THE MOLLUSCAN FAMILY PLANORBIDAE

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Collation, Revision, and Additions
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PREFACE

THE WIDE DISTRIBUTION, large number of species represented, and the economic significance from a medical standpoint, as intermediate hosts of flukes or trematode worms, constitute the family Planorbidae as one of the most important groups of fresh-water Mollusca. It is the largest and most conspicuous of the families of Basommatophorous pulmonate snails.

Unlike the terrestrial pulmonates (Stylommatophora Pulmonata) which have been brought to a high state of precise classification from the anatomical studies of Dr. Henry A. Pilsbry and his co-workers, the Basommatophora are still in a condition of more or less chaos as regards classification, all of the monographs and many of the local studies being based wholly or partly on characteristics of the shell with little regard for relationships which might be gained by a study of the organization of the animal. The condition of this large group as far as classification is concerned is little better than that of the land snails seventy-five years ago.

In 1911 the writer published a monograph of the Lymnaeidae of North and Middle America, basing the classification on characteristics of the genitalia and radula. In that work it was suggested that studies on *Planorbis*, *Physa*, and other groups might follow the publication of the Lymnaeidae volume if it should meet with the approval of the conchological public. That it is still in general use after an interval of more than thirty years is evidence that its reception has been, on the whole, of a favorable nature.

The present volume on the Planorbidae was begun some twenty-five years ago and has been in active preparation for the past ten years. As the work progressed it became evident that adequate treatment of the subject could not be given in a volume similar to that on the Lymnaeidae and so the work has been divided into two parts, part I on the anatomy and classification of the family, and part II* on descriptions of the species of the family inhabiting North and South America and the West Indies.

The study of the internal organization of the family Planorbidae has shown that, as in the case of the land snails, the anatomy gives the only true key to a natural classification. The shell alone cannot be relied upon for this purpose because some of the characteristics are often misleading, affording many cases of parallel development, as the presence of lamellae within the aperture, which feature is found in a number of groups which are unrelated anatomically. There are some shell characteristics, however, which are of value in classification when used in conjunction with anatomical features.

For the anatomical studies recorded in this volume, eighty species and races of the family have been examined, represented by more than 725 specimens. The anatomy of six additional species has been taken from the literature. The number of species examined has been divided among the four subfamilies as follows: Planorbinae 19; Segmentininae 11; Helisomatinae 41; Planorbulinae 10. A large majority of the known genera and subgenera are represented and it is confidently believed that additional anatomical study will not greatly alter the classification herein set forth.

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*See title page of Part II (page 213) for statement regarding change in scope of this part.

The anatomical drawings in this work have all been made by the author with the aid of the camera lucida, and the outlines and much of the detail of the figures are correct from the standpoint of dimensions. Some of the finer details have been filled in by hand on the camera lucida figure. All dissections were made with a Spencer binocular microscope with magnification up to seventy-five diameters. The radulae have all been examined under a Zeiss microscope with magnification up to about 1000 diameters.

In order that the features of the different organs might be fully known they have been separated and otherwise dissected to bring out all relationships. In many cases sections have been made through organs or groups of organs the better to show structural conditions. Some of the figures are diagrammatic, but in the majority of the figures the author has endeavored to portray the form of the organs as they appeared to him under the microscope. Only the shells of the type species of the different genera and subgenera are figured in the plates prepared for Part I.

In the matter of bibliographic citations it has not been deemed necessary to include all references to works in which a genus or other group is listed or described. To have done this would have lengthened the work to a large degree without adding greatly to its value. Only the most important citations, including the first one in which the generic name appears, are included. It will be noted that many groups, which have been ignored or placed in the synonymy by previous authors, have been recognized in this work. This is particularly true of Asiatic groups which have been little known anatomically. Every generic or group name has been given careful study to ascertain its true relationship.

All groups described in this work are arranged under the heading of a genus or of a subgenus, none as sections. Until a greater number of species have been examined for the internal organization this division appears best. Some of the groups herein considered genera may later be placed as subgenera. It does not at present appear to be of any advantage to recognize the terms section or subsection for any of the groupings.

The list of species included in each genus or subgenus has no pretension to completeness, only those species being listed which have either been examined anatomically or appear from the form of the shell to be related. As additional material is examined some of the species listed may be shifted to other groups and additional species may be included.

January, 1942

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*Deceased.

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A MEMORIAL TO
FRANK COLLINS BAKER
(1867 to 1942)

FRANK COLLINS BAKER became Curator of the Museum of Natural History in the University of Illinois on January 1, 1918. From that date onward until his death on May 7, 1942, his chief interests centered around his work and his associations on the Urbana campus. Though he carried on extensive field studies during these years, they were chiefly summer vacation employment, and Urbana remained the focal point of his attention and activity. His appointment as Curator of the University Museum gave him the opportunity to cooperate in the development of a museum devoted primarily to teaching. To this work he brought a broad background of professional experience in every aspect of museum work and at the same time drew freely from his research experiences to create on the Urbana campus a series of collections and exhibits the prime purpose of which was ever that of aiding in student instruction. As in all good teaching one of the first requisites is that of enlisting responsive interest by attractive presentation of fact or material, so likewise in his displays interest was always sought though it was never purchased by cheapening spectacular showmanship. In his synoptic display of the animal series, the dry framework of classification became clothed by artistic and balanced organization of his materials. Groups represented only by fossil remains were treated as integrated with modern expressions of life, not as isolated representations of a dead past.

For one whose career never placed him before classes for delivering formal instruction, he gave evidence of keen appreciation of the museum as a supplement to laboratory and classroom teaching, and at all times offered hearty cooperation to the teaching faculty in creating habitat groups and other exhibits embodying both specific detail and broad principle. Under his curatorship the Museum of Natural History became utilized by diverse student groups. Biology, geology, and geography students found the displays meaningful; students in agriculture came to study the well-organized habitat groups of pests of farm crops, and art students frequented the exhibition halls for sketching.

Mr. Baker's concept of the functions of a museum combined not alone the aspects of display and instruction but a third objective as well, namely, that of research. Throughout his curatorship, he labored to establish and organize research collections. Naturally, the fields of his own interests were most emphasized and these included such diverse interests as the Mollusca, archeology, and paleontology.

In certain specialized areas of these three fields, the University collections have assumed a significance greater than might be expected in a small museum. The collections of Mollusca are especially rich in representatives of the fresh-water and land Mollusca, the direct result of Mr. Baker's active research program. Extensive field collecting was particularly stimulated by his association with the Natural History Survey of Wisconsin in the preparation of his exhaustive two-volume work on the Mollusca of Wisconsin (1928). His long association and collaboration with the Illinois State Natural History Survey gave him access to extensive collections, especially in late years when he was engaged in an intensive field study of the land snails of Illinois which culminated in the Fieldbook of Illinois Land Snails published (1939) by the State Natural History Survey. A revival of interest in researches on the archeology of the State by the University resulted in amassing within the Natural History Museum huge quantities of pottery and artifacts for the care of which Mr. Baker became responsible.

His early interest in the Pleistocene fauna was revived and stimulated by a cooperative program of studies inaugurated by the State Geological Survey. Enormous series of Pleistocene material in quantitative samples were studied by Mr. Baker, whose services in cooperation with the State Geological Survey were recognized by his appointment to the position of Consultant in Pleistocene Paleontology on its staff (1919). The Pleistocene collections under this joint arrangement between Museum and Survey assumed great importance and wide reputation as repository of critical materials, and numerous collectors throughout the country sent samples for critical determination. Thus, at the time of Mr. Baker's death, the Pleistocene collections, which are now deposited in the State Geological Survey, had become one of the significant study collections in this field.

Mr. Baker's interest in research was deep and genuine, and the esteem with which his results are held gives evidence of the effectiveness of his activities in scholarly pursuits. His earliest studies on Mollusca were, in keeping with that period, restricted largely to the study of the shells but he early became an advocate of the study of the soft parts of the living animal which produces the shell and the volume which this sketch accompanies is the culmination of his program of anatomical studies. New apparatus and improved optical equipment made him often express the regret that he could not go back and do again all the earlier studies which he carried on with less adequate laboratory equipment.

Early in his career as a student of Mollusca, Mr. Baker by his own collecting and by personal exchange, began amassing a private collection of fresh-water Mollusca. This collection centered around his chief interest, the fresh-water pulmonate snails. The operation of the old adage, 'To him who hath shall be given,' here finds exemplification, for students of Mollusca regularly sent doubtful specimens to him for classification or verification, and samples of those submitted were added to his cabinet. At the time of his death, the two families Lymnaeidae and Planorbidae were particularly well represented in the Baker Collection, which, as indicated elsewhere in this volume, was presented to the United States National Museum.

A member of many scientific societies, he cherished particularly the election as Corresponding Member of the Zoological Society of London. He was a fellow of the Geological Society of America and likewise of the Paleontological Society of America. At the time of his death he was president of the American Malacological Union. Other societies in which he held membership include: American Association of Museums, Museum Association of Great Britain, Ecological Society of America, American Limnological Society, Ottawa Field Naturalist's Club, and Sigma Xi. He was a fellow of the American Association for the Advancement of Science and held life membership in the Chicago Academy of Sciences and in the Illinois State Academy of Science.

With the years, his zeal for research never waned. In fact, gradually increasing deafness which tended to shut him off from an earlier appreciation of music and from easy communication with his friends gave him opportunity for uninterrupted study in which he could become so completely immersed as to ignore surrounding distractions entirely and to forget adversities, even when he faced some of life's greatest tragedies.

These statements regarding Mr. Baker, as a man and a scientist, would not be complete without some narration of his early years and background.

Frank Collins Baker, son of Francis Edwin and Anna Collins Baker, was born in Warren, Rhode Island, on December 14, 1867. His family later moved to Providence, and there the boy received his early education and for a time attended a business college. Still struggling between the alternatives of business and science as a career, he was for a time employed by the Gorham Silversmiths, and there he learned the techniques of exactness and accuracy which he later maintained were of value in his scientific work.

He attended Brown University for one year (1888-89). Even before this time he had developed a consuming interest in shells which he often remarked were the favorite childhood toys brought to him from distant oceans by a seafaring grandfather. He left Brown to accept the Jessup Scholarship (1889-91) in the Philadelphia Academy of Sciences and there, at the fountainhead of molluscan studies, the die was cast for his scientific career. In later years he often referred to the inspiration which he obtained from mere proximity to Joseph Leidy and other notables in the library and in the programs of the Academy. There likewise he became associated with H. A. Pilsbry, and the tradition for sound molluscan studies, which has always been an important aspect of the Academy program, gripped him.

In 1890, Mr. Baker, as zoologist, was a member of an exploring party from the Philadelphia Academy into Mexico. The travels in Cuba, Yucatan, and Mexico afforded by this expedition had on him the same broadening influence which travel has brought to all the great naturalists and inspired him to consider natural faunal areas instead of political units in subsequent programs of comprehensive taxonomic studies. Thus his monograph on the Lymnaeidae (1911) was not confined to the boundaries of the United States but encompassed a more natural zoogeographical scope of 'North and Middle America,' and the program on the Planorbidae, results of which are embodied in this volume, was extended to include even broader scope in order to secure comprehensive treatment of a taxonomic unit without reference to political subdivisions. After his return from Mexico, Mr. Baker published his first separate book (1895), a small popular work entitled 'A Naturalist in Mexico,' which wove together a narrative of the trip, a description of the country, and scientific observations.

An intimate correspondence with Henry A. Ward of Rochester, part of which has been available to the present writer, ended in an arrangement wherein Mr. Baker was to become associated (1891) as Invertebrate Zoologist with the influential Ward's Natural Science Establishment. Few strictly educational institutions in the early history of this country have wielded the influence exerted by this private concern in the training of natural scientists, especially those headed toward museum work as a profession. While residing in Rochester, he became a frequent visitor in the home of John Hall. On June 12, 1892, he married Lillian May Hall who was his constant companion until her death in 1934.

While his employment by the Ward Establishment was primarily for the identification and organization of the Ward collections of Mollusca, Mr. Baker at the same time selected and organized an extensive synoptic display of museum specimens representing all the groups of the invertebrates, which was being prepared for exhibition at the Chicago World's Columbian Exposition in 1893. Upon completion of this task, Mr. Baker accompanied the exhibit to Chicago where he supervised its installation. At the close of the Exposition, the Ward exhibit was purchased by Marshall Field as part of the nucleus for the beginning of the Field Columbian Museum, and Mr. Baker was engaged as curator in the newly established museum (1894). But that same year he was chosen curator of the old, long established Chicago Academy of Science, where he succeeded and had association with men of the calibre of Robert Kennicott, William Stimpson, and T. C. Chamberlin. It was here that he perfected the techniques of museum display and administration and for the first time had opportunity to develop an intensive program of research, integrated with his professional work. Unfortunately, after about two decades with the Academy, a change in administration placed the Academy in the hands of an individual who acrimoniously opposed the place of research as a museum function. Even this adverse atmosphere brought no reduction in the research program which Mr. Baker had embarked upon, for nights and holidays were free from dictatorial domination. Some measure of his accomplishment during the Chicago period is available in the larger monographs which punctuated the continuous stream of smaller contributions from his desk. Three of his outstanding volumes were published during the twenty-one years of Mr. Baker's association with the Chicago Academy. These are: two volumes on the Mollusca of the Chicago Area (1898 and 1902) and the monograph on the Lymnaeidae (1911). Another undertaking of particular importance—The Life of the Pleistocene—was virtually completed during the years with the Chicago Academy. However, publication of this volume was not afforded until after Mr. Baker came to the University of Illinois (1920), and it was then published by the University Press. The work on this volume marked a new epoch in his research program. Stimulated by an intimate and cordial relation with Professor T. C. Chamberlin of the University of Chicago, Mr. Baker's personal interest in research swung toward the study of faunas of the past and interpretation and reconstruction of environmental conditions under which they existed. The material which served as the original basis for this study was made available in unusual quantity by construction of the Chicago Drainage Canal. Apparently endless material was exposed by the dredging operations, but much of this opportunity for research would have been lost had it not been for Mr. Baker's close personal attention to the dredging as it proceeded. Exposure which he experienced at that time led to infections which affected his hearing. Conditions there established became progressively worse until in later life his hearing was very seriously impaired.

While with the Chicago Academy, Mr. Baker developed a service feature which has become an important aspect of most public museums today and links them closely with the educational program. He began the construction of small portable displays of habitat groups for loan to public schools, thus taking the educational influence of the museum into the schools rather than depending wholly on the unilateral relation of expecting the schools to send their pupils to the museum. The interest in children, and in education, developed by these contacts always remained with him. In the museums under Mr. Baker's direction, the urchin was as welcome a visitor and was as thoughtfully treated as the scholar. Thus, though he never held formal appointment as instructor in any educational institution, he exerted marked influence, and a number of present-day scientists trace the awaking of their interest to his kindly encouragement and enthusiastic attitude toward the field of science. Graduate students in the University of Illinois always found him inspiring and helpful when they approached him with their problems.

Mr. Baker found deep satisfaction in following the careers of men who attributed part of their early zeal for science to boyhood contacts with him and to inspiration growing out of his enthusiasm and kindly interest in their personal problems. One instance of an influence of which he was personally unaware stands out prominently. A mother called at his office in Urbana to present him with a copy of a scientific book written by her son. She explained that the son, who had died while on archeological explorations in a foreign land, definitely attributed his aspiration in the field of science to the benevolent and gracious attention of Mr. Baker to the queries of an unknown and apparently unpromising urchin frequenting the museum of the Chicago Academy.

Mr. Baker resigned from his position with the Chicago Academy in 1915. In that same year, he embarked on a new phase of his career in which his time was given over entirely to field study and research. The newly established New York State College of Forestry, on the campus of Syracus University, employed him as an investigator. For two years he carried on a comprehensive evaluation of the relations of bottom fauna to fish life in Oneida Lake. This program culminated in two volumes of distinctive contributions which were published by the New York State College of Forestry.

Ever since the founding of the University of Illinois, the Museum of Natural History had been in charge of members of the faculty whose foremost obligation had been that of teaching or administration. Under wise guidance of men such as S. A. Forbes and Frank Smith, the Museum had prospered and was able to secure the services of very unusual collectors and competent preparators who added materially to its development. Toward the end of President James's administration, a renewed interest in archeology and in natural resources together with rapid increase in University enrollment led to consideration of the problem of securing a full-time curator for the Museum of Natural History. The position was offered to Mr. Baker who, at the height of his professional career, entered upon his duties in January, 1918.

In 1936 Mr. Baker reached the age established by the University for retirement from active service but his good health and vigor and the best interests of the University combined to bring about postponement of his retirement for three additional years. In 1939, in his seventy-second year, his colleagues helped him celebrate entrance upon status as Curator *Emeritus,* which permitted him to devote his entire time to completion of researches in progress. Letters of congratulation and appreciation from colleagues and from fellow scientists throughout the country were assembled, bound, and presented to him at a dinner in his honor. The esteem with which he was held as an individual and acknowledgments of personal debts of gratitude were as sincely expressed as was the evaluation of his scientific work.

Soon thereafter, illness impaired his opportunity for continuous work in the laboratory, but even under this physical handicap he continued to devote all the time that his strength would allow to the final studies for and preparation of the manuscript for his *magnum opus*—the monograph on The Molluscan Family Planorbidae. Volume I, based on exhaustive anatomical researches, was ready for the editor and work was progressing on Volume II when he was taken critically ill and hospitalization for surgery was unavoidable. Following the operation he never regained his health but became rapidly weaker and died on May 7, 1942.

Slight in stature, unpretentious in attitude, mild in disposition, and kindly, charitable, and unbiased in all of his personal and professional relations, Mr. Baker has left an undying impression of honesty, integrity, and genuineness in the memories of his many friends and associates.

For more than half a century (1889-1942) Mr. Baker continued to publish the results of his researches and observations. Aside from purely incidental notes and compilations, which he continued to publish throughout his career, his early publications dealt largely with distributional studies and problems of taxonomy of the Mollusca. Relatively early he began to shift his interest in Mollusca from purely conchological to malacological lines (about 1897) when he began to study the radulae and anatomy of the soft parts of the molluscs. The interest in Pleistocene paleontology first found expression in a paper published in 1898 and continued through the rest of his life with two posthumous papers on this subject.

Faunal studies with considerable attention to ecological relations of the molluscs began early and found particular expression in his monograph on the Lymnaeidae (1911) and in his ecological studies on the fauna of Oneida Lake. These studies stand as background to the interest which found final expression in his contributions as associate editor of *Naturalist's Guide to the Americas* (1926).

His long identification with the program of molluscan studies, kindly personal qualifications, and familiarity with the history of the subject led to his being commissioned to prepare biographical sketches for five of the distinguished students of Mollusca in the Dictionary of American Biography (Gould, 1929; Kennicott, 1930; Stimpson, 1932; Tryon, 1933; and Sterki, 1933).

Interest in museum administration found expression in a series of papers issued during his years with the Chicago Academy and was revived when he became established in the museum at the University of Illinois.

His publications in archeology were stimulated by his responsibility for the University collections and were concerned largely with analysis of shells and other remains of animal life encountered in excavations of Indian village sites in the Middle West. In this aspect of his work, he collaborated with various specialists but had closest relations with the late W. K. Moorehead whose reports on studies conducted for the University of Illinois were edited by Mr. Baker.

To supplement this analysis it should be recorded that in the period from 1900 to 1915, Mr. Baker edited the Bulletins and other publications of the Chicago Academy of Sciences. From 1913 to 1915 he was assistant editor of *Home and School Reference Work*, published in Chicago in seven volumes, to which he personally contributed 125 articles on birds. Earlier (1900) he prepared a one-page article on Mollusca for the *United Editors Encyclopedia* published in New York. In 1926, in addition to serving as associate editor of *Naturalist's Guide to the Americas*, he prepared the references therein to molluscan distribution. From 1921 to 1926, Mr. Baker wrote numerous reviews of current works on Mollusca for *Ecology*.

In his total contributions, exceeding 350 original articles, more than 250 deal entirely or largely with his chosen field of research, the Mollusca. While many of these are but short, minor notes, some quantitative evaluation of Mr. Baker's productivity may be reflected in the fact that more than a dozen of these works enumerated are of such size as to merit classification as separate books.

Throughout his active career Mr. Baker kept a carefully compiled record of his publications, a copy of which was in his desk at the time of his death. This list, which he prepared, is here published in full with but few slight editorial changes and corrections.

HARLEY JONES VAN CLEAVE

A CHRONOLOGICAL LIST OF THE SCIENTIFIC PUBLICATIONS OF FRANK COLLINS BAKER

ORIGINAL ARTICLES AND BOOKS

1889

1. Conchology department in 'The Old Curiosity Shop' (of which department the writer was editor). California.
2. Notes on Florida shells. Nautilus, 3:53-54.
3. Description of a new species of *Ocinebra*. *Op. cit.*, 3:80-81.
4. A few notes on ornithological collecting. Oologists Exchange, New York, 2(9).
5. Notes on the food of birds. Proc. Acad. Nat. Sci. Philadelphia, 1889:266-270.
6. Remarks upon the round-tailed muskrat, *Neofiber alleni* True. *Op. cit.*, 1889: 271-273.

1890

7. On the Indian River, Florida. Oologists Exchange, 3(11).
8. Directions for collecting alcoholic specimens of the Mollusca. Old Curiosity Shop, 9(3).
9. Remarks on *Urosalpinx perrugatus* Conrad. Nautilus, 4:29-30. Also in Proc. Acad. Nat. Sci. Philadelphia, 1890:46-47.
10. On the modification of the apex of *Murex*. Proc. Acad. Nat. Sci. Philadelphia, 1890:66-72.
11. A catalogue of conchological abbreviations. Nautilus, 4:89-91, 115-117.

1891

12. Notes on a collection of shells from southern Mexico. Proc. Acad. Nat. Sci. Philadelphia, 1891:45-55.
13. Descriptions of new species of Muricidae, with remarks on the apices of certain forms. Proc. Rochester Acad. Sci., 1:129-137.
14. Remarks on the Muricidae with descriptions of new species of shells. Proc. Acad. Nat. Sci. Philadelphia, 1891:56-61.
15. Catalogue and synonymy of the recent species of the family Muricidae. Proc. Rochester Acad. Sci., 1:153-172.
16. The caves of Yucatan. *Op. cit.*, 2:2.
17. Notes on a collection of shells from the Mauritius; with a consideration of the Genus *Magilus* of Montfort. *Op. cit.*, 2:19-40.
18. Catalogue of specimens of Echinodermata, corals, gorgonians, and sponges. Ward's Natural Science Establishment, Rochester, N.Y., iv + 82 pages.

1894

19. Further notes on embryonic whorls of the Muricidae. Proc. Acad. Nat. Sci. Philadelphia, 1894:223-224.

1895

20. A glance at the Chicago Academy of Sciences. Nautilus, 8:109-111.
21. The geographic distribution of the Mollusca. Science (n.s.), 2:179-183.
22. Preliminary outline of a new classification of the Muricidae. Bull. Chicago Acad. Sci., 2:169-189.
23. Syllabus of biological lectures. (Delivered before the North Side Science Section of the Chicago Institute of Education). Chicago.
24. A naturalist in Mexico: being a visit to Cuba, northern Yucatan, and Mexico. Chicago, 1895: viii + 145 pages.
25. Thirty-eighth annual report of the Chicago Academy of Sciences. For the year 1895. 16 pages.

1896

26. On the correct position of the aperture in *Planorbis*. Jour. Cincinnati Soc. Nat. Hist., 19(1):45-48.
27. Notes on the mental development and intelligence in animals. The Observer, 1896:680-682.

1897

28. Thirty-ninth annual report of the Chicago Academy of Sciences. For the year 1896. 26 pages.
29. On the pulsations of the molluscan heart. Jour. Cincinnati Soc. Nat. Hist., 19(2): 73-78.
30. Note on *Natrix grahami* B. and G. (With F. M. Woodruff). Science (n.s.), 5:447.
31. On the effect of music on caged animals. Amer. Nat., 1897:460-463.
32. Critical notes on the Muricidae. Trans. Acad. Sci. St. Louis, 7:371-391.
33. On the modification of the apex in gastropod mollusks. Ann. New York Acad. Sci., 9:685-704.
34. On a collection of mollusks from Grand Tower, Illinois. Nautilus, 11(3):28-30.
35. Further notes on animal intelligence. The Observer, 8:193-194.
36. Collecting about Chicago. Sports Afield, 19(2):112-113.
37. Reason among animals. *Op. cit.*, 19:276-278.
38. Notes on Radulae. Jour. Cincinnati Soc. Nat. Hist., 19(3):81-93.

1898

39. Do cats remember? Sports Afield, 20:215.
40. The molluscan fauna of western New York. Trans. Acad. Sci. St. Louis, 8(5): 71-94.
41. Collecting in Florida. Sports Afield, 20:314-316.
42. Notes on mollusks from Acadia, Missouri. Nautilus, 11:36.
43. Fortieth annual report of the Chicago Academy of Sciences. For the year 1897. 27 pages.
44. The Mollusca of the Chicago area. Part I. The Pelecypoda. Chicago Acad. Sci., Nat. Hist. Survey Bull., 3(1):1-130.
45. A day on the Chicago drainage canal. Nautilus, 12(6):63-65.
46 A new *Sphaerium*. *Op. cit.*, 12:65-66.

1899

47. Collecting fresh-water shells. Popular Sci., 33(5):99-100.
48. Notes on the mollusks of Lilycash Creek. Nautilus, 13(3):30-31.
49. Study of fresh-water mussels. Popular Sci., 33:194-197.
50. Notes on the Mollusca of Owasco Lake, New York. Nautilus, 13:57-59.

1900

51. Notes on a collection of Pleistocene shells from Milwaukee, Wisconsin. Jour. Cincinnati Soc. Nat. Hist., 19:175-177.
52. On a collection of fresh-water shells from Rhode Island. Nautilus, 13:112-113.
53. A new museum tablet. Amer. Nat., 34:283-284.
54. The rock shells. Birds and Nature, 7:191-192.
55. The gross anatomy of *Limnaea emarginata* Say, variety *Mighelsi* Binney. Bull. Chicago Acad. Sci., 2(3):191-211.
56. A revision of the Physae of northeastern Illinois. Nautilus, 14(2):16-24.
57. The teeth of snails. Popular Sci., 34:187-188.
58. Shell collecting near Rochester, New York. Nautilus, 14:69-71.
59. Mollusks in grass. *Op. cit.*, 14:93.

1901

60. The oyster and its relatives. Birds and Nature, 9:26-31.
61. A revision of the Limnaeas of northern Illinois. Trans. Acad. Sci. St. Louis, 9(1):1-24.
62. Snails of the forest and field. Birds and Nature, 9:74-79.
63. Snails of pond, river, and brook. *Op. cit.*, 9:128-133.
64. Snails of the ocean. *Op. cit.*, 9:176-181.
65. The Nautilus and other cephalopods. *Op. cit.*, 9:222-227.
66. New varieties of fresh-water shells. Nautilus, 15(2):17-18.
67. The digitations of the mantle in *Physa*. Bull. Chicago Acad. Sci., 2(4):225-228.
68. Description of a new species of *Limnaea*. *Op. cit.*, 2(4):229-230.
69. The molluscan fauna of the Genessee River. Amer. Nat., 35:659-664.
70. The prong-horned antelope. Birds and Nature, 8:179-181.
71. *Limnaea auricularia* in America. Nautilus, 15(5):59.
72. The educational value of natural history museums. Review of Education, Chicago, 7:155-157.
73. Some interesting molluscan monstrosities. Trans. Acad. Sci. St. Louis, 11:143-146.

1902

74. *Planorbis bicarinatus striatus,* n. var. Nautilus, 15(10):120.
75. Editorial on museum articles. Review of Education, Chicago, 7:361.
76. The Mollusca of the Chicago area. Part II. Gastropoda. Chicago Acad. Sci., Nat. Hist. Survey Bull., 3(2):131-410.
77. Starfishes. Birds and Nature, 12:35-37.
78. The cowries and shell money. *Op. cit.,* 12:86-90.
79. Some snails of the ocean. *Op. cit.,* 12:134-139.
80. The descriptive arrangement of museum collections. Museum Jour., (England), 2:106-110.

1903

81. Shell collecting on the Mississippi. Nautilus, 16:102-105.
82. Corals, sea-fans, and sea-whips. Birds and Nature, 13:83-85.
83. The stony corals. *Op. cit.,* 13:131-133.
84. Coral reefs. *Op. cit.,* 13:179-181.
85. The hydroid corals. *Op. cit.,* 13:225-227.
86. Shells of land and water. A familiar introduction to the study of the mollusks. A. W. Mumford and Co., Chicago. xvi + 175 pages.
87. Pleistocene mollusks of White Pond, New Jersey. Nautilus, 17:38-39.
88. A partial list of the marine mollusks of San Salvador, Bahamas. *Op. cit.,* 17:57.
89. Rib variation in *Cardium.* Amer. Nat., 37(439):481-488.
90. Sea urchins and sand dollars. Birds and Nature, 14:179-181.
91. Notes on *Murex marcoensis* Sowerby. Nautilus, 17-88.

1904

92. The mollusks of Cedar Lake, Indiana. *Op. cit.,* 17:112-113.
93. Some American grasshoppers. Birds and Nature, 15:131-133. (Nom de plume, Collins Thurber)
94. New varieties of American Limnaeas. Nautilus, 18:10-12.
95. The molluscan fauna of the Dells of Wisconsin. Trans. Acad. Sci. St. Louis, 14(2):99-105.
96. Note on *Planorbis truncatus* Miles. *Op. cit.,* 14(2):107-110.
97. The arrangement of the collections of Mollusca in the Chicago Academy of Sciences. Museums Journal (England), 2:354-360.
98. Spire variation in *Pyramidula alternata.* Amer. Nat., 38(453):661-668.
99. New American Lymnaeas, II. Nautilus, 18:62-63.
100. The bluebird. Birds and Nature, 16:158-161. (Nom de plume, Collins Thurber)
101. The bald eagle. *Op. cit.,* 16:232-236. (Nom de plume, Collins Thurber)

1905

102. The belted kingfisher. *Op. cit.,* 17:50-51. (Nom de plume, Collins Thurber)
103. The flicker. *Op. cit.,* 17:131-132. (Nom de plume, Collins Thurber)
104. Critical notes on the smaller Lymnaeas. Nautilus, 18:125-127.
105. The long-billed marsh wren. Birds and Nature, 17:179-180. (Nom de plume, Collins Thurber)
106. New species of *Lymnaea.* Nautilus, 18:141-142.
107. The marsh hawk. Birds and Nature, 17:201-202. (Nom de plume, Collins Thurber)
108. The molluscan fauna of McGregor, Iowa. Trans. Acad. Sci. St. Louis, 15(3): 249-258.
109. Notes on a collection of shells from Bass Lake, Indiana. Nautilus, 19:27-28.
110. The museum and the public school. Museums Journal (England), 5:50-55.
111. A new species of *Lymnaea* from Ohio, with notes on *Lymnaea parva* Lea. Nautilus, 19:51-53.
112. The loggerhead shrike. Birds and Nature, 18:23-24. (Nom de plume, Collins Thurber)
113. The hermit thrush. *Op. cit.,* 18:50-51. (Nom de plume, Collins Thurber)
114. Notes on the genitalia of *Lymnaea.* Amer. Nat., 39:665-679.
115. The yellow-bellied sapsucker. Birds and Nature, 18:119-121. (Nom de plume, Collins Thurber)
116. The cerulian warbler. *Op. cit.,* 18:167-168. (Nom de plume, Collins Thurber)
117. The American flamingo. *Op. cit.,* 18:213-214. (Nom de plume, Collins Thurber)

1906

118. The bob-white or quail. *Op. cit.*, 19:23-24. (Nom de plume, Collins Thurber)
119. The least bittern. *Op. cit.*, 19:71-72. (Nom de plume, Collins Thurber)
120. The blue-gray gnatcatcher. *Op. cit.*, 19:110-111. (Nom de plume, Collins Thurber)
121. A new variety of *Planorbis nautileus* Linn. Nautilus, 19:120.
122. *Lymnaea hinkleyi* n. sp. *Op. cit.*, 19:142-143.
123. Application of De Vries's mutation theory to the molluscs. Amer. Nat., 40: 327-334.
124. Notes on a collection of mollusks from the vicinity of Alpena, Michigan. Trans. Acad. Sci. St. Louis, 16(2):1-15.
125. A new *Sphaerium* from Illinois. Nautilus, 20(2):21.
126. The dickcissel. Birds and Nature, 19:146-147. (Nom de plume, Collins Thurber)
127. The great blue heron. *Op. cit.*, 19:213-214. (Nom de plume, Collins Thurber)
128. *Lymnaea danielsi* n. sp. Nautilus, 20:55.
129. A catalogue of the Mollusca of Illinois. Bull. Illinois State Lab. Nat. Hist., 7(6): 53-136.

1907

130. Descriptions of new species of *Lymnaea*. Nautilus, 20:125-127.
131. The camera in science. Photo Era, 18:185-186.
132. Two new species of *Lymnaea*. Nautilus, 21:52-55.
133. Some observations on museum administration. Science, 26:666-669.

1908

134. Some instructive methods of bird installation. Proc. Amer. Mus. Assoc., 1:52-57.
135. The Chicago Academy of Sciences. Science, 27:423-424.
136. The Chicago Academy of Sciences: its past history and present collections. Chicago Acad. Sci., special publ., 2:1-7.
137. Note on *Lymnaea desidiosa* Say. Nautilus, 22:20-23.
138. Suggestions for a natural classification of the family Lymnaeidae. Science, 27: 942-943.
139. The Chicago Academy of Sciences. *Op. cit.*, 28:138-140.
140. A new American *Planorbis*. Nautilus, 22:45.
141. A small collection of shells from Texas. Science, 28:534-535.
142. Provincial museums. *Op. cit.*, 28:684-685.
143. The relation of the State Academy of Science to the Natural History Survey of the Chicago Academy of Sciences. Trans. Illinois State Acad. Sci., 1:68-69.
144. The Natural History Survey of the Chicago Academy of Sciences. Proc. Amer. Assoc. Mus., 2:15-19.

1909

145. Annual report of the Chicago Academy of Sciences. For the year 1908. Bull. Chicago Acad. Sci., 3:1-21.
146. A new species of *Lymnaea*. Nautilus, 22:140-141.
147. Description of a new fossil *Lymnaea*. *Op. cit.*, 23:19-21.
148. Note on *Planorbis binneyi* Tryon. *Op. cit.*, 23:41-42.
149. The Chicago Academy of Sciences: Its past history and present collections. Museums Jour. (England), 8:423-428.
150. Range of *Lymnaea umbilicata*. Nautilus, 23:80
151. Report on the educational work of some east American museums. Bull. Chicago Acad. Sci., 3:26-34.
152. Mollusks from Kansas and Oklahoma. Nautilus, 23:91-94.
153. Suggestions for an educational exhibit of mollusks. Proc. Amer. Assoc. Mus., 3:56-59.
154. Exhibition cases without shelves. *Op. cit.*, 3:128-130.

1910

155. A new variety of *Lymnaea stagnalis*. Nautilus, 23:112-113; 125-126.
156. Note on free public museums. Science, 31:221.
157. Annual report of the curator. Bull. Chicago Acad. Sci., 3:26-45.
158. Annual report of the librarian. *Op. cit.*, 3:45-46.
159. The ecology of the Skokie Marsh area, with special reference to the Mollusca. Bull. Illinois State Lab. Nat. Hist., 8:437-499.
160. Preliminary note on the life of Glacial Lake Chicago. Science, 31:715-717.

161. Suggestions for an educational exhibit of mollusks. Museums Jour. (England), 9:394-397.
162. The ecology of the Skokie Marsh area with special reference to the mollusks. Trans. Illinois State Acad. Sci., 3:106-108.
163. Description of a new *Lymnaea*. Nautilus, 24:58-60.
164. Mollusks of Unionville, Connecticut. *Op. cit.*, 24:68-69.

1911

165. The Lymnaeidae of North and Middle America, recent and fossil. Chicago Acad. Sci., Special Publ., 3:xvi + 539.
166. Annual report of the curator. Bull. Chicago Acad. Sci., 3:137-150.
167. Annual report of the librarian. *Op. cit.*, 3:151-152.
168. A method of exhibiting large descriptive labels on the outside of museum cases. Proc. Amer. Assoc. Mus., 4:21-23.
169. School loan collections as prepared by the Chicago Academy of Sciences. *Op. cit.*, 4:36-40.
170. Mollusks of Wellesley Island and vicinity, St. Lawrence River. Nautilus, 25:66-67.
171. The molluscan fauna of Tomahawk Lake, Wisconsin. Trans. Wisconsin Acad. Sci., Arts, and Lett., 17(1):200-246.

1912

172. A new *Planorbis* from Michigan. Nautilus, 25:118-120.
173. Post-glacial life of Wilmette Bay, Glacial Lake Chicago. Trans. Illinois State Acad. Sci., 5:108-116.
174. A method of exhibiting insect collections. Proc. Amer. Assoc. Mus., 6:108-111.
175. Recent additions to the catalog of Illinois Mollusca. Trans. Illinois State Acad. Sci., 5:143-145.

1913

176. A new *Lymnaea* from Montana. Nautilus, 26:115-116.
177. *Pseudogalba*, new name for *Simpsonia*. *Op. cit.*, 26:120.
178. Interglacial records in New York. Science, 36:523-524.
179. Notes on post-glacial Mollusca. I. Emmet County, Michigan. Nautilus, 27:7-8.
180. *Galba ferruginea* in Oregon. *Op. cit.*, 27:24.
181. Mollusca of Wyoming County, New York. *Op. cit.*, 27:54.
182. Notes on post-glacial Mollusca. II. Waukesha County, Wisconsin. *Op. cit.*, 27:68.
183. Interglacial mollusks from South Dakota. Science, 38:858-859.

1914

184. Northern Idaho shells. Nautilus, 27:104-106.
185. Mollusks from Magician Lake, Cass and Van Buren Counties, Michigan. *Op. cit.*, 28:8-10.
186. Use of enlarged photographs in museum groups. Proc. Amer. Assoc. Mus., 8: 89-91.
187. An evening with the aquarium and snailery. Nature Study Rev., 10:315-320.

1915

188. On the classification of the Lymnaeidae. *Nautilus*, 29:20-24.
189. *Campeloma lewisii* Walker in Illinois. *Op. cit.*, 29:36.
190. Mollusks from Berrien County, Michigan. *Op. cit.*, 29:47.
191. Pleistocene mollusks from Illinois. *Op. cit.*, 29:87-88.

1916

192. A mollusk injurious to garden vegetables. Science, 43:136.
193. The fresh-water Mollusca of Oneida Lake, New York. Nautilus, 30:5-9.
194. North American faunal areas. Science, 44:273-275.
195. The relation of mollusks to fish in Oneida Lake. New York State Coll. For., Technical Publ., 4:1-366.
196. The auroral display of August 26. Science, 44:568.
197. A new variety of *Lampsilis* from Oneida Lake with notes on the *luteola* group. Nautilus, 30:74-77.
198. Further notes on the post-glacial biota of Glacial Lake Chicago. Trans. Illinois State Acad. Sci., 7:74-78.
199. The relation of the Mollusks of Oneida Lake to the basin of lower South Bay. (Abstract). Ecol. Soc. Amer., 1916.

1917

200. Notes on *Acella haldemani* (Desh.) Binney. Nautilus, 20:135-138.

1918

201. Further notes on the Mollusca of Oneida Lake, New York; the mollusks of lower South Bay. *Op. cit.*, 31:81-93.
202. A molluscan garden pest. Science, 47:391-392.
203. The animal world in a handful of algae. The Guide to Nature, 10:376-380.
204. Notes on nidification in *Gillia* and *Amnicola*. Nautilus, 32:19-23.
205. Description of a new variety of fresh-water mussel from Oneida Lake, New York. Appendix to New York State Coll. For., Technical Publ., 9:247-248.
206. The productivity of invertebrate fish food on the bottom of the Oneida Lake, with special reference to mollusks. *Op. cit.*, 9:1-264.
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1932. George Washington Tryon.
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BOOK NOTICES AND REVIEWS

(In *Ecology*)

1921

The fresh-water Mollusca of the Parish of Aldenham, by A. E. Boycott. 2:230.
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THE MOLLUSCAN FAMILY PLANORBIDAE

PART I

CLASSIFICATION AND GENERAL MORPHOLOGY

I.

GENERAL MORPHOLOGY

A. EXTERNAL APPEARANCE OF THE ANIMAL

CONTRARY TO GENERAL CUSTOM, the characteristics of the animal and its gross anatomy will be considered before taking up the shell and its variations. This procedure seems more logical since it is the animal which secretes and builds up the shell or calcareous covering (see plate 70, fig. 1).

The head and foot protrude from the shell and bear several important organs. The foot is long and variably narrow, broadly rounded in front, and usually tapering to a point behind. There is a large velar area above and in front of the foot which is retained from the embryonic animal, as in *Lymnaea*, and bears the head, eyes, and tentacles. This velum is broad and short and is capable of great extension and retraction; it is usually somewhat semicircular in shape.

The tentacles are very long and filiform, varying from one-half to the whole length of the foot, and are placed at about the junction of the velum with the foot. The eyes are placed on swellings at the inner base of the tentacles. The mantle collar does not extend beyond the edge of the aperture of the shell. The texture of the foot is smooth, not granular as in some of the land snails, and there are no grooves on the body, the animals resembling the Lymnaeas in this respect.

The Planorbidae differ from the related family Lymnaeidae in having certain of the organs on the left side (sinistral), the organs in Lymnaeidae being on the right side (dextral). In this respect the Planorbidae resemble the families Physidae and Bulinidae. The tentacles of the Planorbidae, Physidae, and Bulinidae are also similar and differ from the Lymnaeidae and Ancylidae, in which the tentacles are flattened and triangular.

The breathing organ of the Planorbidae, a modified lung as in the family Lymnaeidae, is supplemented by a prolongation of the anal region (auriform lobe), called the pseudobranch or false gill, which may take over the function of breathing when the animal is submerged and can not obtain free air. This organ is highly vascular, many blood vessels entering it from the lower part of the lung cavity. It is comparatively a recent organ, being post-natal in origin, not having been observed in embryological development.

The pseudobranch varies greatly in shape, being long and narrow, wide, leaf-like, or rounded in different genera. It always bears a portion of the rectum and the anus opens at the upper right side. There is usually a ridge, more or less heavy and distinct, which begins on the upper part of the rectum and ends in the middle or at the base of the pseudobranch. The variations of the pseudobranch are shown on the plates illustrating the anatomy of each genus. A siphon-like extension of the mantle, called the pneumostome or respiratory opening, which may be greatly expanded, provides a tube-like conduit for free air to reach the lung. The pseudobranch is on the left side of the body and the pneumostome is to the right of this organ nearer the median line of the neck.

The genital outlets are on the left side of the neck, the male opening just behind the left tentacle and the female opening a short distance behind the male opening in the side of the neck. In many individuals the penial complex has been observed protruding from the male opening (plate 29, figs. 6, 7, 11, 12), the animal having been killed while in breeding condition. That self-impregnation of the female system by sperm from the extended penial complex is possible is easily believed when the closeness of the two sex outlets is observed.

The body above the foot may be flatly rounded or it may be rounded above and flattened on both sides of the foot (plate 70, fig. 10). Good figures of the animal of *Tropicorbis* are shown on plate 78.

The color of the animal differs in the various genera. Mostly it is bluish-slate or blackish, grayish, or brownish, the color being lighter on the base of the foot and on the tentacles. In some species the color is yellowish. There are often flecks or spots of white on the foot and tentacles. The mantle, especially over the lung and kidney, is in many groups heavily blotched with black or brown.

The shell may be carried perpendicularly, as in *Helisoma* (plate 70, fig. 7), or it may lean to the left side, causing the shell to be pseudodextral or ultradextral, as in *Gyraulus* and *Menetus* (plate 70, fig. 9).

B. GENERAL INTERNAL ANATOMY

The internal anatomy includes the following systems: Reproductive, Digestive, Respiratory, Renal, Circulatory, Muscular, and Nervous. The most important internal structure for classification purposes is the reproductive system and this will be first considered.

[a] The Reproductive System

Like other Basommatophora, the Planorbidae are hermaphroditic with the organs of the two sexes mostly separated. The different organs may be tabulated as follows:

- Female organs......
  - vagina
  - uterus
  - oviduct
  - nidamental gland
  - spermatheca
  - spermathecal duct
  - albumen gland
- Male organs........
  - penial complex
  - vas deferens
  - prostate
  - prostate duct
  - seminal vesicle
- Penial complex.......
  - vergic sac
  - verge
  - sperm canal
  - diaphragm or muscular ring
  - preputium
  - penial gland
  - penial gland duct
  - pilasters
  - muscles
- Common to both male and female..
  - ovotestis
  - ovisperm duct or hermaphrodite duct

Male Organs. *External form.* In the natural position the penial complex lies over the vagina and uterus (plate 39, fig. 3). When pulled away from this position its form is seen to be more or less cylindrical and to consist of a large bulbous lower portion, preputium (PR) and a smaller pyriform portion, the vergic sac (VS, plate 24, fig. 11). A narrow tube, the vas deferens (VD) is inserted at the summit of the vergic sac. This descends to near the male opening where it is concealed in the muscular tissue of the neck of the animal and appears again near the female opening (plate 24, fig. 15). In some species the vas deferens is enlarged as it enters the vergic sac, the enlargement being similar to the epiphallus of the land snails (plate 39, fig. 7, *Menetus*).

In one group of species (the Helisomatinae) there is usually a duct (penial gland duct, plate 24, fig. 11, DC) which normally lies coiled at a point between the vergic sac and the preputium (plate 27, fig. 9, DCO). This may be very long, as in *Helisoma trivolvis* (plate 24, fig. 11) or short, as in *Helisoma anceps* (plate 23, fig. 3, DC). In another subfamily (Planorbinae) there is no penial gland duct except in two or three genera.

There are one or two retractor muscles of the penial complex (plate 24, fig. 11, RM; plate 39, fig. 9, RM; plate 34, fig. 2) and a number of muscles believed to be supporting muscles to retain the penial complex in position. The retractor muscles enter the columellar muscle but the supporting muscles are attached to the muscular wall of the forepart of the body. The supporting muscles may in a measure perform the office of additional retractor muscles in some genera, especially in helping to retract the preputium after eversion. There do not appear to be any protractor muscles; the penial complex becomes turgid by blood pressure.

The penial complex assumes many shapes in the genera belonging to the subfamily Helisomatinae. The preputium may be pushed upward and the vergic sac may occupy a position on the side of the preputium as in *Helisoma campanulatum* (plate 27, figs. 5-8).

The vas deferens is continued near the female complex and borders the uterus and oviduct where it is a small tube (plate 24, fig. 15, *Helisoma trivolvis*). Just above the spermatheca the prostate appears. This organ varies greatly in the different genera. In *Helisoma* (plate 24, fig. 15, PRS) it is somewhat elongated and fan-shaped and the compound diverticula empty directly into the sperm duct along a very small portion of that tube. A cross section of the prostate in *Helisoma trivolvis* illustrates this condition (plate 24, fig. 13; see also plate 27, figs. 4 and 12, cross sections of *Helisoma campanulatum*). The section is seen to be distinctly fan-shaped. In some other genera the prostate duct is separated from the sperm duct and vas deferens and the prostate is greatly lengthened. The prostate is composed of many or few diverticula arranged in a single series, each diverticulum being attached to and emptying into the separate prostate duct, which in turn empties into the vas deferens below the prostate (plate 14, figs. 7, 9; plate 1, figs. 1, 7).

Beyond the prostate the vas deferens is continued as a somewhat larger tube, the sperm duct (plate 27, fig. 14, SPD; plate 24, fig. 15). At its distal end the sperm duct unites with the oviduct to form the ovisperm duct or hermaphrodite duct (plate 27, fig. 14; plate 34, fig. 6).

About midway of the ovisperm duct is a glandular enlargement which has been called the seminal vesicle (SV). Many students of both fresh-water and land pulmonates simply call this region an enlargement of the ovisperm duct, but it is distinctly glandular and different from the ovisperm duct in structure. It also occupies the position above the prostate, where it lies in other animals. It is recognized as the seminal vesicle by Simroth (1912, p. 501) and by Larambergue (1939, p. 94). Taylor (1900, p. 359) calls the small sac-like organ into which the duct of the albumen gland enters, the seminal vesicle, but as this organ is an adjunct of the male system in all animals it could scarcely be located in an organ of the female system. The swelling near the albumen gland is the carrefour. The seminal vesicle is variable in form in the different species and genera and provides another feature for classification purposes (see plate 35, fig. 5, *Carinifex jacksonensis;* plate 1, fig. 1, *Planorbis planorbis;* plate 14, fig. 7, *Gyraulus albus*).

Female Organs. The vagina (VG), usually a thick walled, wide tube, passes imperceptibly into the uterus (U) which is usually much enlarged. A large sacculated body, the nidamental gland (NG, sometimes called egg gland) follows the uterus and is usually placed over the uterus and the oviduct. The oviduct (OD) lies back of the gland and is much narrowed as it passes backward to join the ovisperm duct. The method of junction of the oviduct and sperm duct with the ovisperm duct varies in different genera.

The albumen gland (AL) is a large, more or less elongated organ, composed of many small alveoli. In its natural position it lies over the stomach and a loop of the intestine passes under it causing a channel to be formed on the under side of the albumen gland (plate 38, fig. 9, *Menetus opercularis;* plate 15, fig. 1, *Gyraulus hirsutus*). The organic relations between the albumen gland and the oviduct are somewhat complicated. A small duct extends from the albumen gland and enters a large bulbous swelling which is attached to the end of the oviduct before that organ combines with the sperm duct to form the ovisperm duct. This gland or bulb is the carrefour which receives the products of the albumen gland and from which they enter the oviduct (see plate 34, fig. 6, *Carinifex ponsonbyi;* plate 35, figs. 6, 7, *Carinifex jacksonensis*). Taylor (1900, p. 359) erroneously calls the carrefour the seminal vesicle.

The spermatheca or receptaculum seminis (S) is a bulbous or pear-shaped organ with a narrow duct of variable length which enters the vagina at its junction with the uterus. Its function is said to be that of receiving the sperm (in the form of a spermatophore) during copulation and to store it safely until the eggs descend from the ovotestis, at which time they are fertilized by the stored sperm. The vagina is usually very short but may be of considerable length in some species.

Organs Common to Both Systems. The ovotestis (OT) is embedded in the liver and fills about one whorl of the shell. It varies in form much as does the prostate, the two organs being more or less synchronous in this respect, a valuable feature in classification. In the Helisomatinae it is many-lobed, the diverticula branching fan-wise from the ovisperm duct (plate 27, fig. 4, *Helisoma campanulatum;* plate 34, fig. 9, *Carinifex ponsonbyi*). In the Planorbinae and Segmentininae the diverticula are in pairs; the two diverticula are attached directly to the ovisperm duct (plate 16, fig. 9, *Gyraulus deflectus obliquus*). During the breeding season the diverticula may be filled with both ova and sperm, the ova either ripe for expulsion or developing (plate 10, fig. 2, OT, *Drepanotrema hoffmani*). The ovisperm duct is a small tube of variable length, enlarged near the middle to form the seminal vesicle.

Both ova and sperm are produced in the same diverticulum. They are said to arise simultaneously from indifferent epithelial substance and may be found developing together in a single diverticulum (see Crabb, 1927, p. 75). It is thought by most malacologists that the spermatozoa ripen first, descend during copulation, and are stored in the spermatheca of the female system until the ova ripen and descend through the oviduct, and that fertilization occurs when the ova and sperm meet in the lower part of the uterus or vagina, just before the depositing of the egg capsule. Some cytologists declare that fertilization occurs in the ovotestis diverticulum and that the fertilized egg descends and is deposited without the necessity for copulation. See Clapp 1927 for a discussion of this subject. Typical eupyrene spermatozoa and nucleated ovum of *Gyraulus circumstriatus* (Tryon) are shown on plate 52, figs. 14-16.

The Penial Complex. The male organ, which I have called the penial complex, contains a number of features which are of great value in systematic diagnosis. The whole organ is divisible into two parts, a lower swollen or bulbous portion called the preputium (PR) and an upper portion called the vergic sac (VS). The latter contains the penis proper or verge (V), which may be short and fat (plate 1, fig. 5, *Planorbis planorbis*) or very long and narrow (plate 10, fig. 6, *Drepanotrema hoffmani*). All grades of length and diameter between these extremes are to be found in the different genera.

The verge may be modified at its extremity by the presence of a dagger-like object called a stylet (plate 16, fig. 6, ST, *Gyraulus deflectus obliquus;* plate 14, fig. 1 and fig. 6 *Gyraulus albus*). In these examples the outlet canal for the passage of the spermatozoa is at the side. In other genera there may be a fleshy papilla or appendage at the end of the verge (PA) with the outlet of the canal in the middle at the base of the papilla (plate 2, figs. 5, 6, *Segmentina nitida*). In still other genera the termination of the verge is simply rounded with the canal outlet in the center (plate 38, fig. 15, *Menetus cooperi calioglyptus*). Other slight modifications are found in some genera.

Between the vergic sac and the preputium there is an organ which I have called the diaphragm (D). This is a muscular ring which separates the two parts of the penial complex. This may be a simple ring with a central perforation (plate 39, fig. 7, *Menetus cooperi*) or it may be a dependent papilla (plate 23, fig. 6, *Helisoma anceps;* plate 24, fig. 10, *Helisoma trivolvis;* plate 16, fig. 5, *Gyraulus deflectus obliquus*). The preputium always has several vertical ridges on the inside called pilasters (PL) which may serve to guide the verge or the penial gland during protrusion.

In 1926 (Trans. Wis. Acad., V. 22, pp. 200, 201) the writer called attention to a peculiar gland found in the preputium of the genus *Helisoma*. Subsequent study has shown that this organ is found in several other groups or genera of American, European, and Asiatic planorbids. This gland is of variable shape, pyriform, rounded, or elongated (plate 23, fig. 2, *Helisoma anceps;* plate 24, figs. 8 and 14, *Helisoma trivolvis*). In section it is seen to be cup-shaped, to be lined on the sides with folds and to have many small folds in the bottom of the cup. The gland is attached to the inner wall of the preputium either midway between the male opening and the muscular ring (diaphragm), or somewhat nearer this ring in some species.

From the base of the cup, and piercing the integument of the preputium, is a duct of variable length (DC), which, if long, is folded on the outside of the preputium (plate 27, fig. 9, *Helisoma campanulatum*); or, if short, simply lies on the surface of the preputium (plate 23, fig. 2, *Helisoma anceps*). When coiled on the outside of the preputium it is bound to that organ by short muscles. Sections through the cup are shown on plate 23, fig. 1, plate 24, fig. 1, and plate 27, fig. 1. The duct terminates at the muscular ring or diaphragm (D), pierces the wall of the lower part of the vergic sac, and terminates just above the ring (plate 23, fig. 6, *Helisoma anceps;* plate 24, fig. 10, *Helisoma trivolvis*), or in a groove in the ring (plate 36, fig. 9, *Parapholyx effusa*).

The function of the penial gland is at present insufficiently known. It was once thought by the writer to be connected with the formation of the spermatophore and was called the spermatophore gland (Baker, 1931, p. 581), but this belief scarcely agrees with the structure of the gland. In section this organ is seen to have two parts, each of which may have a different function. In *Helisoma trivolvis* (plate 24, fig. 4) the gland shows a large cup-shaped cavity, the walls of which are lined with vertical folds (GF). The bottom of this cup is lined with folds laid crosswise. The long duct begins at the bottom of the cup and terminates in the vergic space (DC) of the vergic sac (VS) just above the muscular ring or diaphragm (D).

In some species, as *Helisoma duryi* and its varieties, the duct begins in a small cavity or cup at the end of the gland (plate 33, figs. 3, 10), the walls of which have vertical folds. The larger cup-shaped cavity has no connection with the smaller cavity or its duct. In some species, notably in the genus *Menetus*, there is no external duct, connection with the vergic space being effected by an open channel (plate 42, figs. 3, 4). Another group of *Menetus* has a short duct on the inside of the preputium (plate 39, fig. 7). In *Menetus* and some other groups there is a small channel in the muscular ring (plate 39, fig. 7, D). *Helisoma anceps* shows this feature well (plate 23, figs. 2, 6). *Parapholyx effusa klamathensis* (plate 36, figs. 9, 10) also shows the canal in the muscular ring.

It appears possible that one of the functions of the penial gland might be to expand the opening in the muscular ring or diaphragm which is normally nearly or quite closed, and prepare it for the protrusion of the verge. The penial gland duct possibly carries a fluid, secreted by the vertical folds in the gland cup, to the diaphragm to facilitate the passage of the verge.

But there is another function of the gland. It has been observed that during copulation not only is the verge extruded from the male opening, but also the whole penial gland. This has been observed in many species of *Helisoma* (*H. duryi normale*, plate 33, fig. 16; *H. trivolvis lentum*, plate 29, figs. 7, 11, 12; *Promenetus exacuous*, plate 41, fig. 9). In all species of Planorbidae the verge is extruded during copulation. In a specimen of *Drepanotrema lucidum* examined (plate 11, figs. 1, 2, 6, 7) the verge and penial gland protruded together from the male opening. It is probable that the gland portion with the cup-like cavity lined with vertical folds is an excitatory organ or sarcobelum, for in the species possessing this gland there is no special apparatus for this purpose such as occurs in other species which have a horny stylet or fleshy papilla at the end of the verge (*Gyraulus*, *Anisus*, and other genera).

Another feature observed in connection with the penial gland is that the penial complex is often seen in a bilobed condition, the gland being pushed upward in the preputium causing the vergic sac to appear as though attached to the side of the preputium. This condition occurs mostly in *Helisoma* (plate 25, figs. 1, 6, 7, 9; plate 24, figs. 1, 2). The evolution of this feature was observed in specimens of *Helisoma campanulatum* and is shown on plate 27, fig. 7 being the normal form and figs. 6, 5, and 8 showing the gradual change to the bilobed condition.

Much remains to be learned about the function of the penial gland. Observations of the living snail in aquaria should help to solve some of the questions. It may be observed, however, that this is not so easily accomplished as might be supposed. More than a dozen aquaria were kept under observation by the writer for several years, and while the animals were seen in apparent coitus on several occasions, the protrusion of the gland was not seen. Perhaps histological studies would help, especially before and after breeding. The subject is worthy of a doctor's thesis.

As was recorded in the study of the family Lymnaeidae (Baker, 1911), there is great variation in the form of the genitalia of the genera of the family Planorbidae. As in the Lymnaeidae, also, this modification occurs mostly in the male organs, principally the penial complex, but includes also the prostate and seminal vesicle. The female organs are uniform in position and shape, only the spermatheca and its duct vary in form and length to any degree. The male organs, therefore, afford useful features upon which to base a natural classification of the family, since the characters of the different groups are constant and uniform.

[b] The Digestive System

The digestive system of the Planorbidae is similar in many respects to that of the family Lymnaeidae. The system naturally divides into three parts, the first consisting of the buccal sac, the oesophagus, and the salivary glands, the second part the region of the stomach with the liver connections, and the third part the intestine and rectum (see fig. 1, plate 48).

The buccal sac is usually pear-shaped, the oesophagus entering it at the upper middle portion. There are retractor and protractor muscles and nerves received from the buccal ganglia. The salivary glands are paired, a duct entering the buccal sac on each side near the oesophageal connection. The salivary glands, usually cylindrical and elongated, are composed of many small lobules. The two glands are joined behind and form a continuous loop or ring. These organs are very uniform in the different species of the family (see plate 70, figs. 12, 13). The oesophagus is usually rather long (about one-fourth as long as the intestine), beginning as a tube of small diameter and enlarging as it approaches the stomach region.

The stomach is a large muscular body composed of three parts, first the crop, which is an enlarged portion of the oesophagus, then the gizzard, which is an indistinctly bilobed body of large diameter, and third the pyloris, or opening into the intestine. The gizzard is not as distinctly bilobed as in *Lymnaea* but is of the same nature. When opened it is found to contain small particles of siliceous matter, evidently sand taken in with the food to serve for the breaking up of the ingested food.

On the under side of the pyloris, near the duct of the liver, there is a finger-like process or blind sac which appears to be the stylotheca containing the crystalline style. This blind sac is present in all species of the family examined. Internally the sac contained a gelatinous substance or was empty. The liver or digestive gland covers the posterior part of the stomach region in its natural position. It has two unequal lobes which form the posterior part of the animal and in which the ovotestis is concealed. The liver is composed of a great number of small lobules, more or less digitiform. It is well supplied with blood vessels which form a plexus on and in the organ. A large duct enters the pyloric portion of the stomach at the point of junction with the blind sac.

The intestine is very long. It bends around the stomach from the end of the pyloris and passes backward for a distance. It then forms a single loop which bends forward and extends to the fore part of the animal on the left side (the right side in the Lymnaeidae). The rectum, the greatly enlarged portion of the intestine, supports a central ridge or crest on the upper side which extends to and over the pseudobranch. The anal opening is always near this ridge on the pseudobranch, to the right and above this organ.

Variation in the digestive system is noted only in the form of the stomach region, short and rotund in some species (plate 48, fig. 1, *Helisoma trivolvis*) or elongated and narrow in other species (plate 48, fig. 8, *Bathyomphalus contortus*). The loop of the intestine sharply borders the stomach in some species (fig. 1) though in some species it extends forward without a loop (fig. 8).

[1] The Jaw

The mouth of the Planorbidae is provided with two important organs which afford characteristics for classification, the jaw and the radula. The horny jaw lies in the upper part of the mouth at the fore end of the buccal sac (plate 70, fig. 13). As in *Lymnaea*, the mouth is somewhat T-shaped in repose. In the upper part of the T lies the superior jaw, which is wide and low, of a brownish color, striated vertically on its front part, the striations producing a saw-like condition on its lower, cutting edge (plate 49, fig. 1, *Helisoma anceps*). The lateral jaws, two narrow, brown, horny ribbons, emargin the lips or sides of the mouth. They are connected with the lateral margins of the superior jaw by a narrow projection from the upper part of the lateral jaws. These side jaws form a question-mark figure, as will be noted in the figures on plate 70. The jaws, superior and lateral, are attached to a cartilage which in turn is attached to the roof of the mouth. The jaws are moved by several distinct muscles.

The jaws of the Planorbidae fall into two principal types or variations. The most common is the group described above, with large superior jaw and two smaller lateral jaws. Another type is horseshoe-shaped and in this there is but one division which appears to represent the fusion of the lateral and superior jaws of the first type. The striations of the superior jaw of the first group become separate vertical plates in the second group, producing a segmented jaw. This segmentation extends to the lower part of the side of the horseshoe, showing that the lateral jaws are included in the segmentation (see plate 50, fig. 16, *Gyraulus parvus*).

A peculiar jaw, not included in the usual segmented type of the family, is that of *Carinifex* in which the jaw is bow-shaped (or roundly horseshoe-shaped) and is composed of many narrow plates fastened to a heavy cartilage (plate 49, fig. 19, *Carinifex ponsonbyi*; fig. 18, *Carinifex jacksonensis*). Although belonging to the subfamily Helisomatinae the jaw is practically of the Planorbinae type. Figure 17 on plate 49 shows the large size of the cartilage in this genus (*C. jacksonensis*).

This type of segmented jaw is suggestive of the polyplacognath group of land snails. It is said to be a very ancient type of jaw which would seem to indicate that the Planorbinae group of the family is more ancient than the Helisomatinae group (except *Carinifex* which has the primitive form of jaw). The marginals of the radula also indicate a primitive form of radula.

[2] The Radula

The radula of the Planorbidae is ribbon-like as in the Lymnaeidae. It lies on a subquadrate cartilage near the rear end of the buccal sac. The front end of the radula extends toward the mouth of the snail and the rear end is bent downward into a radular sac which forms a rounded protrusion or bump at the back of the buccal sac (see plate 70, figs. 12, 13). The radula grows forward from this sac as the functional teeth at the front end of the ribbon become worn by use. There are protractor and retractor muscles which pull the radula backward and forward, over its cartilage, during the act of cutting up food particles. In use, the radula is moved from behind forward, like the tongue of a cat lapping food from a plate, as described by Sterki many years ago.

The lingual ribbon of the Planorbidae carries many teeth in transverse rows as in the family Lymnaeidae. There may be as many as 200 rows with 85 teeth in a row or a total of 17,000 teeth in one ribbon. The central tooth is always bicuspid and in some groups (as in *Drepanotrema*) there are one or more accessory cusps on either side of the central cusps. There is a series of duplicating teeth on each side of the central tooth. This row is divisible, as in the Lymnaeidae, into lateral, intermediate, and marginal teeth. The lateral teeth are usually tricuspid and comprise an inner, short entocone, a large median mesocone, and a smaller outer ectocone (see plate 57, fig. 1). The cusps are usually dagger-like and may be wide or narrow. The intermediates are those teeth between the typical lateral and marginal teeth which show certain modifications, as splitting of the ectocone or entocone into smaller cusps. The marginals are usually somewhat claw-like with a variable number of small cusps. The mesocone usually persists in the earlier marginal teeth and may be recognized by its large size and central position.

The law of mesometamorphosis applies to the Planorbidae as well as to the Lymnaeidae. As stated by Pilsbry this law is as follows:

> All modifications of the teeth proceed from the median line of the radula outwards toward the edges, the outer marginal teeth being the last to be modified (Guide to Study of Helices, p. xiii).

The marginals of the Planorbidae are of the same primitive type as are those of the Lymnaeidae, showing a close relationship between these two families and also their common descent from the tectibranchiate stock of marine mollusks. The lateral teeth of the Planorbidae show a wider degree of variation than do the lateral teeth of the Lymnaeidae, indicating, perhaps, that the Planorbidae may be somewhat younger in development.

In studying the teeth of the Planorbidae it must be remembered that only the unworn teeth show the true characteristics of the radula. Also the teeth must be in their natural position on the radula ribbon and not tilted or otherwise disturbed.

The Planorbidae are divisible into two groups by the form of the marginal teeth. One group, including the genus *Helisoma* and other divisions of the subfamily Helisomatinae, have long and narrow reflections reaching far below the base of attachment and with the distal end and the outer margin multiserrate (see plate 57). The other group, including the genus *Planorbis* and other divisions of the subfamily Planorbinae as well as some of the subfamily Segmentininae, have short, wide reflections high up on the base of attachment and only a few serrations or cusps on the lower margins (see plate 69).

The lateral teeth are very uniform in both groups, these being mostly tricuspid, the cusps rounded or sharp and dagger-like. In several groups (as *Drepanotrema* and *Segmentina*) the laterals are modified by the addition of several cusps, causing the teeth to be 6 or 7 cuspid. These exceptions appear to be due to a splitting of the three cusps of the normal lateral teeth (entocone, mesocone, ectocone) found in the majority of planorbid genera. As with the other organs, the radulae offer sound criteria for classification purposes.

[c] The Renal System

The kidney or renal organ (nephridium) of the family Planorbidae is a large and conspicuous part of the snail's anatomy, occupying a considerable portion of the body whorl of the animal. It lies to the left of the lung cavity, the genitalia being between the kidney and the ureter (see plate 14, fig. 4, U, NG). Viewed from the ventral side, the kidney consists of two parts, a small upper saccular portion with the pericardium at the right (SK) and an elongated lower portion (TK). A section through the middle of this portion of the kidney (plate 44, fig. 9) shows a central tube or lumen flanked on each side by a large vein, the pulmonary vein on the right side (AP) and the renal vein on the left side (RA). The central tube, the tubular portion of the kidney, is regularly marked by internal septa which project into the lumen for a greater or less distance. The tubular portion is surrounded by thick walls of spongy tissue, the most conspicuous part being a distinct ridge (RK). To the left of this ridge (in the section) there is another conspicuous ridge on the roof of the mantle.

At the lower end of the tubular portion is the short ureter (UR). This is a small tube which turns to the left, usually more or less upward, and discharges into the mantle cavity. The figures on plates 44 to 47 show the various forms of ureter and the relationships of the different parts of the kidney. In 1940, Mattox, working on another group of snails, pointed out the fact that the kidney may reflect specific characters.

A series of sections through the kidney of *Australorbis glabratus* (plate 45, figs. 7 to 11) show the internal form of the kidney at different points in its length. In fig. 1, plate 45, an arrow indicates the place where each section is made. Figure 7 (E) is a section through the sacculate part of the kidney below the pericardium, and shows the lumen partly filled with folds extending from the walls of the kidney. In fig. 8 (D) the section shows the tubular portion of the kidney with a few folds extending from the walls, also the large pulmonary vein at the right and the smaller renal vein at the left. In figs. 9 and 10 (C, B) the same features are shown. In fig. 11, near the lower part (A), the kidney is flattened and broadened and the veins are smaller. All figures show the variation in the form of the ridge in different portions of the kidney. The blood vessels (veins) lie in close proximity to the tubular part of the kidney and pick up the blood to be carried to the heart.

The folds in the tubular portion of the kidney are metameric in their presence and one section may pass through a portion of the kidney where these are present, or it may pass between two sets of folds, as shown in figs. 16 and 17 on plate 45, as well as on other plates. The ridge on the kidney is mostly confined to members of the subfamily Helisomatinae and offers a valuable criterion for the separation of this planorbid group. The Planorbinae are mostly without this ridge.

The ureter of the Planorbidae is described as straight, but no exit of this nature was found in any species examined. All had a short ureter, partly reflexed, as shown in the figures on the plates.

[d] The Circulatory System

The circulatory system of the Planorbidae is similar to that of the Lymnaeidae and other Basommatophorous Pulmonata. The heart lies to the right of the kidney (instead of to the left as in *Lymnaea*) and consists of a ventricle and an auricle enclosed in an oval pericardium (plate 44, fig. 2, PC, AU, VT). The aorta (AO) extends backward from the ventricle and divides into two branches or arteries, the visceral artery which supplies the digestive, genital, and other systems in the posterior part of the body, and the cephalic artery which bends around and forward, carrying blood to the organs in the head, foot, etc. These arteries branch frequently, the branches becoming smaller, and terminate in contact with the venous system either by small arterioles or through lacunae or blood sinuses which connect the arterial system with the venous system.

The venous system consists of blood vessels which convey the blood back to the heart after circulation through the kidneys, lung, and other parts of the system. A large branchial vein borders the kidney on the right side, carrying blood to the auricle. A large renal vein also borders the left side of the kidney, entering the saccular portion (see plate 44, fig. 2, AP, RA). Venous sinuses are present and store the blood after circulation to be carried to the renal and respiratory systems for purification.

In the Planorbidae the blood (haemolymph) contains a substance (haemoglobin) which gives it a pinkish or red color. This is an active substance occurring abundantly in the respiratory system and differs from the bluish blood (haemocyanin) which occurs in most mollusks. Its presence in *Planorbis* is said to be associated with the poorly oxygenated habitat occupied by most species of this group in stagnant pools or lakes and ponds poorly supplied with oxygen. This statement, however, is open to question, since many species of the Planorbidae live in habitats abundantly supplied with oxygen, in company with Lymnaeas and other fresh water pulmonates. The pseudobranch is probably helpful in supplying oxygen to the blood, as it is highly vascular (plate 14, fig. 4, P).

[e] The Respiratory System

Respiration in the Planorbidae is effected as in the Lymnaeidae and other aquatic pulmonate mollusks. Free air is admitted into a large mantle cavity abundantly lined with blood vessels forming a plexus on the dorsal wall of the mantle cavity. This lung cavity lies on the right side of the mollusk, next to the kidney, and is bordered on the left by the pulmonary vein (plate 44, fig. 2, L). The lung cavity is placed on the right side of the body in sinistral species (*Planorbis, Physa*) but on the left side in dextral species (*Lymnaea*).

In the Planorbidae the presence of the secondary branchium, the pseudobranch, enables the animal to respire without coming to the surface. This organ is of various shapes, but is always an outgrowth of the branchial cavity walls and lies to the left of the pulmonary siphon to which it is attached (plate 14, figs. 3, 4, P). It may be a simple rounded fold or it may be flat with a distinct ridge down its center. It is abundantly supplied with a plexus of blood vessels which absorb oxygen from the water.

The rectum passes through the pseudobranch and its outlet (anus, A) is usually above and about at the middle of the pseudobranch. The rectum usually has a large crest or ridge on its upper surface which diminishes in size at the lower part where it extends over and to the edge of the pseudobranch (see plate 25, fig. 3, *Helisoma pilsbryi;* plate 28, fig. 8, *Helisoma scalare;* plate 35, fig. 4, *Carinifex jacksonensis*).

The breathing orifice or pulmonary siphon (pneumostome) is an outgrowth of the mantle which is capable of forming a tubular conduit or siphon through which free air may be admitted to the lung (see the plates mentioned above). The respiratory, renal, and circulatory systems are intimately connected and should be considered together to understand the conditions governing the respiration and blood circulation of the animal.

[f] The Nervous System

The nervous system of the family Planorbidae differs little from that of the family Lymnaeidae (see Baker, 1911, plates 1 and 5). A nerve ring surrounds the oesophagus posterior to the buccal sac (plate 48, fig. 18). There are two cerebral ganglia above the oesophagus (CG). Below the oesophagus there are two pedal ganglia (PG), two buccal ganglia (BG), two visceral ganglia, and a single abdominal ganglion. Two pleural ganglia are connected with the visceral, pedal, and abdominal ganglia. The left cerebral ganglion sends nerves to the penial complex (plate 48, fig. 17, *Helisoma anceps*), which divide to send branches to the vergic sac, penial gland duct region, and retractor muscle, as well as to other parts of this complex.

In the Planorbidae these nerves are sent off from the left instead of the right ganglia, because the group is sinistral. In the Lymnaeidae, a dextral group, the nerves arise from the right ganglia (see Baker, 1911, plate 5).

[g] The Muscular System

The muscular system of the family Planorbidae does not differ from that of the family Lymnaeidae except in positions due to the sinistrality of the animal. The most important muscles for classification purposes are those of the male generative system.

C. THE SHELL

The shells of the Planorbidae are mostly orb-shaped, wheel-shaped, or disc-shaped, rarely becoming a conical spiral as in *Lymnaea* and *Physa*. Several physoid types occur, as the *Helisoma scalare* of Florida. Such types sometimes occur in other species of the family as abnormal or pathologic forms, and have been noted in the genera *Helisoma* and *Carinifex*. Scalariform individuals may also occur in any species and have been noted particularly in the smaller species of the genus *Gyraulus*.

The shell may be closely coiled, like a watch spring, or loosely coiled, and of few or many whorls. It may be so flat that one wonders how an animal can find enough room to function in so small a space, as *Drepanotrema cultratum*, or it may be almost globose, as *Helisoma pilsbryi*. It may be as thin as paper or thick and very solid.

The shells of the larger species, especially in *Helisoma*, are carried almost perpendicularly as in *Helisoma trivolvis macrostomum* (shown on plate 70, fig. 7), or it may lie almost flat as in *Planorbula jenksi* (shown on plate 70, fig. 11). In all species of the family Planorbidae the genital organs are on the left side and the animal is sinistral. But the shells are not all strikingly sinistral. Such large groups as *Helisoma*, *Planorbarius*, and *Indoplanorbis* are obviously sinistral, usually exhibiting a distinct right and left side when in locomotion. But the smaller species are tipped to one side, to the left, and are apparently dextral and are usually described as pseudodextral or ultradextral. In such species the upper side (right) is umbilical and the lower side (left) is apical. These shells, while truly sinistral, appear as dextral. In most works on this family the shells have all been considered dextral and figured as such. Quite a literature has developed in the controversy as to whether the shells of *Planorbis* are dextral or sinistral (see Baker, 1896. Jour. Cincinnati Soc. Nat. Hist., 19, p. 45).

In size the planorbids range from the tiny *Armiger crista*, less than 2 mm. in diameter, to the large *Helisoma trivolvis macrostomum*, which attains a diameter of 30 mm. The whorls may be rounded on the periphery or this region may be sharply carinated or squarely flattened. The lower (umbilical) surface may be so flattened that no umbilical opening is indicated, or it may be deeply indented forming a distinct umbilicus. Sutures may be deeply indented or scarcely visible. The aperture is most frequently rounded, ovate, or half-moon shaped. It may be armed with lamellae or entirely free from such obstructions. The outer lip may be thin and sharp or it may be strengthened by a heavy ridge or callus. There may be, also, more or less of a callus on the parietal wall. As most species are planorboid in form there are few modifications of the columella, as are found in the family Lymnaeidae.

The sculpture of the planorbid shell consists mostly of growth lines which may be very fine and thread-like or coarse and rib-like. In some species there have been developed costae or ribs more or less evenly distributed. In a few species the epidermis forms paper-like crests or frills, as in *Helisoma anceps royalense*. Spiral impressed lines are found in most of the species of the family. These are usually rather heavy and conspicuous but in some species they are very fine. In a few species the spiral lines are very faint or absent, as in *Menetus opercularis*. Malleated individuals are comparatively rare in the Planorbidae although they are common in the Lymnaeidae. The epidermis or periostracum of the planorbids is usually rather thick and heavy. In some groups the shell appears devoid of an epidermis, the surface being shining and waxy. The remarks on sculpture in the Lymnaeidae Monograph (pp. 3, 4) apply equally well to the Planorbidae.

The color of the shells of the family Planorbidae is usually some variety of horn color, light or dark. In some groups, as *Australorbis*, the color is rich brown or chestnut. Some shells are light milky in color. A few species border on red, others are ashy. The range of color is about like that in the family Lymnaeidae, but there are no species known comparable to the greenish shell and purplish aperture of *Bulimnea magasoma*, the handsomest of the fresh water pulmonates. Zebra markings occur among the planorbids as among the lymnaeids.

II.

GENERAL ECOLOGY

ECOLOGY now has such a wide significance and includes so many diverse subjects that it is necessary to define what is embraced under this term in this chapter. It is here made to include everything that affects the animal either from external or internal sources, including such subjects as the habitat, climate, altitude, chemical conditions of the water body, pollution, parasites, relations in food chains, reproduction, development, etc.

GENERAL ENVIRONMENTAL CONDITIONS

Representatives of the family Planorbidae may be found in almost any body of fresh water, from the largest lakes to the smallest pools. Streams of all sizes harbor one or more species of the family. Certain groups, as *Menetus*, *Planorbula*, *Tropicorbis*, and some *Gyraulus*, are abundant in small pools which may become wholly or partially dry during dry seasons. Many of the large forms, such as *Helisoma campanulatum*, *Helisoma corpulentum*, *Helisoma pilsbryi*, and some varieties of *Helisoma anceps*, prefer larger bodies of water like the larger lakes. *Helisoma trivolvis* is common in small lakes or bays of larger lakes, in shallow areas where the shore is bordered by *Typha* and sedge, where food in the form of algae and other vegetation is abundant. In such habitats the snails may be seen with the foot attached to the under side of the surface film, the shell hanging downward, the animal busily eating such small organisms as may lie on the surface. In Florida, members of the subgenus *Seminolina* live in limestone pools of limited size.

Almost all of the members of the family Planorbidae are littoral animals and are not usually found in water deeper than fifteen feet, the usual limit of rooted vegetation in water bodies. The maximum numbers occur in shallow areas not exceeding six feet in depth. A few inhabit deeper water and in the deep lakes of Europe and Asia, as lakes Geneva, Constance, and Léman in Switzerland, Lake Balaton in Hungary, and Lake Baikal in Siberia, they may occur in abysmal depths of from forty to 350 meters. In our own lakes, deep dredgings have produced no members of the family Planorbidae. The family is on the whole a distinctly shallow-water group.

The Planorbidae are able to withstand unfavorable features of their environment better than most groups of mollusks, owing to their ability to breathe free air. Thus water of some alkalinity and salinity, as well as water containing sewage, may be used by these animals successfully as habitats. The Lymnaeas also share this ability to live under unfavorable conditions. It has been observed, however, that chemicals and oil, also wood wastes from factories, are inimical to the Planorbidae and Lymnaeidae and none have been seen which could resist this deadly type of habitat. Clear, cold mountain streams, especially if rapid, contain no planorbids, and usually no other mollusks, as far as personal observations have indicated. Many such in New England have been examined and a few in Idaho and Montana.

Altitude does not seriously affect the distribution of the members of the family Planorbidae. In the Rocky Mountains they occur in lakes at altitudes of from 9,000 to 10,000 feet. Lake Titicaca, in Peru, which contains many mollusks, including a peculiar group of Planorbidae (*Taphius*) is at an altitude of 12,846 feet. The Swiss lakes are at comparatively high altitudes as are also some of the lakes of Asia which contain mollusk faunas of some size.

Quite a literature has accumulated on the general ecology and particular habitat relationship of the Planorbidae and other fresh-water mollusks. The remarks on the lymnaeas in the 1911 monograph on that family may be consulted with advantage. A number of special papers and books have been published which bear on this subject. These are listed in the bibliography and may be consulted under the following names: Adams, 1909; Baker, F. C., 1910, 1911, 1916, 1918, 1920, 1922, 1924; Dybowski, 1875; Forel, 1869, 1874; Lindholm, 1909, Taylor, J. W., 1894-1900.

VARIATIONS IN DIFFERENT ENVIRONMENTS

The planorbid snails do not exhibit as much variation due to differences in the environment as do the Lymnaeidae (see Baker, 1911, pp. 29-32). The shell aperture often increases in size in large lake localities where the animal is subject to heavy wave action. This may be observed in *Helisoma anceps percarinatum* and in *Helisoma anceps sayi* which are lake dwellers in contrast with typical *Helisoma anceps* which is usually a river or creek inhabitant. *Helisoma campanulatum davisi* is a small pool or swamp dweller while typical *Helisoma campanulatum* is a lake inhabitant and usually has a larger, more expanded aperture. Some species of this family show preferences for particular types of habitat. Thus *Planorbula armigera* is usually found in ephemeral pools or small bodies of water, or in protected places in larger ponds and lakes. *Planorbula crassilabris* may often be found on a lake shore fully exposed to the waves. *Promenetus umbilicatellus* is an inhabitant of ditches, pools, and swampy places, while *Promenetus exacuous* is usually found in larger bodies of water.

Great variation is often seen in specimens of the same species from one habitat. Thus *Helisoma duryi seminole*, in Lake Eustis and Lake Griffin, Florida, varies from a typical planorboid form to a distinct physoid form by the elongation of the spire. In Lake Titicaca, in Peru, *Taphius andecolus* exhibits many variations in the form of the aperture, the whorls, and the condition of the umbilical region. In *Carinifex* the individual variations are numerous among specimens of one species from the same habitat. Among some of the species of the genus *Australorbis* of South America and the West Indies there is often great variation in the axial height of the shell.

These examples might be greatly multiplied but enough have been presented to show that variation is the rule among individuals of the family Planorbidae and that this variation may not be due alone to conditions of the environment but rather to the inherent 'law to vary' which is found in all living things. The family Planorbidae does not appear to offer as good a field for the distinguishing of the so-called habitat or ecological variations as does the family Lymnaeidae.

LOCOMOTION

Locomotion in the family Planorbidae is accomplished by the same means as in the family Lymnaeidae (see Baker, 1911, p. 32). The method most usually observed is that of gliding. The planorbids have been observed to rise suddenly and descend abruptly, as do the lymnaeids, by varying the amount of air in or on the body or shell. The members of the family are usually very active, crawling about on aquarium walls quite rapidly, eating everything in their path. In locomotion the planorbids resemble the physas more than the lymnaeids, the latter usually being rather sluggish in motion. Young and immature planorbids are usually very active, much more so than fully mature individuals.

FOOD

Like the lymnaeids the food of the planorbids is largely vegetal. Little is known, however, concerning the food supply of this family. They have been observed eating pond-lily leaves (principally *Castalia*), *Potamogeton*, both the large floating leaf species and the submerged leaf species, and algae of various kinds. Both old and young snails will eat avidly of the algal scum which collects on the glass sides of an aquarium. The radula can be plainly seen, the animal using it from behind forward as described by Dr. V. Sterki many years ago.

Stomachs and crops that have been opened and examined have usually contained a quantity of fine sand (especially in the crop) which probably helps in grinding the food before it enters the intestine. Ostracods (six in one specimen of *Helisoma subcrenatum* from Pass Lake, Fidalgo Island, Washington), distomids, vegetable fibers, and a quantity of flocculent undigested animal matter have been noted in the stomach. Specimens of *Helisoma duryi seminole* from Florida had the stomach and gizzard filled with small grains of sand and nothing else. Some planorbids are scavengers, though not to the extent observed among the lymnaeids. No evidences have come under observation indicating that the group is carnivorous (see Baker, 1911, p. 42 for notes on the food of lymnaeas).

FOOD FOR OTHER ANIMALS

Together with other fresh-water mollusks, the family Planorbidae furnishes food for a large number of other forms of animal life. Chief among the animal groups feeding on mollusks are certain species of fish (see F. C. Baker, 1916). Fresh-water snails, including planorbids, have been found in the stomachs of the following food and game fish:

Whitefish (*Coregonus clupeaformis* (Mitchill))
Small Mouth Buffalo (*Ictiobus bubalus* (Raf.))
Common Sucker (*Catostomus commersonii* (Lacépède))
Yellow Bullhead (*Ameiurus natalis* (LeSueur))
Common Bullhead (*Ameiurus nebulosus* (LeSueur))
Freshwater Drum (*Aplodinotus grunniens* Raf.)
Pumpkinseed (*Lepomis gibbosus* (Linn.))
Bluegill (*Lepomis macrochirus* Raf.)

Many smaller fish, not of direct value as food or game fish, are yet of great value as food for the larger food fish. Many of these include the planorbids and other fresh-water snails in their diet. Such small fish known to eat snails are:

Fresh Water Killy (*Fundulus diaphanus* (LeSueur))
Killifish (*Fundulus dispar* (Agassiz))
Viviparous Top Minnow (*Gambusia affinis* (Baird & Girard))
Manitou Darter (*Percina caprodes zebra* (Agassiz))

Five species of the planorbids have been specifically identified in the stomach contents of fish. These are:

Gyraulus parvus (Say)
Gyraulus deflectus obliquus (DeKay)
Promenetus exacuous (Say)
Helisoma anceps (Menke)
Helisoma campanulatum (Say)

Many species of birds, especially water birds, consume some mollusks in their diet. Ducks, such as the Lesser Scaup (*Nyroca affinis* (Eyt.)) and others feeding in shallow water, eat fresh-water snails. The waders, such as the Upland Plover (*Bartramia longicauda* (Bechst.)) and the Killdeer (*Oxyechus vociferus* (Linn.)), feed on snails. The Red-winged Blackbird (*Agelaius phoeniceus* (Linn.)) has been known to feed on a planorbid (probably a *Gyraulus*).

Other groups of animals which include fresh-water snails in their diet are turtles, frogs, newts and salamanders, crayfish, leeches, and dragonfly nymphs. It is quite probable that many other animals which frequent fresh-water snail habitats feed on the smaller species or the young of larger species. The stomach contents of many fish and birds have been listed as simply snails or *Planorbis* without identification of the species involved. It is obvious that the planorbids, and other snails of the fresh waters, are a valuable food source for the larger animals.

LENGTH OF LIFE

The life span of the members of the family Planorbidae is not definitely known. Specimens of *Helisoma trivolvis lentum* were hatched in an aquarium and lived sixteen months. At this time they were about 8 mm. in diameter and had four whorls. An adult *lentum* has five whorls and is about 20 mm. in diameter. It appears possible that these specimens would have attained full maturity in another year, or two and a half years from time of hatching. *Helisoma duryi normale* has been hatched in an aquarium and has lived for over a year. An adult *Planorbarius corneus* (the red snail) has been kept alive with goldfish for two years. Mature individuals of *Helisoma trivolvis* have remained alive for nearly two years in a well-balanced aquarium.

Just how long any of the planorbids live in their natural habitat is not known, four or five years it is probable. The lymnaeids are said to live for three or four years. Experiments with the larger snails of the family Planorbidae, *Helisoma* particularly, would be of value.

THE PLANORBIDAE AS HOSTS FOR PARASITIC WORMS

The family Planorbidae furnishes some of the best examples of the rôle of snails in the life history of certain trematode worms known as flukes. A group of worms known as blood flukes (*Schistosoma*) cause serious disturbances in man. Three species are known from different parts of the world. These parasites require a mollusk as the host of the parthenogenetic generations of their life cycle. In this life cycle the *Schistosoma* in the human host lays eggs which are voided in the faeces or the urine. Eventually the larvae in the eggs become clothed with a ciliated epithelium, and, on coming into water, the egg shell bursts and the miracidium escapes, whereupon it begins to swim about rapidly (Faust, 1932, p. 350).

These miracidia are adapted to specific groups of snails. When in their swimming they reach the proximity of certain snails they show a specific response to that species of mollusk, probably due to a mucous secretion of the animal. In most cases they readily attack, and, in the course of half an hour or an hour, penetrate the soft tissues of the snail. In certain cases of other trematodes (*Clonorchis* and *Metagonimus*), however, it is necessary for the embryonated eggs to be swallowed by the snail, whereupon they hatch in the lumen of the oesophagus, bore their way through the wall, and gradually migrate through lymph channels into the lymph spaces bathing the hepatic glands. In the meantime, they have metamorphosed into the simple sacculate sporocysts. These first generation sporocysts give rise to a parthogenetic progeny (either second generation sporocysts or rediae). From this second generation there develops (also parthogenetically), a progeny of larvae known as cercariae. Thus, from the penetration of a single miracidium there may be developed as many as ten thousand or more cercariae. Then later, on reaching maturity, they erupt from the tissues of the snail, and, either by direct or indirect routes, produce infection in human or reservoir hosts (from Faust, 1932, pp. 350-351).

Although the three human species of blood flukes (*Schistosoma*) are closely related, they utilize entirely different species of mollusks for the parthenogenetic stages. Thus, *Schistosoma haematobium*, with a distribution in northern Africa, the Congo Basin, the Sudan, Mesopotamia, Palestine, Sicily, Corsica, and possibly southern France, parasitizes species of the genera *Bulinus* and *Physopsis*. *Schistosoma japonicum*, with a distribution in China, Japan, Formosa, and the Philippine Islands, uses members of the genus *Oncomelania*.

The third species, *Schistosoma mansoni*, occurring in the same localities in Africa as *S. haematobium*, is also found in northern South America and many of the West Indian islands whither it was brought from Africa by slaves during the days of the slave traffic. This species originally parasitized small planorbids belonging to the genus now known as *Afroplanorbis*. In the West Indies a genus of large snails known as *Australorbis* is parasitized by the *Schistosoma mansoni*, which has become a serious pest in these regions. A genus of smaller snails, *Tropicorbis*, related to the African group *Afroplanorbis*, is also used as intermediate host. The small snails of the genus *Drepanotrema* have also been found with cercariae. Attempts to use the genus *Helisoma* as a host for *Schistosoma mansoni* were unsuccessful, although species of this genus are parasitized by other forms of trematode worms.

Aguayo (1938, p. 210) has summarized the species of snails used as intermediate hosts by *Schistosoma* and other trematodes. *Schistosoma haematobium* is shown to use a species of planorbid, '*Planorbis dufuorii*' as well as *Bulinus* and *Physopsis*. The *Schistosoma mansoni* intermediate hosts include *Afroplanorbis boissyi*, *A. pfeifferi*, *A. sudanicus*, *Australorbis glabratus*, *A. olivaceus*, *A. antiguensis*, *Tropicorbis centimetralis*, and *Drepanotrema cultratus*.

The liver flukes of the genus *Fasciola* parasitize certain genera of Lymnaeidae (*Radix*, *Pseudosuccinea*, *Fossaria*, and *Stagnicola*) as well as one *Physa*, *P. cubensis*. The large fluke of the Orient, *Fasciolopsis buski*, which is closely related to *Fasciola*, uses only the small planorbids belonging to the old genus *Segmentina* which now includes the groups *Polypylis*, *Helicorbis*, and *Pingiella*, true *Segmentina* not being found in the East. Four species are listed as intermediate hosts, *Planorbis coenosus* (=*Helicorbis*), *Segmentina hemaesphaerula* (=*Polypylis*), and '*Segmentina schmakeri*' and '*S. nitidella*' which have not yet been examined for their anatomy and hence their position is doubtful (probably *Polypylis*). The value of correct specific identifications of the intermediate hosts of these trematode worms is of the first importance as has been clearly indicated by Ingles (1933) in a study of the parasites of frogs.

Elaborate studies have been made by Dr. E. C. Faust of the Department of Tropical Medicine in Tulane University, New Orleans, and by the late Dr. William A. Hoffman of the School of Tropical Medicine of the University of Puerto Rico, on various phases of the Schistosomiasis mansoni problem in Puerto Rico, where the mollusk *Australorbis glabratus* (Say) (=*Planorbis guadeloupensis* Sowb.) is the intermediate host. For these studies see Faust, 1933; Hoffman and Faust, 1934; and Faust, Jones, and Hoffman, 1934.

Papers by parasitologists in which molluscan hosts are mentioned are numerous. A few are here indicated. Faust (1918) has observed cercariae of four species in *Helisoma trivolvis* in Illinois and one species in *Helisoma subcrenatum* (not *trivolvis*, as stated) in Montana (Faust 1917). In a list of the described cercariae of the United States (1919) Faust mentions two species of the family Planorbidae, *Planorbis parvus* (*Gyraulus*) and *Planorbis trivolvis* (*Helisoma*), as well as several Physidae and Lymnaeidae which are known hosts. Fourteen species of cercariae infest *Helisoma trivolvis* and three species occur in *Gyraulus parvus*. Miller (1936) found *Helisoma trivolvis* from Illinois and *Helisoma trivolvis lentum* (not *lantum*, typographical error) from Louisiana to be hosts of many American cercariae. O'Roke (1917) found *Helisoma trivolvis* (probably the race *lentum*) carrying cercariae in Kansas, and McCormick (1923) found *Helisoma trivolvis* and *Gyraulus parvus* to be infested in Ohio. Ward (1918), in Ward and Whipple's Fresh-water Biology (pp. 365-424), summarizes the cercarial stages of parasitic flatworms, gives keys for the determination of the larval stages and indicates the species of mollusks which have served as intermediate hosts. *Physa*, *Lymnaea*, and *Planorbis* are listed, including many of the Planorbidae. However, this text was compiled at the very beginning of studies on trematode life histories on this continent. More recently there have been numerous detailed studies on the stages in fresh-water snails. Many other works might be quoted but a sufficient number have been indicated to show the rôle played by the fresh-water snails, particularly the Planorbidae, in the life cycle of the trematode worms. Some additional titles are listed in the bibliographies accompanying the papers mentioned in this chapter.

During the anatomical investigations made for this work careful note was made of the presence of larvae of trematode worms, principally cercariae and a few rediae. Over a thousand specimens of mollusks were examined but only a few contained parasitic worms. The following species, arranged under subfamilies, were observed to be infested.

Subfamily Planorbinae

No specimens of this subfamily were found with cercariae or rediae.

Subfamily Segmentininae

Segmentina nitida from marshes in a meadow in Czneriakow, a suburb of Warsaw, Poland. Sent by Mr. A. Jankowski. Cercariae were abundant, mainly in the ovotestis which was almost destroyed. All specimens examined were infested.

Drepanotrema hoffmani from pond near Isabela, Puerto Rico. Sent by Dr. William A. Hoffman. Heavily infested with stylet cercariae.

Australorbis glabratus from near San Juan, Puerto Rico. Sent by Dr. Hoffman. Various degrees of infestation.

Subfamily Helisomatinae

Helisoma anceps, from Unionville, Connecticut. Collected by F. C. Baker. One specimen with lung cavity filled with rediae and one specimen with cercariae in liver and genitalia.

Helisoma trivolvis lentum, from near Urbana, Peoria, and St. Joseph, Illinois. Cercariae in liver and ovotestis.

Helisoma subcrenatum from Cottonwood Pass, near Gypsum, Colorado. Sent by Junius Henderson. Four out of six specimens with cercariae in different parts of the body, mostly the liver. Some specimens from a sluggish creek one mile west of Devon, Montana, collected by J. Henderson and Hugo Rodeck, contained cercariae, mostly in the liver.

Helisoma plexatum, from Teton River, north of Rexburg, Idaho, collected by J. Henderson; one out of six infected.

Helisoma hornii, from Paul Lake, Kamloops District, British Columbia. Sent by Dr. D. S. Rawson, University of Saskatchewan. About one-third were affected by cercariae.

Helisoma pilsbryi from Chetek Lake, Barron Co., Wisconsin. Collected by F. C. Baker. Cercariae in eight specimens with the liver and ovotestis mostly affected.

Helisoma corpulentum from Miles Bay, Lake of the Woods, Canada, Fall Lake, Ontario, Canada, and Knife Lake, St. Louis Co., Minnesota. Collected by Dr. A. R. Cahn. Many infested with cercariae.

Helisoma corpulentum multicostatum, from Lake Kahnipiminanikok, Ontario, Canada. Collected by Dr. A. R. Cahn. One out of six with cercariae.

Helisoma whiteavesi from Kashabowie Lake, Ontario, Canada. Collected by Dr. Cahn. One out of four infested with cercariae.

Helisoma campanulatum wisconsinense from Pirate Island, Lake Nipissing, Ontario, Canada. From the Biological Board of Canada. One out of five specimens with cercariae.

Subfamily Planorbulinae

Menetus cooperi callioglyptus from Quatana, Vancouver Island, British Columbia. Received from Dr. W. A. Clemens. Two-thirds of the specimens examined (about a dozen) were infested with cercariae, in several examples almost consuming the liver, albumen gland, and ovotestis. In several specimens the cercariae were most numerous about the stomach. Several hundred were observed in some specimens.

Menetus cooperi from small lakes on Mt. Constitution, Orcas Island, Puget Sound, Washington. Collected by Dr. Dale Foster. Of fifteen specimens examined, one contained cercariae.

Menetus dilatatus from Unionville, Connecticut, fourteen miles west of Hartford. Collected by F. C. Baker. One specimen in sixteen contained cercariae.

Menetus sampsoni from slough of Meramec River east of Stanton, Franklin Co., Missouri. Collected by Leslie Hubricht. Twelve out of fourteen specimens were infested with cercariae, the liver and genitalia being principally affected. In several specimens nearly all of the internal organs had been destroyed.

Same species from small lake near Hutchins, Dallas Co., Texas, collected by Dr. E. P. Cheatum. Fifty per cent of specimens examined were affected by cercariae.

Promenetus exacuous from small lake in Wainwright Park, Alberta, Canada. Received from A. LaRocque, Canadian National Museum, Ottawa. Nearly all specimens examined were infested with cercariae, some in the fore part of the body, many about the stomach, but mostly confined to the liver and genitalia. Specimens of *exacuous* from Maine, Wisconsin, Michigan, New York, and Ontario did not contain larval worms.

It is unfortunate that parasitological assistance was not available when these anatomical studies were in progress in order that the particular species of parasitic trematode worms involved might have been ascertained. Many species of cercariae remain to be discovered from the tissues of planorbid and other fresh-water mollusks.

The effect of fluke infestation on the anatomy of the snail is variable. The cercariae may infest only the liver, in which case, often, the cercariae finally leave the snail which recovers from the damage inflicted by the parasite. In many other cases, however, the liver, genitalia, and stomach are affected and in large measure destroyed. Specimens have been examined in which the genitalia were completely destroyed or the genitalia and liver obliterated. In one case (*Menetus cooperi*), almost the whole snail was so filled with cercariae (several thousand) that the normal organization could not be distinguished, the cercariae being packed in the space occupied by the organs and in aggregation taking their form. This was particularly true of the genitalia. Faust (1920, p. 79) has given a good account of the pathological changes in the gastropod liver due to fluke infestation. Wesenberg-Lund (1934) and Miriam Rothschild (1936) have recorded instances of gigantism in snails apparently attributable to trematode infections.

Several parasitologists have essayed the rôle of conchologists in an endeavor to understand the specific limitations of the groups of molluscan species acting as hosts for parasitic trematode worms. Among these are the late Dr. Adolpho Lutz (1918) of the Instituto Oswaldo Cruz and Dr. A. Vianna Martins (1938) of the Laboratorio do Instituto Biologico Ezequiel Dias. Dr. Lutz describes all species under the common generic name *Planorbis*, the modern genera *Australorbis* and *Tropicorbis* being the principal groups discussed. In the main, the work of Dr. Lutz is good and the species have been carefully distinguished. The work of Dr. Martins is a study of the genus *Australorbis* of Pilsbry, based in part on the earlier work of Dr. Lutz. Unfortunately the two genera *Tropicorbis* and *Australorbis* have been confused by this author and many species lumped under *Australorbis*, to which they have little relation anatomically. It is obvious that specific identifications must be accurately made if any value is to be attached to these forms as intermediate hosts of parasitic worms.

In Part II of this work the recognized species, and also the synonyms, of species of both *Australorbis* and *Tropicorbis*, as well as of other groups, will be discussed and the species figured.*

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*The author's death came before he could finish Part II. However, 60 plates made for Part II are printed as an Appendix to this work (see page 213 et seq.). H.E.C.

III.

NIDIFICATION AND EMBRYOLOGICAL DEVELOPMENT

THE EARLY STAGES of cell growth and development in the planorbids (*Helisoma trivolvis*) have been well described and figured by Holmes (1900, pp. 369-458). Crabb (1927, pp. 67-108) has described and figured the early stages of *Lymnaea stagnalis appressa* (=*jugularis*) and Lankester (1874) has given us the full development of the European *Lymnaea stagnalis*. More recently (1934) Lowrance has very fully described the early development of *Stagnicola kingi*. Little work has been done, however, on the embryonic development of the different species of the family Planorbidae and especially on their nidification, period of development, and the time element in the growth of the young animal in its shell.*

A dozen or more aquaria were operated during the years 1930 to 1934 and careful data were gathered concerning the period of egg deposition, number of capsules laid, changes taking place within the egg capsule, and growth of the young snails within the egg and after hatching.

A. DEVELOPMENT OF *Helisoma scalare* (JAY)

In 1932, Dr. E. A. Andrews, of the Johns Hopkins University, sent the writer a piece of pond lily leaf upon which was a large egg capsule of *Helisoma (Seminolina) scalare* (Jay), containing twenty-eight eggs in various stages of development. This capsule was deposited in an aquarium but the parent came from Lake Butler, Florida. This egg capsule was observed as opportunity afforded until all of the embryos were hatched or had died. From this capsule a fairly good idea of the development of this planorbid was obtained. Observations began when the specimen was received on March 2 and the last specimen was hatched on March 17. The different stages are figured on plate 51 and are described in the explanation of that plate.

Development was observed to be sporadic in many of the eggs. There were resting stages between periods of great activity of rotation about the interior of the egg, the rotation beginning in this species the latter part of the gastrula stage, the second day of development, and becoming marked from the early trochophore stage. This rotation is caused by the vibration of the numerous cilia attached to the foot of the embryo (CL in figures).

Observations on the egg capsule began on March 2, when twenty-eight fertile eggs were counted. The observations, made several times a day, showed the following degrees of development:

March 2-3. 24 eggs in segmentation stages. 4 in early trochophore stage.
4. Same condition as on March 3.
5. 20 eggs in gastrula stage; 4 in trochophore stage; 4 in preveliger stage.
7. 18 in gastrula stage; 5 in trochophore stage; 3 in veliger stage; 2 postveliger.
8. 18 in gastrula stage; 4 trochophore; 3 veliger; 3 embryos with shell.

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*After this manuscript was in press, a very significant experimental study, by H. B. Roney, on the development of *Helisoma* eggs, under controlled conditions, appeared in *Ecology*, v. 24, pp. 218-243.—H.J.V-C.

March 10. 18 in gastrula stage; 4 trochophore; 3 veliger; 3 embryos with shell.
11. 18 in gastrula stage; 4 veliger; 3 postveliger; 3 embryos with shell.
12. 18 in gastrula stage; 3 veliger; 4 postveliger; 3 embryos with shell.
13. 18 in gastrula stage; 3 veliger; 3 postveliger; 3 embryos with shell; 1 hatched.
14. 18 in gastrula stage; 3 veliger; 3 postveliger; 2 embryos with shell; 1 hatched.
15. 18 in gastrula stage; 2 veliger; 2 postveliger; 2 embryos with shell; 2 hatched.
16. 18 in gastrula stage; 2 postveliger; 3 embryos with shell; 1 hatched.
17. All hatched or dead, many of the gastrula stage filled with Protozoa.

In the above table it will be observed that only ten embryos completed their development. Eighteen embryos did not continue their growth after reaching the gastrula stage, for what reason is not apparent. In the stage shown in fig. 9 on plate 51 the snail is very active, moving about in the egg and grazing like the adult snail. The radula can be seen working with its peculiar lapping motion, the heart is beating regularly, and the pulmonary siphon is functioning, for it can be seen to emit bubbles. One young snail four days out of the egg was transferred to an aquarium. This specimen was very active, crawling about the glass sides of the jar. The eyes were black and very conspicuous.

Several of the embryos that completed their development showed the following history.

EGG NUMBER 1

March 2-3. Segmentation and gastrula. Like fig. 2, 3.
4. Early trochophore stage.
5. Trochophore stage.
7. Posttrochophore stage. Like figs. 4, 5.
8. Veliger stage. Like figs. 6, 7.
9. Veliger stage. Like fig. 9.
March 10. Embryo stage. Like fig. 10.
11. Embryo stage. Like fig. 10.
12. Embryo stage. Like fig. 11.
13. Young snail. Like fig. 12.
14. Young snail. Like fig. 12.
15. Young snail. Like fig. 12.
16. Hatched from egg. Like fig. 13.

EGG NUMBER 8

March 2-4. Early segmentation and gastrula stages. Like figs. 2, 3.
5. Posttrochophore stage. Like figs. 4, 5.
7. Veliger stage. Like fig. 6.
8. Veliger stage. Like fig. 6.
9. Veliger stage. Like figs. 7, 8.
March 10. Veliger stage. Like fig. 9.
11. Embryo stage. Like fig. 10.
12. Embryo stage. Like fig. 10.
13. Young snail. Like fig. 12.
14. Young snail. Like fig. 13.
15. Young snail. Like fig. 13.
16. Hatched. Like figs. 13, 14.

Both of the above embryos completed their development in fifteen days. Probably some early cell divisions took place the day before observations began, which would increase the development period to sixteen days. The temperature of the room was 70-75 degrees Fahrenheit. The other eggs in this capsule showed approximately the same development. The embryo in egg number 5 migrated to egg number 6 at the late embryo stage and both embryos occupied the same chamber until they were hatched, three days later.

Several adult *Helisoma scalare* received from Dr. Andrews, collected in Lake Butler, Florida, were placed in an aquarium where they bred and laid eggs which successfully completed their development. Eggs were first observed on March 13 (see plate 52, fig. 1). The egg capsules were deposited on the glass sides of the aquarium and were numbered so that development could be easily and accurately observed. Thirteen egg capsules were deposited early in March:

No. 1. 10 eggs, capsule 3.5 by 2.5 mm.
2. 6 eggs, capsule 3.5 by 2.5 mm.
3. 8 eggs, capsule 3.0 by 3.0 mm.
4. 10 eggs, capsule 5.0 by 3.0 mm.
5. 4 eggs, capsule 3.5 by 2.5 mm.
6. 10 eggs, capsule 4.5 by 3.5 mm.
7. 10 eggs, capsule 5.0 by 3.0 mm.
No. 8. 11 eggs, capsule 4.5 by 3.5 mm.
9. 2 eggs, capsule 4.5 by 2.5 mm.
10. 9 eggs, capsule 5.0 by 3.5 mm.
11. 5 eggs, capsule 4.5 by 3.5 mm.
12. 13 eggs, capsule 5.0 by 4.0 mm.
13 14 eggs, capsule 5.0 by 3.5 mm.

Egg capsule No. 3 with eight eggs developed as follows:

March 13. Freshly deposited capsule.
14. Early segmentation.
15. Gastrula stage.
16. Gastrula and trochophore stages.
17. Gastrula and trochophore stages.
18. Trochophore and preveliger stages.
19. Veliger stage.
20. Early embryo stage.
21. Embryo stage.
March 22. Embryo with shell of about one whorl.
23. Embryo with shell half filling egg.
24. Embryo with shell three-fourths filling egg.
25. Embryo with shell almost filling egg.
26. Embryo with shell filling egg.
27. Four embryos hatched.
28. Last embryo hatched.

The period of development was fifteen days.

Capsule No. 6, with ten eggs, occupied a longer period (18 days) in hatching.

Capsule No. 8, with eleven eggs, had all embryos hatched in seventeen days, from March 15 to March 31. Capsule No. 11, with five eggs, developed and hatched the young snails in thirteen days, from March 15 to March 27. All other capsules occupied fifteen to eighteen days. The shell when the young are hatched measures about 1.0 by 0.7 mm.

About two weeks later (April 2) six capsules were deposited measuring as follows (see plate 52, figs. 2, 3):

Capsule 4.5 by 3.0 mm. with 10 eggs.
Capsule 5.5 by 3.0 mm. with 7 eggs.
Capsule 6.0 by 4.0 mm. with 14 eggs.
Capsule 5.0 by 3.0 mm. with 9 eggs.
Capsule 5.0 by 3.0 mm. with 19 eggs.
Capsule 5.0 by 3.0 mm. with 9 eggs.

One capsule with nine eggs developed as follows, the process occupying but twelve days:

April 2. Freshly deposited eggs.
3. Segmentation.
4. Segmentation and gastrula stages.
5. Gastrula and trochophore stages.
6. Posttrochophore and preveliger stages.
7. Preveliger and veliger stages.
April 8. Postveliger and early embryo stages.
9. Embryo with small shell.
10. Embryo filling egg.
11. Embryo filling egg.
12. Embryos hatching.
13. Young snails all hatched.

On May 22 the aquarium was examined for its entire contents. There were ninety-six young snails of *scalare* only sixteen of which were living. There were three adult specimens measuring 8 to 10 mm. in length. These, curiously enough, were in shape more like *Helisoma duryi seminole* than typical *scalare*. The shells were very wide with broad spire and decided umbilicus. The young snails in the aquarium were approximately seven and one-half weeks old. A few of these were measured and the number of whorls was counted:

Height 2.0; diameter 2.5 mm. Whorls 2.
Height 3.0; diameter 3.0 mm. Whorls 2½.
Height 2.5; diameter 2.8 mm. Whorls 2½.
Height 2.5; diameter 2.8 mm. Whorls 2¼.

When hatched the shells usually measure 1 mm. in height and 0.7 mm. in diameter and have a trifle more than one whorl. The young *scalare,* therefore, had more than doubled in size in less than eight weeks. On August 15, after a hot summer, seven specimens remained in the aquarium. Five of these measured as follows:

Height 4.7; diameter 5.0 mm. Whorls 3⅕.
Height 4.0; diameter 4.1 mm. Whorls 3.
Height 5.0; diameter 5.1 mm. Whorls 3.
Height 6.0; diameter 5.0 mm. Whorls 3⅕.
Height 6.0; diameter 6.0 mm. Whorls 3½.

These measurements indicate that the shells had almost trebled in size in about twelve weeks, although but one more whorl was added.

On June 26, during a hot period of weather, two adult snails of this species died, leaving one adult, which lived over winter isolated in a small aquarium. On March 5, 1933, several egg capsules were laid by this individual approximately nine months after its isolation. Two empty egg capsules were observed on the side of the aquarium and twenty-one young snails were crawling about. The young shells measured 2 mm. in height and 2.5 mm. in diameter and had two whorls. All lived from March 5 to May 21 when three died. On June 25 the last adult died but nine of the young remained alive.

On September 3, 1933, four of the young *scalare* were living. The young snails at this time, about twenty-three weeks old (160 days) measured 5.0 mm. in height and 4.5 mm. in diameter and had three and one-half whorls. Between September 3 and September 17 these young snails formed eighteen egg capsules containing the following number of eggs: 6, 11, 13, 9, 10, 5, 7, 7, 12, 11, 2, 5, 9, 10, 10, 7, 9, 7. Embryos in but two of the capsules completed their development. The parent snails of this last brood, it will be noted, were the offspring of an isolated adult *scalare*. The young snails lived until January, 1934.

The development of *Helisoma scalare* is similar in many respects to that described by Lankester for *Lymnaea stagnalis* (1874) and by Lowrance (1934) for *Stagnicola kingi*. There are, of course, differences in the form of the embryos as would be expected in two such diverse families. Lowrance found that young snails of *Stagnicola kingi* hatched in from fourteen to sixteen days (p. 10) but that with increased temperature (26 degrees centigrade) this period was cut to from nine to eleven days. *Lymnaea stagnalis* may require as much as twenty days or more for development.

B. NIDIFICATION AND DEVELOPMENT IN OTHER SPECIES OF *Helisoma*

Plates 51 and 52

Living material belonging to five additional species and races of *Helisoma* was studied in aquaria during the years 1931, 1932, and 1933. The species included were:

Helisoma trivolvis lentum (Say)
Helisoma trivolvis fallax (Haldeman)
Helisoma duryi normale Pilsbry
Helisoma duryi eudiscus Pilsbry
Helisoma tenue californiense F. C. Baker

Several species were from different localities and these as well as each race were kept in separate aquaria. Observations were made several times each day at intervals of three or four hours. Each jar was labeled and the egg capsules lettered or numbered as they were deposited by the animals. Notes were kept of developments in each capsule. The data which follow have been condensed from the original notes.

The information sought in these studies was to ascertain the time required for development and the rate of growth of the shells of the young snails during their life in the aquaria.

[a] Self-fertilization or Autofecundation

That self-fertilization or autofecundation is possible among the fresh-water pulmonates has been suggested by several zoologists during the past hundred years or more, but until comparatively recent time few experiments have been carried on to test the reality of this method of reproduction. Colton (1912, p. 173; 1918, p. 48) has shown that *Lymnaea*, *Physa*, and several groups of Planorbidae (*Gyraulus*, *Menetus*) lay fertile eggs by this method when isolated. Crabb (1927) has presented elaborate data on this subject, and more recently Larambergue (1939) has issued an elaborate monograph particularly relating to *Bulinus contortus*. On pages 541-543 he presented a list which includes all of the authentic examples of autofecundation. This list includes all families of Basommatophora as well as a few among the Stylommatophora. Crabb (1927) studied *Lymnaea stagnalis appressa* (=*jugularis*) to determine whether snails kept in strict isolation reproduced by self-fertilization or by parthenogenesis. His conclusions were that there was no evidence of parthenogenesis in this snail.

It is to be noted, however, that reproduction by parthenogenesis does occur in some groups of snails. Boycott (1919) has asserted that *Paludestrina jenkinsi* develops by this method. More recently Van Cleave (1937) and Mattox (1937, 1938) have shown that the viviparoid snail *Campeloma rufum* develops solely by parthenogenesis although other species of the genus have been found to be bisexual. The reproductive method in *Campeloma* was observed by morphological and histological studies and there is no question concerning the parthenogenetic method of reproduction in the species examined.

Some years ago, Chadwick (1903, p. 265) conducted some interesting experiments on *Planorbis vortex*, a common English planorbid. On February 2, 1901, he isolated an adult specimen in a jar three-fourths filled with boiled water, a small quantity of weed was introduced, the rest of the jar was filled with pure oxygen and the vessel was perfectly sealed. It remained in this condition for eighteen months, or until August, 1902. In June, 1902, aften sixteen months of complete isolation, the snail deposited some eggs which were hatched in early July, producing twenty-seven young snails, many of which were still thriving under these confined conditions on December 10, 1902. In evaluating this set of observations, and many others along this line, it should be remarked that only those experiments in which individual eggs were isolated have any conclusive value in establishing the occurrence of self-fertilization. This is especially true when forms are considered for which there are no observations as to the length of time the spermatozoa remain viable following copulation.

Crabb states (1927, p. 91) that self-fertilization is the normal method of reproduction in *Lymnaea* and other fresh-water pulmonates and that cross-fertilization seldom or never occurs. With this general statement the writer can not fully concur. It is doubtless true in many cases of reproduction during isolation but that it is the chief method among free snails when in aggregation in their native environment or even in the laboratory is scarcely possible. The writer has observed many species of *Lymnaea*, *Physa*, and the planorbids *in coitu*. If the method of reproduction mentioned by Crabb is the chief or possibly the only method, why should the male portion of the genitalia be so elaborately developed with prostate and the penial complex provided with such diverse accessories in its makeup? The spermatheca has been found to contain a spermatophore containing sperm which was obviously deposited during copulation. Self-copulation probably occurs when a snail is isolated, at least in those species having a penial complex of sufficient length to reach the female opening, which is the case in many species of the Planorbidae.

Crabb states that he was unable to raise progeny from isolated *Planorbis trivolvis* (*Helisoma*), four individuals being carefully reared in isolation for 377 days without the laying of a single egg capsule. Ten to fifteen small empty egg masses were deposited. Even the control culture, consisting of two snails, formed no capsules. *Lymnaea stagnalis*, on the contrary, was very prolific.

> My isolated laboratory stock lays about every third day for a period of about twenty-five days, rests a few days, then begins another cycle of laying. This is continued throughout the year. Of fifty-four *L.s.appressa* isolated from the same egg mass, seven laid their first eggs fifty-eight days after hatching. However, they do not reach their maximum laying capacity until they are about one hundred days old (Crabb, p. 73).

Colton's experiments on *Lymnaea* (*Pseudosuccinea*) *columella* indicated that the interval between hatching and egg laying was widely variable (1912, p. 175). Thirteen isolated individuals had the following interval between hatching and egg laying: 32, 26, 35, 49, 58, 92, 50, 50, 56, 57, 63, 74, and 74 days. Twenty-six days was the shortest interval and ninety-two days the longest interval.

In the family Planorbidae the intervals are much longer, not only of the specimens placed in isolation, but for those in aggregation. *Helisoma scalare* laid thirteen egg capsules in early March, 1932. In early April, six additional capsules were produced. An isolated individual which lived over winter (nine months) without egg laying, deposited two fertile egg capsules on March 5, 1933. Between September 3 and September 17 the young snails, 160 days old, laid eighteen egg capsules containing from six to thirteen eggs in each capsule.

Specimens of *Helisoma trivolvis lentum* were placed in aquaria in 1930. On February 16, 1931, a capsule was laid, on February 22 four capsules were deposited and on March 7 two capsules were laid. No other eggs were laid by these specimens which lived until September 17, 1933, or a period of 943 days. A young specimen from the parent *lentum* was isolated January 16, 1932. It was about 325 days old. Between May 27 and June 9, 1932, this individual, after inhabiting the aquarium for 132 days, laid twenty egg capsules aggregating 325 eggs. On June 20, 1932, the parent snail was removed to another aquarium and on June 22 laid two egg capsules and on June 27 deposited two more capsules. These capsules were laid fifteen and twenty days after the large laying period in the first aquarium. Two-thirds of the eggs laid completed their development. A few of the second generation remained alive for about two years but laid no egg capsules.

These examples seem to indicate that the large planorbids do not breed as often as do the lymnaeids and are not as available for studies in development as are members of the Lymnaeidae. Just how the smaller species of the genera *Menetus*, *Gyraulus*, and *Tropicorbis* would react to such investigations is not known.* It is probable that had Crabb kept his *Helisoma trivolvis* longer they might ultimately have laid eggs.

[b] The Development of *Helisoma*

The notes that follow describe some of the results of aquarium observations on a few of the species of the genus *Helisoma*. No attempt has been made to go into the finer details of embryological development. This has been done by Holmes (1900) and others.

[1] *Helisoma trivolvis lentum* (Say)

Several specimens of the *lentum* race were received in 1930 from Dr. E. C. Faust of the Tulane Medical School, New Orleans. They were collected from the canal at New Orleans. This city is also Say's original locality for this species. The snails were placed in aquaria and kept under observation for several years. On February 16, 1931, an egg capsule was observed, apparently freshly laid, with twenty-five eggs. It measured 7.5 by 6.0 mm. On February 22 four additional egg capsules were laid, one 4 by 3.5 mm. with nine eggs, one 7 by 4 mm. with fourteen eggs, one 9 by 4.5 mm. with nineteen eggs, and one 10 by 4.5 mm. with twenty-four eggs. On March 7, two other egg capsules were observed, one with fifteen eggs and the other with nineteen eggs. All eggs were fertile and contained embryos in the early stages of development.

On September 12, 1931, twenty-five young snails were counted, ranging in diameter from 4.5 mm. with two and one-fourth whorls to 16 mm. with four whorls. On November 28, 1931, nineteen specimens were counted ranging in size from 5.5 mm. in diameter with three whorls to 14 mm. with four and one-fourth whorls. On January 16, 1932, the nineteen specimens were again measured, the smallest being 5.5 mm. in diameter with three whorls and the largest 14 mm. with four and one-fourth whorls. On March 19, 1932, the same number of specimens remained in the aquarium, the smallest being 6 mm. in diameter with three and one-fourth whorls and the largest 14.5 mm. with four and one-fourth whorls. On June 10, 1932, only fourteen specimens remained in the aquarium, five having died. The smallest was 6.5 mm. in diameter and had three and one-fourth whorls and the largest was 12.5 mm. with four whorls. August 15, 1932, only six specimens were alive, the smallest 6.5 mm. in diameter and the largest 10 mm. in diameter. On October 23 and December 26 the six specimens were still alive. Their size had not increased.

On March 5, 1933, five specimens were living, the largest 10.5 mm. in diameter with four whorls. On June 25, 1933, three were living, the largest being 11 mm. in diameter with four and one-fourth whorls. On September 17, 1933, two specimens were living. These two specimens had lived over two years in the aquarium. Of the original 125 eggs laid in February and March, 1931, only 25 young snails survived until September, 1931, and only two snails were alive two and one-half years later. Mortality among the young snails appears to be heavy in their early postembryonic life.

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*Rearing methods for securing uninfected snails to be used in life history studies on parasitic worms have been practiced in many parasitological laboratories. W. H. Krull (1931) has published the procedure for successful rearing of *Gyraulus parvus* and found that this species may be reared to full size in from four to five weeks under laboratory conditions (Occas. Pap. Mus. Zool., Uni. Michigan, No. 226).—H.J.V-C.

[2] *Helisoma trivolvis fallax* (Haldeman)

October 2, 1931, fifteen specimens of this race, collected near Cambridge, Massachusetts, were received from Dr. Harold A. Rehder, then in Harvard University (now Assistant Curator of Mollusca, United States National Museum). Egg capsules were observed February 6, 1932, one measuring 4.5 by 3.5 mm. and containing six eggs, and one 5.6 by 7 mm. with thirteen eggs. The eggs of both capsules passed through their development and were hatched by February 12. On February 28 another capsule was laid measuring 5.2 by 4 mm., containing ten eggs, but was eaten by Protozoa after three days of development. March 4 a capsule was laid measuring 5 by 6 mm. with twelve eggs, and on March 10 another capsule was laid, 3.5 by 5.5 mm., containing eleven eggs. On March 13 a capsule containing nine eggs was observed. On March 19, twenty-two young and five adult snails were counted in the aquarium, the young ranging in size from 1.8 mm. to 3 mm. in diameter.

An examination on May 22 revealed seventeen young snails living. All of the adult snails were dead. The living young snails measured as follows:

2 specimens 2.5 mm. in diameter with 2 whorls.
3 specimens 2.5 mm. in diameter with 2½ whorls.
1 specimen 2.8 mm. in diameter with 2¼ whorls.
3 specimens 3 mm. in diameter with 2½ whorls.
1 specimen 3.2 mm. in diameter with 2½ whorls.
4 specimens 3.5 mm. in diameter with 3 whorls.
1 specimen 3.8 mm. in diameter with 3 whorls.
2 specimens 4 mm. in diameter with 3 whorls.

On June 26, 1932, the seventeen young *fallax* were still alive. On August 15 there were fourteen living young snails which measured as follows:

1 specimen 2 mm. in diameter with 2 whorls.
1 specimen 3 mm. in diameter with 2 whorls.
1 specimen 3.5 mm. in diameter with 2½ whorls.
2 specimens 4 mm. in diameter with 2½ whorls.
5 specimens 4.5 mm. in diameter with 3 whorls.
2 specimens 5 mm. in diameter with 3 whorls.
2 specimens 5 mm. in diameter with 3¼ whorls.

On October 23, 1932, only four young *fallax* remained living:

1 specimen 3.5 mm. in diameter with 2½ whorls.
1 specimen 4.5 mm. in diameter with 3 whorls.
1 specimen 5 mm. in diameter with 3 whorls.
1 specimen 5 mm. in diameter with 3¼ whorls.

On March 1, 1933, these four snails were still living and measured as follows:

1 specimen 4 mm. in diameter with 2½ whorls.
1 specimen 5 mm. in diameter with 3 whorls.
1 specimen 5.2 mm. in diameter with 3½ whorls.
1 specimen 5.5 mm. in diameter with 3¼ whorls.

On May 1, 1933, only three living snails remained:

1 specimen 4.9 mm. in diameter with 3 whorls.
1 specimen 5.5 mm. in diameter with 3½ whorls.
1 specimen 5.6 mm. in diameter with 3½ whorls.

On June 25 one young snail remained which measured 6 mm. in diameter and had three and one-half whorls.

This small subspecies of *Helisoma trivolvis* lived in the aquarium 495 days or about seventeen months. It grew from a size of 1.5 mm. in diameter when hatched to 6 mm. when it died, and increased from one and one-fourth to three and one-half whorls. Adult *fallax* measures 15 mm. in diameter and has five full whorls. The last remaining young was, therefore, somewhat more than one-third grown. Full maturity would probably have been attained the third year after hatching.

Conclusions of this sort, in which length of life span is estimated from growth rates in aquaria, are only tentative and are possibly subject to considerable error. Very early experiments on snail development tended to show that the size of reared snails is influenced by the volume of the water and the container in which they grew. Conclusive evidence of rate of growth in nature could be determined by measuring representative samples, from normal habitats, taken periodically as practiced by Van Cleave (1932) and his students in the interpretation of life history data.

[3] *Helisoma duryi normale* Pilsbry

Specimens of this planorbid, collected on the Tamiami Trail, forty miles west of Miami, Florida, were sent to the writer by Mr. W. F. Shay of the Department of Science, Normandy High School, St. Louis. They were placed in aquaria in January, 1931. On January 31 several egg capsules were observed, one containing fifteen embryos in various stages of development, three in veliger stage and twelve with well-formed shells. By February 2, eleven snails had been hatched and were crawling on the glass sides of the aquarium. By February 6 most of the veliger larvae had been hatched. Another capsule contained fifteen eggs with one veliger stage, one gastrula stage and thirteen embryos with well-formed shells. These latter hatched on February 4. Another capsule contained ten eggs, five embryos with partly formed shells and five embryos with fully formed shells. These were hatched by February 5.

On September 1, 1931, three capsules were observed on the side of the aquarium, one with nine eggs, 7 by 4.5 mm. in area, one with ten eggs, 6 by 5 mm. and one with eight eggs, 5.7 by 3.2 mm. On September 12, two additional capsules were deposited, one with seven eggs (6 by 3.2 mm. in area) and one with four eggs (4.7 by 2.7 mm.). Of the first series of three capsules, two died and were eaten by Protozoa and one completed its development. Of the second set, one capsule carried out its full development. In this capsule, the veliger stage was reached on September 15 and the embryo with a well-formed shell on September 19. On September 20, the four snails were actively feeding in the egg capsule, the walls of the egg capsules were broken, and the snails were crawling about in the broken interior. On September 21, the snails had left the egg capsule and were feeding on the side of the aquarium. It is probable that this capsule had been laid for a day or two before first observed because the interval of nine or ten days seems too short for complete development.

On January 17, 1932, a recently laid capsule containing sixteen eggs was discovered and was observed until all of the embryos had been hatched (see plate 42, fig. 12). In this capsule fifteen days elapsed between early segmentation and exit from the egg. By the middle of February the young snails measured 1.1 by 1 mm. and actively glided about the aquarium. The body in the shell is pinkish, the foot hyaline, slightly yellowish, the liver brownish, and the eyes black and prominent. The tentacles are long and mobile. The radula can be plainly seen at work and the jaw appears blackish through the translucent head.

From the above capsule and from several others hatched at about the same time, forty young snails were released in February. Observations were made on the shells several times in March and April. On May 22 there were seven living snails and thirty-three empty shells, indicating that mortality had been heavy, principally during the month of May. The seven living snails had the following shell measurements:

1 specimen 1.5 mm. in diameter with 2 whorls.
1 specimen 2.5 mm. in diameter with 2½ whorls.
1 specimen 2.8 mm. in diameter with 3 whorls.
1 specimen 3.4 mm. in diameter with 2¾ whorls.
2 specimens 3.5 mm. in diameter with 3 whorls.
1 specimen 4 mm. in diameter with 3½ whorls.

On June 26 the seven snails were still alive. By August 15 one had died. The six snails gave the following measurements:

2 specimens 4 mm. in diameter with 3 whorls.
2 specimens 4.5 mm. in diameter with 3¼ whorls.
1 specimen 5 mm. in diameter with 3¼ whorls.
1 specimen 5.5 mm. in diameter with 3¼ whorls.

On December 26, 1932, but four snails remained alive. These showed the measurements below:

1 specimen 4 mm. in diameter with 3 whorls.
1 specimen 5 mm. in diameter with 3¼ whorls.
1 specimen 5.2 mm. in diameter with 3¼ whorls.
1 specimen 6 mm. in diameter with 3½ whorls.

On March 12, 1933, three snails were living which measured as follows:

1 specimen 4.8 mm. in diameter with 3 whorls.
1 specimen 5.7 mm. in diameter with 3¼ whorls.
1 specimen 6.1 mm. in diameter with 3½ whorls.

On June 25, 1933, the same three snails showed some growth:

1 specimen 5.5 mm. in diameter with 3¾ whorls.
1 specimen 6.5 mm. in diameter with 3½ whorls.
1 specimen 6.5 mm. in diameter with 3½ whorls.

On August 6, 1933, but two snails remained alive. These measured:

1 specimen 6 mm. in diameter with 3½ whorls.
1 specimen 6.8 mm. in diameter with 3½ whorls.

These young snails lived 570 to 580 days after hatching and increased in diameter from 1.1 mm. to 6.8 mm. and in number of whorls from one to three and a half. An adult *normale* measures about 20 mm. in diameter and has five whorls, so that the young snails were about one-third grown after a development period of one year and seven months. If this growth is normal, it must require three or four years for this race to attain maturity, unless there is considerable acceleration in growth during the second or third years. The temperature in which the young snails were reared was ordinary room heat between 70 and 75 degrees F. This temperature reached 90 degrees or more in the hot summer months. The matter of food is also important since only filamentous algae were placed in the aquaria, the snails feeding mostly, however, on the green algal deposit which formed on the glass sides of the aquaria.

[4] *Helisoma duryi eudiscus* Pilsbry

Specimens of this race of *duryi* were received from Mr. T. Van Hyning, of the Florida State Museum, collected at Silver Springs, Marion County. They were received at the laboratory on October 2, 1931. On December 13 an egg capsule was laid measuring 2 by 2.5 mm. in area with five eggs. On February 6, 1932, another capsule was laid measuring 2 by 4 mm. with nine eggs, and on February 12 a capsule with seven eggs. On February 10 a large capsule measuring 5 by 4 mm. was deposited containing twelve eggs. One capsule (Feb. 10) developed to the gastrula stage and then ceased growth. Another was disintegrated and the space was filled by Protozoa. A third capsule (Feb. 12) completed its development, all of the embryos being hatched.

A single adult *eudiscus* was left in the aquarium and on June 11, 119 days after the laying of the last egg capsules, egg laying began again with the deposition of a capsule measuring 4 by 3.5 mm. and containing two eggs, each egg 1 mm. in diameter. On June 13 the eggs had reached the gastrula stage. From June 14 to June 26 the eggs remained in the same stage and at the last date the eggs appeared to disintegrate.

[5] *Helisoma tenue californiense* F. C. Baker

Specimens of this race were received from Dr. S. S. Berry, collected from Prospect Park, near Redlands, San Bernardino Mts., California. They were placed in an aquarium on February 12, 1932, and laid nine egg capsules on the next day. The nine capsules contained 199 eggs as noted below:

No. 1. 4 by 4 mm. in diameter containing 15 eggs.
2. 5 by 3.5 mm. in diameter containing 18 eggs.
3. 4 by 7 mm. in diameter containing 21 eggs.
4. 6 by 3.5 mm. in diameter containing 28 eggs.
5. 4 by 5 mm. in diameter containing 15 eggs.
6. 4 by 4 mm. in diameter containing 11 eggs.
7. 4 by 7.5 mm. in diameter containing 27 eggs.
8. 4.5 by 7 mm. in diameter containing 26 eggs.
9. 5 by 8 mm. in diameter containing 38 eggs.

Development was fairly regular and occupied fifteen days, from February 13 until February 28. A typical development is indicated below:

Feb. 14. Segmentation begun.
15. Segmentation and gastrula stages.
16. Gastrula and trochophore stages.
17. Trochophore and preveliger stages.
18. Early veliger stages.
19. Veliger stages.
20. Early embryo stages.
21. Early embryo stages.
22. Embryos with shell forming.
Feb. 23. Embryos with shell forming.
24. Embryos with shell ⅓ filling membrane.
25. Embryos with shell filling ⅓ and ½ of membrane.
26. Embryos with shell filling ¾ of membrane.
27. Embryos with shell completely filling membrane.
28. All hatched.

On February 15 three capsules were laid by the adult snails. They contained three, eleven, and thirteen eggs respectively and development occupied thirteen to fifteen days, from February 28 until March 12. On February 18 a capsule 9 by 6 mm. was laid containing forty eggs, and on February 20 four capsules were deposited measuring 6 by 5, 9 by 6, 6 by 5, and 6 by 4.5 mm. They contained thirty-five, thirty-three, twenty-eight, and twenty eggs respectively. On March 1 and 2, two capsules were laid containing thirty-one and twenty-three eggs. All of these eggs completed their development in from twelve to fourteen days.

On June 5, 1932, the aquarium was examined and the shells counted and measured. There were ninety-six living young snails and forty-five empty shells, 141 specimens in all which had hatched from the capsules enumerated above. The living young snails gave the following measurements:

8 specimens 1.5 mm. in diameter with 1½ whorls.
18 specimens 2.0 mm. in diameter with 2 whorls.
3 specimens 2.3 mm. in diameter with 2 whorls.
40 specimens 2.5 mm. in diameter with 2 whorls.
20 specimens 3.0 mm. in diameter with 2 whorls.
6 specimens 3.0 mm. in diameter with 2½ whorls.
1 specimen 4.0 mm. in diameter with 2½ whorls.

Between June 5 and June 26, fifty-four young snails died, leaving forty-two active young and three adult snails. On August 15, only fourteen young snails were alive, the great mortality being largely due to the very hot summer. The measurements of these survivors are shown below:

1 specimen 2.1 mm. in diameter with 2 whorls.
2 specimens 2.5 mm. in diameter with 2 whorls.
3 specimens 3.0 mm. in diameter with 2½ whorls.
6 specimens 3.5 mm. in diameter with 2½ whorls.
2 specimens 4.0 mm. in diameter with 2½ whorls.

On October 23, 1932, two young snails died leaving twelve active young. On December 28, 1932, four additional snails died leaving eight young which gave the following measurements:

1 specimen 3.5 mm. in diameter with 2½ whorls.
1 specimen 4.0 mm. in diameter with 2½ whorls.
1 specimen 4.0 mm. in diameter with 3 whorls.
1 specimen 4.2 mm. in diameter with 3 whorls.
3 specimens 4.5 mm. in diameter with 3 whorls.
1 specimen 4.9 mm. in diameter with 3 whorls.

On March 12, 1933, only five young snails remained alive, as noted below:

1 specimen 4.0 mm. in diameter with 2½ whorls.
1 specimen 3.5 mm. in diameter with 3 whorls.
2 specimens 5.0 mm. in diameter with 3 whorls.
1 specimen 5.0 mm. in diameter with 3¼ whorls.

On May 1, 1933, but two specimens remained alive, measuring:

1 specimen 4.0 mm. in diameter with 3 whorls.
1 specimen 5.2 mm. in diameter with 3¼ whorls.

On June 25, 1933, one specimen only remained, measuring 6.1 mm. in diameter with three and one-half whorls. This specimen had lived from February 28, 1932, until June 25, 1933, an interval of 482 days or sixteen months. It had grown from a diameter of 0.8 mm. to 6.1 mm. and the whorls increased from one to three and one-half. Adult *californiense* measures 20 mm. in diameter and has five whorls which would indicate that the young specimen sixteen months old had made about one-third of its growth. As in the cases of the other species described in this chapter, factors of volume of water, food, and temperature may have retarded the normal growth of the young of this race. At this ratio full maturity would be attained between the third and fourth years of life.

[6] Other Records of Egg Laying

Helisoma pilsbryi infracarinatum F. C. Baker. Specimens of this species were received from Mr. A. LaRocque, of the Canadian National Museum. They were collected in the Rideau River near Ottawa, Canada. On June 20 two egg capsules were deposited each measuring 6 by 4.5 mm. in size and containing eighteen and twenty eggs. On

May 7 a capsule was laid which measured 7 by 4.5 mm. in area and contained twenty-two eggs. Development was not observed.

Helisoma traskii (Lea). Six shells of this species, preserved in alcohol, received from Mr. Stanley Siegfus of Bakersfield, California, had eleven egg capsules on the shells, containing 394 eggs. A capsule containing fifty eggs is figured (13) on plate 52. The specimens were from the Buena Vista Canal, outlet of Kern Lake, California, near the type locality for *traskii*. The capsules and eggs are noted below:

1 shell with 2 capsules containing 16 and 24 eggs.
1 shell with 2 capsules containing 45 and 42 eggs.
1 shell with 1 capsule containing 10 eggs.
1 shell with 2 capsules containing 35 and 85 eggs.
1 shell with 3 capsules containing 35, 22, and 20 eggs.
1 shell with 1 capsule containing 50 eggs.

Moquin-Tandon (1855, pp. 425-439) collected egg capsules from water bodies in the environs of Toulouse, France, and observed the development of some of the embryos. Some of his observations are recorded below:

Segmentina nitida (Müller). Nine egg capsules containing 3, 4, 5, 6, 7, and 8 eggs, the capsules measuring 0.25 to 1.5 mm. in diameter. Development occupied ten to twelve days.

Hippeutis fontanus (Lightfoot). Several capsules with 3, 4, 5, and rarely 6 eggs in each capsule.

Gyrorbis complanatus (Linn.) (= *Planorbis planorbis* (Linn.)). Eight capsules containing 10, 11, 13, 16, 17, and 21 eggs.

Gyrorbis carinatus (Beck in Möller) (= *Planorbis carinatus*). Capsules containing ten to twenty eggs each. Development occupied ten to fifteen days.

Gyrorbis vortex (Linn.) (= *Anisus vortex* (Linn.)). Ten to twelve eggs in a capsule which were 4 mm. in diameter. Development required ten to twelve days.

Planorbis albus Müller (= *Gyraulus albus* (Müller)). Capsules 3 to 4 mm. in diameter containing four to ten eggs.

Planorbis contortus Linn. (= *Bathyomphalus contortus* (Linn.)). Capsules 3 mm. in diameter containing six to eight eggs. Development occupied ten to twelve days.

Planorbis corneus (Linn.) (= *Planorbarius corneus* (Linn.)). Egg capsules 9, 11, 12, 13, and 15 mm. in diameter containing twelve to forty eggs each. Development required fifteen to sixteen days.

Brooks (1880) has recorded the early stages in the development of the small snail *Gyraulus parvus* (Say) (= *Planorbis parvus* Say).

IV.

DISTRIBUTION IN TIME AND SPACE

A. GEOLOGICAL HISTORY AND DISTRIBUTION

THE ANCESTRY of the Planorbidae, as of other members of the pulmonate mollusks, is shrouded in mystery. It is said that the ancestors of the Planorbidae, as of other groups of the Basommatophora, were originally aquatic, then migrated to the land and finally again returned to aquatic habitats. Perhaps this was accomplished through such groups as the Auriculidae (*Carychium* for example) which have the Basommatophorous organization but inhabit the land.

In America the family apparently first appears in the Morrison formation which is considered of Jurassic or Early Cretaceous age, probably Jurassic. In Europe, a species, *Planorbis mendipensis* Moore, is known from the Liassic of England. The family is not uncommon in the Bear River formation, believed to be at the top of the Lower Cretaceous (Comanchean), or at the base of the Upper Cretaceous, and also in the several divisions known to belong to the Upper Cretaceous, as Judith River, Belly River, and others. During Tertiary time the family was well represented. Eocene, Miocene, Oligocene, and Pliocene formations have yielded many characteristic species. The Pleistocene planorbid fauna is practically the same as the recent fauna.

As the few specimens of planorbid shells from Jurassic or Lower Cretaceous time are not notably different in general characteristics from those of later geological periods or from the modern fauna, it is obvious that the family in some form must have existed in earlier strata, Triassic and Carboniferous (Pennsylvanian and Mississippian). A *Physa* (*prisca* Walcott) and other fresh-water groups are reported from the Mississippian of Nevada and fresh-water and land mollusks are known from various localities from strata of Pennsylvanian age. Planorbids, however, have not yet been reported from these older geological periods.

In Europe this family is fairly common in rocks of Mesozoic and Cenozoic age, but earlier records are very few in number. A Triassic planorbid has already been mentioned. In the Upper Oolite another species appears, *Planorbis fisheri* Forbes. In the Eocene a number of species of this family occur, and in the Oligocene more than eleven species are known. The family is not uncommon in later periods. On the continent a large number of species and races of this family have been recorded from nearly all of the later geological periods. Wenz (1923) has listed all of these but many of the species have obviously been placed in the wrong genera, especially some of the large forms which are listed under the genus *Planorbina*, for it does not occur in Europe. It is quite probable that these large species are members of the genus *Planorbarius* and are related to the large *Planorbarius corneus* so common in the recent fauna.

In America (see Henderson, 1935) sixty-three species of fossil planorbids have been described. Of these two are of Jurassic or Comanchean age, two from Comanchean, five from Upper Cretaceous, eight from Eocene, six from Oligocene, five from Miocene, thirty from Pliocene, and five simply described as 'Tertiary.'

It is obviously very difficult to place fossil mollusks in appropriate genera in a classification based on anatomical characteristics. Nearly all of the fossil planorbids of America and Europe have been described as '*Planorbis*.' With the greatest of care it is possible to place some of these species in their correct genera as understood at the present time. Some forms, however, can only be tentatively placed, basing the decision on the similarity of the fossil species to some known living species of which the anatomy is known. Even among modern species this method is fraught with danger because of similar resemblances of the shells of several genera, as in *Planorbula* and *Tropicorbis*, where some species of the latter genus have internal lamellae in the aperture similar to species of the genus *Planorbula*. The two genera are far apart anatomically.

Among American fossils the following genera are known to be represented by several species and races:

Tropicorbis, 1 species; *Paraplanorbis*, 1 species; *Platytaphius*, 2 species; *Gyraulus*, 6 species; *Helisoma*, 8 species; *Carinifex*, 2 species; *Vorticifex*, 8 species; *Perrinilla*, 2 species; *Parapholyx*, 2 species; *Pompholopsis*, 1 species; *Menetus*, 5 species; *Planorbifex*, 1 species.

Many of the species now known as *Planorbis* may later be placed in more appropriate genera. It is proposed in Part II of this work to review critically all of the American fossil Planorbidae, including several from the West Indies and Central America, and to endeavor to place each species in its correct genus.*

The geographical distribution of the extinct species of the family Planorbidae is not very different from that of the recent species of the family. Fossil species of the family have been recorded from Europe, Asia, Africa, Australia, some of the islands of the Pacific Ocean, North and South America, and the islands of the West Indies.

B. GEOGRAPHICAL DISTRIBUTION

Like the Lymnaeidae, the Planorbidae are world-wide in their geographic distribution. There is scarcely a known region in which some of the planorbid snails do not live. The distribution by genera, however, is more or less limited. Typical *Planorbis* and *Planorbarius* are mostly confined to Europe and western Asia, with possibly some forms of circum-Mediterranean distribution. *Helisoma* is wholly American but is known from both North and South America and from some of the West Indies. A fossil species has been reported from northeast Siberia (Lindholm, 1933). This genus is numerous in North America, principally the northern part of the United States and Canada. *Planorbula* is found only in eastern North America from Alabama northward. *Carinifex* and *Parapholyx* are west American in distribution. *Menetus* is American and does not extend south of the United States. A small group of *Helisoma* (*Seminolina*) occurs only in the peninsula of Florida.

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*As explained elsewhere, Mr. Baker's death prevented him from completing Part II of this monograph.

Australorbis is known from South America and the West Indies but is not found north of the Isthmus of Panama. *Tropicorbis* occurs in South and Central America, in Mexico, the West Indies, and in the southern part of the United States bordering the Gulf of Mexico. Curiously enough, a closely related group, known as *Afroplanorbis*, is found in northern and central Africa and resembles *Tropicorbis* so closely, in both shell and anatomy, that it is a question whether the two groups are not identical generically. *Anisus* is mostly European and Asiatic. *Segmentina* is typically European, west Asian, and north African. Several groups related to *Segmentina*, as *Polypylis, Helicorbis, Pingiella*, and *Intha*, are confined to eastern Asia and some of the Pacific islands. *Taphius* occurs only in Central America and in northern South America. *Gyraulus* is the most widely distributed of any of the genera of Planorbidae, being known from North America, Europe, Asia, Africa, and some of the islands of the Pacific as well as from the West Indies. It is typically a northern group (palaearctic) but a few species extend southward into the tropical regions.

The present study of the distribution of the members of the family Planorbidae shows conclusively the value of the anatomy in the classification of the species. It is of interest to note that in considering the distribution of the genera, details of the anatomy have been the only means by which the different groupings could be made with certainty. Hence our knowledge of distribution has become more definite and better understood than was possible when shell characters were given chief taxonomic value. The shell alone is not sufficient to distinguish groups because there are parallels in growth tendency which render shells of widely separated genera confusingly similar in appearance. Instances of this are found in the species of *Tropicorbis* and *Planorbula, Australorbis* and *Helisoma, Segmentina* and *Polypylis,* etc.

Dispersal of Species

The presence of species of mollusks in isolated places has been somewhat of a puzzle to many zoologists. How, for example, are ponds without inlet or outlet and more or less widely separated, populated by one or more species of planorbids or other fresh-water species? In what manner have the same species of *Tropicorbis, Australorbis,* or *Drepanotrema* found their way to so many of the islands of the West Indies, isolated by large and deep areas of salt water? Examining the distribution of *Australorbis,* for example, we find it occurring in eastern and northern South America and also in many of the groups of islands—the Lesser Antilles, the Greater Antilles, Puerto Rico, and Jamaica. Some species of *Tropicorbis* have the same distribution.

Natural dispersal by migration is out of the question. Driftwood might answer for land snails (at least to a limited degree) but not for fresh-water forms. A former connection with South America occurred too remotely to answer satisfactorily the question. When we examine the migration routes of the migrating birds, especially the wading birds and ducks, we are struck by the similarity of the geographic routes of the birds with the geographic distribution of the snails. One route is from Venezuela, South America, through the Caribbean and West Indian islands as follows: Trinidad, Grenada, St. Vincent, St. Lucia, Martinique, Dominica, Marie

Galente, Antigua, St. Christopher, St. Thomas, Puerto Rico, Haiti, Jamaica, and Cuba. The three genera *Australorbis*, *Tropicorbis*, and *Drepanotrema* inhabit most of the islands mentioned. Another route is from Venezuela northward up the eastern coast of Panama, close to Costa Rica, Nicaragua, Honduras, Guatemala, eastern Mexico to the gulf coast of the United States. The genus *Tropicorbis* has this distribution and many of its species are widely distributed. Some migrant birds pass up the west coast of Central America and Mexico.

It is the writer's belief that the populating of many if not all of the islands of the West Indies with planorbid and other fresh-water mollusks has been brought about through the agency of migrating birds. They stop at these islands to feed and rest, the snails become attached to the feet or other parts of the bodies of the birds, to be liberated when the birds make other stops. Young snails have been found attached to the feet of many birds. In the case of the Basommatophorous mollusks a single snail introduced into a pond would be sufficient to insure population since self-fertilization is easily accomplished. By this means in a few years a body of water would be a prolific habitat for the species. Aquatic insects, especially beetles, would perform the same service, especially in populating closely associated ponds or streams. Young snails have been found attached to the wings (elytra) of beetles.

Natural migration doubtless takes place in connected streams and other bodies of water and will account for the dispersal of related species within the drainage of a water system. Floods often carry species of snails over natural divides. In the distribution and dispersal of the Mollusca, all agencies must be taken into account. The scarcity of records of snails on the bodies of migrating birds is primarily due to the fact that those who kill the birds, sportsmen and hunters, pay no attention to what may be attached to the feet of their victims. Ornithologists, too, do not carefully examine the bodies of the specimens and the snails fall off or are brushed off during the preparation of the skin for the cabinet. Careful examination of the bodies of birds would doubtless provide many valuable evidences for avian dispersal of fresh-water and other mollusks.

V.

HISTORICAL SKETCH OF CLASSIFICATIONS

IN THE EARLY VOLUMES on the Mollusca, the planorbids, as well as other genera, were largely classified by the shells and were placed in families with wide limits as to the genera involved. Thus in 1851-1856, in S. P. Woodward's *Manual of the Mollusca,* nearly all of the genera of fresh-water pulmonates—*Limnaea, Chilina, Physa, Planorbis,* and *Ancylus*—appear in the family Limnaeidae. In *A History of British Mollusca,* by Forbes and Hanley, in 1853 (volume iv) the fresh-water pulmonates of the genera *Limnaea, Planorbis, Physa,* and *Ancylus* are all placed in the family Limnaeidae.

W. G. Binney, in 1865, published a work on *The Land and Fresh-Water Shells of North America,* in which the fresh-water pulmonates are all placed in the family Limnaeidae with Limnaeinae, Planorbinae, and Ancylinae as subfamilies, *Physa* being included in the subfamily Limnaeinae.

In 1870, W. H. Dall proposed a classification in which four subfamilies were recognized: Limnaeinae, Planorbinae, Camptocercinae, and Pompholiginae. In 1872, George W. Tryon, Jr., in a *Monograph of the Fresh-water Univalve Mollusca of the United States,* placed all groups under the family Physidae, but separated the principal groups as subfamilies: Limnaeinae, Pompholiginae, Megasystrophinae, Planorbinae, and Ancylinae. In this grouping he was following Haldeman (1842-1844) who placed *Planorbis* and other groups in the family Physidae.

Paul Fischer, in the *Manuel de Conchyliologie* (1883), listed most of the fresh-water pulmonates under the family Limnaeidae, within which he recognized Ancylinae, Limnaeinae, and Planorbinae as subfamilies. *Physa* he relegated to a separate family. Tryon, a year later (1884), in the third volume of his *Structural and Systematic Conchology,* placed all of the fresh-water pulmonates under the family Limnaeidae with subfamilies Limnaeinae (including *Physa, Aplexa, Bulinus,* etc.), Pompholiginae, Planorbinae, and Ancylinae. A. H. Cooke, in 1895, evidently following Paul Fischer, separated Physidae as a family but places the subfamilies Limnaeinae, Planorbinae, and Ancylinae in the Limnaeidae. F. C. Baker in 1902 and Dall in 1905 separated *Physa* and *Aplexa* to form the family Physidae but placed *Limnaea* (*Lymnaea*), *Planorbis,* and allied genera in the family Limnaeidae. *Ancylus* was made a separate family, Ancylidae, by Baker.

In 1902, Westerlund placed all of the Basommatophorous mollusks in the family Limnaeidae with four subfamilies, Limnaeinae, Physinae, Planorbinae, and Ancylinae. Dybowski (1903) proposed a classification of the Basommatophora in which six families were recognized, Limnaeidae, Limnophysidae, Amphipeplidae, Planorbidae, Ancylidae, and Physidae. Bryant Walker (1918) in his 'Synopsis' recognized four families, Lymnaeidae, Planorbidae, Physidae, and Ancylidae.

From 1920 onward, most of the important monographs and lists have accepted the four-family division of the Basommatophora, Lymnaeidae, Planorbidae, Physidae, and Ancylidae (Germain, 1921-23; Kennard and

Woodward, 1926; Pilsbry and Bequaert, 1927; F. C. Baker, 1928; Haas, 1929; Lindholm, 1926; Thiele, 1931; and others). Germain (1931), in his *Mollusks of France*, recognized five families, the four previously alluded to and Bulinidae, the groups of which were thought to constitute a family. Many other works might be listed, especially by European writers, as Lindholm, Westerlund, Clessin, Dybowski, Odhner, Pallery, Preston, Soos, and others. The most important of these are listed in the synonymy under the different genera. The large monographs, such as Clessin (1886) and Sowerby (Reeve, 1872), do not help much in family distinctions and the lesser faunal lists of both continents, of which there are many, simply copy the classification as published in some of the works mentioned above.

In the matter of generic distinctions among the planorbids there is little of note in the earlier works. In 1884, Tryon listed most of the group names as subgenera of *Planorbis*, recognizing *Segmentina* as a distinct genus. *Pompholyx*, *Carinifex*, and *Choanomphalus* are listed as genera with some subgenera, mostly fossil groups. In 1905, Dall considered all groups but *Segmentina* as subgenera of *Planorbis*. Germain, 1921, followed Dall. Kennard and Woodward (1926) did likewise. In 1926, F. C. Baker recognized the groups *Helisoma*, *Planorbula*, *Menetus*, and *Gyraulus* as being of generic rank and in 1928 fully described these groups, giving anatomical reasons for their distinction. Among European works, Lindholm in 1926 recognized as of generic rank *Planorbis*, *Tropidiscus*, *Spiralina*, *Anisus*, *Gyraulus*, *Bathyomphalus*, *Armiger*, *Hippeutis*, and *Segmentina*, a great step in advancement over previous works as regards classification. Thiele in his Handbuch (1931) was too conservative, listing all groups as sections under the genera *Planorbis* and *Anisus*. Mori (1938) in his classification of Japanese Planorbidae followed Thiele. It is to be observed, however, that all of these genera or subgenera as treated by early authors, were diagnosed from shell characters for the most part.

In a review of the classifications of the Basommatophorous group the change in number of families and genera recognized is noteworthy. From one family in 1870 (Limnaeidae or Physidae) this grouping has grown to five at the present time, indicating a tendency to recognize smaller group differences and also indicating advance in knowledge concerning these groups. Many generic and subgeneric names have been proposed during the past ninety or one hundred years but these were founded almost wholly on shell characteristics. No such analytical studies as those on the land mollusks by H. A. Pilsbry and by H. B. Baker were made until after the year 1920.

Studies of the anatomy of the Planorbidae began in Europe many years ago but were confined to only a few species. Most of the early papers or works on anatomy simply gave as illustration a familiar example, as, for example, *Planorbis corneus* and *Limnaea stagnalis* figured by Moquin-Tandon in 1855. Baudelot (1863) published good figures of the genitalia and other organs of *Planorbis corneus* (= *Planorbarius*). In 1867, Ficinus, an almost forgotten writer, published an article on the penis of Planorbidae in which he divided the European species of *Planorbis* into two groups, (1) with a penial stylet, including *Planorbis vortex*, *leucostoma*, *spirorbis*, *albus*, and *contortus*, and (2) without a stylet, including *Planorbis corneus*, *nitidus*, and *fontanus*. He erected the genus *Appendicularia* for *Planorbis* *nitidus* and *P. fontanus* because of the presence of the flagella on the penis. This is, as far as known to the writer, the first attempt to classify the Planorbidae by reference to details of the anatomy.

In 1891, Buchner published the first comprehensive account of the genitalia of the family Planorbidae. He divided the male organ into four types, (1) *corneus* with a small penis, (2) *nitidus* and *complanatus* with flagella and sperm outlet at the side, (3) *marginatus* and *carinatus* with sperm outlet in the center, and (4) *contortus*, *vortex*, *rotundatus*, and *albus* with a stylet. He did not distinguish the peculiar gland of *corneus* from the penis. The difference between the prostate diverticula of *Planorbis corneus* and the smaller species, *vortex*, *carinatus*, *nitidus*, etc., was especially mentioned but no reference was made of the presence of a separate prostate duct. There was a good account of the excretory organ (kidney). Simroth's account (1912) of the genitalia of the Planorbidae was based on Buchner's work and added nothing to our knowledge of the antomy of the group.

In 1917, L. Soos published a paper on the anatomy of the Hungarian Planorbidae, giving figures of the genitalia of *Planorbis corneus*, *Tropidiscus planorbis*, *Segmentina nitida*, *Bathyomphalus contortus*, *Gyrorbis spirorbis*, and *Gyraulus albus*. The radulae and the digestive system were also considered. This is the best work on the anatomy of the Planorbidae which had appeared up to this time.

During the decade from 1921 to 1930, several notable papers appeared on the anatomy of the family. Annandale (1922) and Annandale and Prashad (1919-1921) added to our knowledge of the anatomy of the Indian Planorbidae. In 1923, Rao published an exhaustive treatise on the anatomy of Annandale's new genus *Indoplanorbis*. Connolly (1925) figured the genitalia and radula of *Planorbis pfeifferi* which indicated that it was related to the West Indian genus *Tropicorbis*. F. C. Baker, in 1926, published notes on the genitalia, jaws, and radulae of certain American Planorbidae and in 1928 (Moll. of Wis., I, pp. 306-387) presented descriptions and figures of the genitalia, jaws, and radulae of the species of Planorbidae inhabiting the Middle West. The subfamily Helisominae (Helisomatinae) was proposed as new on page 309 of that work. The classification of the genitalia is based on that of Buchner with the addition of two types, one new and one following Annandale.

In 1929, Odhner published an account of the Mollusca of the Täkerns in which the genera were separated by characteristics of the genitalia, radulae, and other anatomical features. On page 22 a key appeared in which the groups were briefly diagnosed from the anatomical standpoint. This was the most modern treatment which the family had received and the key is the first attempt to separate the genera by the use of anatomical differences.

During the decade 1931 to 1940, several critical papers appeared on the anatomy of the Planorbidae, adding greatly to our knowledge and clearing up many doubtful points in the classification based on the anatomy. In 1931, Germain issued his work on the land and fresh-water mollusks of France in which outline figures of the genitalia, and some of the radulae, were given. No attempt was made, however, to base a classification on the anatomical data. Also in 1931, appeared F. C. Baker's paper on the classification of the larger planorbes of Europe and America, in which *Planorbis corneus* and the American *Helisoma* species were discussed and the genitalia and radulae figured. The peculiar penial gland of the genus *Helisoma* was discussed at length. The same author, in 1933, made a study of the peculiar genitalia of *Indoplanorbis exustus* of India adding some features to the previous paper by Rao. Later, the same author published short papers placing certain disputed species in their proper generic position, based on their anatomy. Thus, in 1935, *Planorbis umbilicatellus*, long thought to be a *Gyraulus*, was shown to be a member of the genus *Menetus* and a new subgenus was proposed for *Menetus exacuous* (*Promenetus*). In 1936, *Planorbis obstructus* was shown to belong in the genus *Tropicorbis* and the true relationship of *Parapholyx* was indicated.

In 1935, A. Soos published a paper on the Planorbidae of Hungary which included good figures of the genitalia of the species inhabiting that country. In 1934, a paper from the pen of H. A. Pilsbry discussed the planorbid fauna of Florida, their genitalia were figured, and a new name (*Seminolina*) was proposed for the group which is not found outside of the Florida peninsula. The classification of other groups, *Tropicorbis, Menetus, Carinifex*, and *Parapholyx* was discussed and a new genus *Australorbis* was proposed for the large snails inhabiting South America and the West Indies. The European genus *Anisus* was ably discussed. A new subfamily, Planorbulinae, was established. Characteristic keys to the genera of American Planorbidae were given, based on anatomical features. It is not overstating to say that this paper is the most comprehensive account of the family Planorbidae from a modern standpoint that has yet appeared.

From the foregoing summary it is plainly obvious that a detailed study of the classification of the family Planorbidae, based on anatomical information, comparable to the methods used by Pilsbry on the land mollusks, is still to be prepared. An attempt to supply this deficiency is the purpose of the present work. It is believed that a foundation has been laid upon which to build a natural classification of the family Planorbidae.

VI.

A NEW CLASSIFICATION OF THE FAMILY PLANORBIDAE

GENERAL DISCUSSION

DURING THE PAST FIFTY YEARS, the classification of the land shells (Stylommatophora), under the able leadership of Dr. Henry A. Pilsbry, of the Academy of Natural Sciences of Philadelphia, has been brought to a high degree of accuracy and completeness. This has been accomplished by the study of anatomical details of the genera and species, bringing together groups which are allied by features of the natural organization of the animal. While the shell has helped in many cases it has been the internal features, chiefly the genitalia, that have given criteria for generic and higher distinctions. The results obtained by these studies have been accepted by nearly all malacologists and conchologists.

No such comparable work has been done on the fresh-water pulmonates (Basommatophora), and the few attempts to apply anatomical criteria for generic distinctions, as used in the Pulmonata, have met with more or less criticism. It is obvious, however, that only by the careful study of the internal organs of the animal can a natural classification be secured. This was attempted by the writer for the Lymnaeidae in 1911 and some gratifying results were obtained. The family Planorbidae offers better characteristics for purposes of classification than does the Lymnaeidae, there being a greater diversity of structural features among the different genera.

For the data in the present work a large number of species of the family Planorbidae, from different parts of the world, were dissected. These represent a majority of the generic groups so far published, in addition to several new genera. As in the study of the land mollusks, the genitalia have been of the greatest assistance. Few new groups were necessary because those already published, of which there were many, were adequate to represent the different anatomical features involved.

In the new classification here presented, great stress is laid on the differences in the male genitalia, the size of the preputium and vergic sac; the characteristics of the prostate diverticula and the prostate duct; the presence or absence of a stylet on the verge; flagella present or absent on the vergic sac; a penial gland in the preputium and whether this has an internal or an external duct or none at all; the opening of the sperm canal in the verge, whether at the end or on the side; the number of retractor muscles of the penial complex; and the nature of the ovotestis, whether the diverticula are in a double series or are multiple.

Other anatomical features also aid in classification, as the shape of the kidney, whether it is smooth or has a ridge; the condition of the jaws, whether simple or fragmented; the form of the radula teeth; the shape of the stomach and the turns of the intestine from stomach to anus. The pseudobranch also offers some criteria although this organ is fairly uniform in the family. It does effectively separate the Planorbidae from the Bulinidae, the pseudobranchs of the two groups being markedly different. For generic purposes, the shell offers less assistance than the organs of the animal, although the shell sometimes presents characteristics of generic importance.

It has been possible to recognize four subfamilies of the family Planorbidae based on fundamental anatomical differences, and all of the genera, as far as they have been examined, readily fit into this subfamily classification. A few groups, as *Taphius*, *Biomphalaria*, *Platytaphius*, and *Trochorbis*, are still unknown anatomically, but it is believed that when examined they will be found to fit into this classification. Many species of the family still remain of which the animal characteristics are unknown and it is possible that new genera or subgenera will need to be made for their inclusion. It is confidently believed that the classification herein presented will form a reliable foundation on which to build future knowledge which may be obtained concerning this interesting family.

ANATOMICAL KEYS TO GROUPS*

Key to Subfamilies

1a. Prostate a single row of diverticula usually placed on a separate prostate duct...2
b. Prostate with multiple diverticula usually placed on the sperm duct............3
2a. Vergic sac with flagella..............................Segmentininae (see p. 47).
b. Vergic sac without flagella..............................Planorbinae (see p. 46).
3a. Prostate forming a fan-shaped pattern in cross section, penial gland duct on outside of preputium, ovotestis consisting of several diverticula arranged fanwise......................................Helisomatinae (see p. 47).
b. Prostate forming a finger-shaped pattern with few diverticula, penial gland duct inside preputium, ovotestis with paired diverticula....Planorbulinae (see p. 48).

Key to Genera of Planorbinae†

1a. Prostate diverticula on separate duct, simple, unbranched at end...............2
b. Prostate diverticula not on separate duct, branched at end..*Australorbis* (see p. 90).
2a. Verge with stylet, outlet of sperm canal at side..............................3
b. Verge without stylet, outlet of sperm canal at end............................6
3a. Shell with many closely coiled whorls not increasing greatly in diameter........4
b. Shell with few loosely coiled whorls rapidly increasing in diameter..............5
4a. Left side of shell flat without central depression..........*Anisus* s.s. (see p. 57).
b. Left side of shell with deeply excavated depression...........................(Subgenus) *Bathyomphalus* (see p. 62).
5a. Left side of shell with rounded whorls on a plane surface...*Gyraulus* s.s. (see p. 66).
b. Left side of shell with whorls depressed as though reamed out.......................................(Subgenus) *Torquis* (see p. 72).
6a. Vergic sac less than one-fourth length of preputium.......*Planorbis* (see p. 51).
b. Vergic sac longer than preputium..7
7a. Vergic sac about as long as preputium, shell 5 mm. or more in diameter, not costate...8
b. Vergic sac much longer than preputium, shell 3 mm. or less in diameter, usually costate......................................*Armiger* (see p. 75).
8a. Species inhabiting Africa............................*Afroplanorbis* (see p. 86).
b. Species inhabiting America.................*Tropicorbis* s.s. (see p. 85).......9

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*In using this type of alternative key the options are always arranged in couplets, the contrasting conditions being arranged as 'a' and 'b' under the same numeral. The reader always starts with 1a. If the description under 1a fits the specimen or concept under consideration, the numeral at the end of that line indicates the next couplet to be tried (except in those instances where 1a leads directly to an identification). If the statement under 1a does not fit, the alternative under 1b should, and so on through the key until a group name is reached at the end of one of the options. This form of continuous and consecutive key is less confusing than the type in which descriptions to be compared are widely separated from each other and does not offer the technical difficulties of composition inherent in the indented or step form of key.—H.J.V-C.

†Some subgenera which have distinctive morphological characters are included in this key and in all succeeding keys to genera.

9a. Shell with closely coiled whorls slowly increasing in diameter, orbicular........10
b. Shell with loosely coiled whorls rapidly increasing in diameter....................................(Subgenus) *Lateorbis* (see p. 85).

10a. Aperture without internal lamellae at any stage of growth..*Tropicorbis s.s.* (see p. 85).
b. Aperture with internal lamellae during a part of the shell's growth...................................(Subgenus) *Obstructio* (see p. 85).

Key to Genera of Segmentininae*

1a. Genitalia with penial gland in preputium..2
b. Genitalia without penial gland in preputium..5

2a. An external penial gland duct on preputium..3
b. Without penial gland duct on preputium..4

3a. External duct very short, half as long as preputium; penial gland a simple cup attached to wall of preputium; flagella more than twice as long as vergic sac, sausage-shaped, attached to short ducts.........*Intha* (see p. 112).
b. External duct about four times as long as preputium; penial gland sac-like, bifurcated; flagella consisting of small cylindrical sacs attached to very long ducts...*Pingiella* (see p. 109).

4a. Preputium narrow, club-shaped; vergic sac longer than preputium; verge slender with vergic appendage at end..................*Segmentina* (see p. 96).
b. Preputium wide, pear-shaped; vergic sac shorter than preputium; verge wide at upper part, without penial appendage................*Hippeutis* (see p. 100).

5a. Flagellum long and narrow; vergic sac and preputium of about the same length; shell more than 5 mm. in diameter................................6
b. Flagellum wide and short; vergic sac about twice as long as preputium; shell very small, 1.5 mm. in diameter........................*Acrorbis* (see p. 121).

6a. Flagellum as long as penial complex, swollen or club-shaped at summit..*Polypylis* (see p. 104).
b. Flagellum shorter than penial complex, not swollen at summit, often bifid at the end.................................*Drepanotrema* (see p. 114).......7

7a. Shell with rounded periphery.....................*Drepanotrema s.s.* (see p. 118).
b. Shell with angulated or carinated periphery..(Subgenus) *Fossulorbis* (see p. 118).

Key to Genera of Helisomatinae†

1a. Preputium with penial gland but without penial duct....*Planorbarius* (see p. 166).
b. Preputium with external penial gland duct..2

2a. Penial complex with one retractor muscle..3
b. Penial complex with two retractor muscles..6

3a. Penial complex with but little constriction between vergic sac and preputium; penial gland duct about half as long as preputium...*Helisoma s.s.* (see p. 124)...4
b. Penial complex with notable constriction between vergic sac and preputium; penial gland duct as long as the preputium...(Subgenus) *Seminolina* (see p. 129).

4a. Penial complex with vergic sac and preputium equal in length, the preputium much wider than the vergic sac; penial gland duct several times as long as preputium, in a coil between vergic sac and preputium........................5
b. Penial complex with vergic sac shorter than the preputium, which is elongate; penial gland short and thick, not longer than preputium.....................6

5a. Shell with simple aperture, not campanulate...(Subgenus) *Pierosoma* (see p. 134).
b. Shell with campanulate or bell-shaped aperture (Subgenus) *Planorbella* (see p. 150).

6a. Penial duct on outside of preputium very short, slender, placed between vergic sac and preputium; penial gland an elongated cup with wide aperture..*Carinifex* (see p. 154).
b. Penial duct twice as long as in 6a, thick, wide, extending from upper part of preputium to vergic sac; penial gland pipe-shaped, with a long "stem" attached to a short "bowl"...........................*Paraphólyx* (see p. 161).

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*One subgenus is included among the groups differentiated in this key.

†Several subgenera are also differentiated in this key.

Key to Genera of Planorbulinae*

1a. Penial gland sausage-shaped with round, closed duct.......... 2
b. Penial gland flattened, ovate, with open, channel-like duct.......... 3

2a. Penial duct very short leading from gland direct to muscular collar or diaphragm.......... *Menetus* s.s. (see p. 183).
b. Penial duct long, extending up the side of the preputium to the muscular collar or diaphragm.......... (Subgenus) *Micromenetus* (see p. 187).

3a. Penial gland connected with muscular collar by an open duct as long as the gland, lying above a single diagonal projection of the left pilaster; seminal vesicle composed of many diverticula forming a mulberry appearance on the surface.......... *Planorbula* s.s. (see p. 173).
b. Penial gland connected with muscular collar by an open slit in the muscular wall of the preputium, the two pilasters sending branches from both sides to this slit; seminal vesicle consisting of many short diverticula stretched along a large part of the oviduct.......... *Promenetus* (see p. 178).

SYSTEMATIC LIST OF GENERA AND SUBGENERA RECOGNIZED IN THIS WORK

In the following list the genera and subgenera are arranged in the sequence which appears most in accord with their structural features. Several groups are unknown anatomically and these are marked by an asterisk. They are placed in the subfamilies and near the genera with which they appear to be affiliated. The fossil species, it is obvious, can never be known anatomically and these are placed near those genera which they most nearly resemble. The fossil groups are marked by a dagger. Two groups of uncertain affinities, one recent and one fossil, are placed at the end of the family sequence. The type species is indicated following the name of each genus or subgenus.

Family PLANORBIDAE H. and A. Adams, 1855

Subfamily Planorbinae Pilsbry, 1934

Genus Planorbis Geoffroy, 1767	*Helix planorbis* Linn.
Genus Anisus Studer, 1820 (Gray, 1847)	
Subgenus Anisus SS	*Helix spirorbis* Linn.
Subgenus Costorbis Lindholm,† 1926	*Planorbis strauchianus* Clessin
Subgenus Bathyomphalus (Ag.) Charp., 1837	*Helix contorta* Linn.
Genus Odontogyrorbis Lörenthey,† 1906	*Planorbis kramberger* Halaváts
Genus Gyraulus (Ag.) Charp., 1837	
Subgenus Gyraulus SS	*Planorbis albus* Müller
Subgenus Torquis Dall, 1905	*Planorbis parvus* Say
Genus Armiger Hartmann, 1840	*Nautilus crista* Linn.
Genus Taphius H. and A. Adams, 1855	*Planorbis andecolus* Orb.
Genus Tropicorbis Pilsbry and Brown, 1914	
Subgenus Tropicorbis SS	*P. liebmanni* Dunker = *orbiculus* Morelet
Subgenus Obstructio Haas, 1939	*Planorbis janeirensis* Clessin
Subgenus Lateorbis F. C. Baker (New)	*Planorbis pallidus* C. B. Adams
Genus Afroplanorbis Thiele, 1931	*Planorbis sudanicus* Martens
Genus Syrioplanorbis F. C. Baker,† new name for Heterodiscus West., preoccupied	*Planorbis libanicus* West.
Genus Biomphalaria Preston,† 1910	*Biomphalaria smithi* Preston
Genus Australorbis Pilsbry, 1934	*Planorbis glabratus* Say
Genus Anisopsis Sandberger,‡ 1875	*Planorbis calculus* Sandberger

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*One subgenus is included in this key.

†The anatomy is not known for any member of this group.

‡A group represented by fossils only.

Subfamily SEGMENTININAE F. C. Baker (New)

Genus Segmentina Fleming, 1817	*Planorbis nitidus* Müller
Genus Hippeutis (Ag.) Charp., 1837	*Planorbis complanatus* Drap.
Genus Polypylis Pilsbry, 1906	*Planorbis largillierti* Phil.
Genus Helicorbis Benson,† 1855	*Planorbis umbilicalis* Benson
Genus Trochorbis Benson,† 1855	*Trochorbis trochoideus* Benson
Genus Pingiella F. C. Baker (New)	*Pyramidula peipinensis* Ping and Yen
Genus Intha Annandale, 1922	*Intha capitis* Annandale
Genus Drepanotrema Fischer and Crosse, 1880	
Subgenus Drepanotrema SS	*Planorbis anatinum* Orb. (=*yzabalensis* C. and F.).
Subgenus Fossulorbis Pilsbry, 1934	*Planorbis cultratus* Orb.
Genus Paraplanorbis Hanna,‡ 1922	*Planorbis condoni* Hanna
Genus Platytaphius Pilsbry,† 1924	*Planorbis heteropleurus* P. and V.
Genus Acrorbis Odhner, 1937	*Acrorbis petricola* Odhner

Subfamily HELISOMATINAE F. C. Baker, 1928

Genus Helisoma Swainson, 1840	
Subgenus Helisoma SS	*Planorbis anceps* Menke (=*bicarinatus* Sowb.)
Subgenus Seminolina Pilsbry, 1934	*Physa scalaris* Jay
Subgenus Pierosoma Dall, 1905	*Planorbis trivolvis* Say
Subgenus Planorbella Haldeman, 1842	*Planorbis campanulatus* Say
Genus Carinifex W. G. Binney, 1863	*Planorbis newberryi* Lea
Genus Vorticifex Meek,‡ 1870	*Carinifex tryoni* Meek
Genus Perrinilla Hannibal,‡ 1912	*Helisoma cordillerana* Hannibal
Genus Parapholyx Hanna, 1922	*Pompholyx effusa* Lea
Genus Pompholopsis Call,‡ 1888	*Pompholopsis whitei* Call
Genus Planorbarius Froriep, 1806	*Helix cornea* Linn.

Subfamily PLANORBULINAE Pilsbry, 1934

Genus Planorbula Haldeman, 1840	
Subgenus Planorbula SS	*Planorbis armigerus* Say
Subgenus Haldemanina Dall, 1905	*Planorbis wheatleyi* Lea
Genus Promenetus F. C. Baker, 1935	*Planorbis exacuous* Say
Genus Menetus H. and A. Adams, 1855	
Subgenus Menetus SS	*Planorbis opercularis* Gould
Subgenus Micromenetus F. C. Baker (New)	*Planorbis dilatatus* Gould
Genus Planorbifex Pilsbry,‡ 1934	*Planorbis vanvlecki* Arnold

Groups of Uncertain Affinities

Genus Choanomphalus Gerstfeldt,† 1859	*Choanomphalus maacki* Gerstfeldt
Genus Poecilospira Mörch,‡ 1853	*Valvata multiformis* Zeiten.

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†The anatomy is not known for any member of this group.

‡A group represented by fossils only.

VII.

SYSTEMATIC ACCOUNT OF THE SUB-FAMILIES, GENERA, AND SUBGENERA

RECENT AND FOSSIL

PLANORBIDAE, together with the Physidae and Bulinidae, are animals with spiral shells; the genitalia and the respiratory and excretory organs are on the left side. The shell of Planorbidae is typically sinistral in some groups (*Helisoma*) and pseudodextral or ultradextral in many groups. The shell is carried almost vertically in the typically sinistral groups but leans toward the left in other groups, principally the smaller forms. In these groups the spire is beneath and the umbilicus is above, these being respectively the right and left sides of the shell. The central tooth of the radula is always bicuspid. In *Physa* it is multicuspid.

The chief feature separating the Planorbidae from the other members of the Limnophila is the presence of an accessory breathing organ, the pseudobranch, which takes over the office of a gill when the animal is submerged and can not obtain free air. The flattened, 'planorboid' shell is, of course, another distinctive feature of the family.

The groups of genera related to *Bulinus* and *Physopsis* have in the past been included in the family Planorbidae because of the similarity of the radulae and the presence of a pseudobranch. But this organ in *Bulinus* is different from the pseudobranch in Planorbidae, being in the form of folds or ridges while in the Planorbidae it is smooth and leaf-like. There are also differences in the genitalia, principally in the penial complex. These differences suggest that *Bulinus*, *Physopsis*, and other related groups should form a separate family Bulinidae. This has been recognized by Germain in his mollusks of France (1931) and by Larambergue in a recent publication (1939). The Indian genus *Indoplanorbis* has been shown by the latter author to be related to *Bulinus* and its place appears to be with the Bulinidae.

Subfamily PLANORBINAE H. A. Pilsbry, 1934

The subfamily of H. and A. Adams is equivalent to the family Planorbidae as now recognized by systematists. In the Planorbinae the prostate diverticula are all simple sacs placed in a single row along the whole length of a long prostate duct which is separated from the sperm duct into which it enters. The ovotestis has the diverticula arranged in a double row. An apparent exception is found in the genus *Australorbis* where the single row of glands is placed directly on the sperm duct and the ends of the prostate diverticula are branched. The kidney is usually rounded and without a superposed ridge. Here again *Australorbis* is an exception, having a ridged kidney as in *Helisoma*.

Type genus *Planorbis* Geoffroy.

There is considerable variation among the different genera grouped in Planorbinae, principally in the jaws, the radulae, and the presence of a penial stylet. These differences may be tabulated as follows:

Radula with serrated marginals placed high up on the reflection: *Planorbis, Bathyomphalus, Anisus, Gyraulus, Armiger.*

Radula with claw-like marginals on a long reflection: *Australorbis, Tropicorbis.*

Radula with interstitial cusps on laterals or marginals: *Australorbis, Tropicorbis.*

Jaw in three pieces, a superior and two lateral jaws: *Tropicorbis, Australorbis, Afroplanorbis.*

Jaw fragmented with many plates: *Planorbis, Bathyomphalus, Anisus, Gyraulus, Armiger.*

Verge with stylet: *Anisus, Bathyomphalus, Gyraulus.*

Verge without stylet: *Planorbis, Armiger, Tropicorbis, Afroplanorbis, Australorbis.*

Several groups are unknown anatomically and hence their position in the system can not be definitely known until the animal has been examined. Such are *Costorbis*, *Syrioplanorbis*, *Taphius*, and *Biomphalaria*. The fossil group supposed to belong to this subfamily, *Odontogyrorbis*, can only be placed by shell resemblances and this points to the Planorbinae.

Genus PLANORBIS Geoffroy, 1767

Genotype by tautonomy *Helix planorbis* Linn.

1767. *Planorbis* GEOFFROY, Traité Coq., Paris, p. 12. No type designation.

1774. *Planorbis* MÜLLER, (part) Verm. Terr. Hist., II, p. 152. No type designation.

1833. *Anisus* FITZINGER, (part) Beitr. Landesk. Oester. III, p. 111 (Non Dejean, 1821, Coleoptera).

1847. *Spiralina* HARTMANN, Herrmannsen. Ind. Gen. Mal., II, p. 286. As synonym of *Planorbis*.

1850. *Tropidiscus* STEIN, Schn. u. Muscheln Berlins, p. 76. As subgenus. Type designated by Clessin, 1886 — *Planorbis marginatus* Drap.

1852. *Anisus* [FITZINGER] HERRMANNSEN, Ind. Gen. Mal., Suppl. p. 9. Type: *Planorbis umbilicatus* Müller. As fixed by Gray, 1847. Not *Anisus* Studer, 1888.

1855. *Gyrorbis* MOQ.-TAND., (part) Hist. Nat. Moll. Terr. et Fluv. France, II, p. 428. No type cited. As genus.

1855. *Omalodiscus* BENSON, Jour. Asiatic Soc. Bengal, XXIV, p. 127. Type designated by Kennard and Woodward, 1924, *Omalodiscus marginatus* Drap.

1883. *Tropidiscus* FISCHER, Man. Conch., p. 509. No type designation. As section.

1885. *Tropidiscus* WESTERLUND, Fauna Palaearc. Reg., V, p. 64. No type cited. As subgenus of *Planorbis*.

1886. *Tropidiscus* CLESSIN, Syst. Conch.-Cab., XVII, p. 34. Type *Planorbis marginatus* Drap. As subgenus.

1898. *Planorbis* (Geoffroy) VON MARTENS, Biol. Centr. Amer., Moll., p. 380. No type cited. As genus.

1902. *Tropidiscus* WESTERLUND, Rad. Jugoslav. Akad., 151, p. 120. Genotype *Helix planorbis* Linn. As subgenus.

1905. *Placorbis* DRAPARNAUD, Nat. Hist. Moll. France, p. 138. (vide Lindholm, Archiv. für Mollusk., 58 year, Heft 6, p. 252).

1905. *Tropidiscus* DALL, Alaska Moll., p. 85. Type *Planorbis umbilicatus* Müller = *Planorbis complanatus* Stein.

1906. *Omalodiscus* DALL. Nautilus XIX, p. 105. Comments on nomenclatorial position but cites no type.

1917. *Tropidiscus* SOOS, Ann. Musei Nat. Hungarici, XV, pp. 40, 141. Type *Tropidiscus planorbis* (Linn.). As genus.

1921. *Tropidiscus* GERMAIN, Rec. Ind. Mus., XXI, p. 7. Type *Planorbis planorbis* (Linn.). As subgenus.

1923. *Planorbis* (of Müller 1774) WENZ, Fossil. Cat., Part, 22, p. 1523. Genotype *Planorbis planorbis* (Linn.). As genus.

1926. *Tropidiscus* (of Stein) LINDHOLM, Archiv. für Mollusk., 58 year, Heft 6, p. 252. Ideogenotype *Helix planorbis* Linn. As genus.

1927. *Planorbis* KENNARD and WOODWARD, Syn. British Non-Marine Moll., p. 66. Type by tautonomy *Helix planorbis* Linn. As genus.

1929. *Planorbis* (of Müller 1774) Haas, Trab. Mus. Cien. Nat. Barcelona, XIII, p. 379. Type evidently intended to be *Planorbis planorbis* (Linn.). As genus.

1930. *Planorbis* H. B. Baker, Oc. Papers, Mus. Zool. Univ. Mich., No. 210, p. 42. Type by absolute tautonomy *Helix planorbis* Linn. As genus.

1931. *Planorbis* Germain, Moll. Terr. et Fluv. France, II, pp. 516, 521. No type designation. As genus and subgenus.

1931. *Tropidiscus* Thiele, Handbuch, IV, Teil 2, p. 481. Type *Planorbis planorbis* (Linn.). As subgenus.

1935. *Tropidiscus* Soos, Allat. Kozlem., XXXII, p. 29. *Planorbis carinatus* Müller and *Planorbis planorbis* (Linn.) cited. As subgenus under genus *Anisus*.

1936. *Planorbis* (of Müller 1774) Haas, Abh. Senckn. Natur. Gesell., No. 431, p. 25. *Planorbis planorbis* (Linn.) by absolute tautonomy. As genus.

Shell (plate 77, figs. 26-28) discoidal with few whorls, regularly increasing in diameter; upper and lower (left and right) sides flattened; a carina encircles the body whorl on the left side; aperture small, rounded, or oval, the right side in advance of the left side.

Animal. External appearance. The body is small, the foot short, rounded before and pointed behind; tentacles long and filiform; eyes sessile at the inner base of the tentacles; when removed from the shell the animal of *Planorbis planorbis* has a blackish or lead-colored mantle, a yellowish liver, and a pinkish ovotestis.

ANATOMICAL CHARACTERISTICS

PLATE 1

GENITALIA. Male Organs (fig. 1). Seminal vesicle (SV) 3.5 mm. long and 0.7 mm. wide, elongate-cylindrical, covered for the most part by small pustule-like glands. Sperm duct (SPD) very long (14 mm.) adherent to the oviduct. The prostate (PRS) is about 5 mm. long and consists of forty to forty-five diverticula placed in a single row on a long prostate duct (PD) which is separated from the sperm duct. Both sperm duct and prostate duct enter the smaller vas deferens near the vagina (fig. 1, VD, PD). The prostate diverticula are cylindrical in form and a trifle more than 0.5 mm. in length. A cross section through the prostate and oviduct shows the relationship between the sperm duct and the prostate duct (fig. 7). The vas deferens is a long (12 mm.) narrow tube (VD).

The penial complex is elongated (fig. 2), the preputium (PR) is long (3 mm.), cylindrical, and the vergic sac (VS) is short (0.7 mm.) and somewhat less in diameter than the preputium. There is one long and narrow retractor muscle (RM) attached to the vergic sac near the junction of the latter with the preputium. A group of five or more small muscles near the base of the preputium and a longer, narrow muscle attached to the upper part of the preputium have been called supporting muscles (SM). They are not attached to the columella muscle but to the fore part of the head. The long, narrow muscle may play a part in retracting the preputium after copulation.

Internally (fig. 4) the preputium has two vertical pilasters and a large number of longitudinal muscular ridges (PL). The walls of the preputium are thin but the walls of the vergic sac are thickened, especially at the summit where the vas deferens enters. The verge (V) is short and wide in repose and nearly fills the vergic sac. A section through the verge and a part of the vas deferens shows the sperm canal to be located in the center and to have a central exit (fig. 5). The absence of a distinct muscular ring or diaphragm is noteworthy.

Female Organs. The spermatheca (S) in the specimens examined is about 1.5 mm. long and 1 mm. wide, globular or pear-shaped, and attached to the uterus by a short, narrow duct about 1 mm. long (SD). The vagina (VG) is very short (less than 0.5 mm.) and wide. The uterus (U) is as wide as the vagina and is about 5 mm. long. The nidamental gland (NG) is as long as the uterus and surrounds a large part of the oviduct (see fig. 1). It is greatly lobulated. The free oviduct (OD) is short (about 2 mm.) and about as narrow as the sperm duct. Beneath the albumen gland the sperm duct and the oviduct are joined to form the ovisperm duct (fig. 6). The albumen gland is large (3.5 by 2 mm.) and is a mass of small sacs (AL). A small duct enters the carrefour (CF) which in turn enters the oviduct in front of the junction of that organ with the sperm duct.

Hermaphrodite Organs. The ovotestis (OT) consists of many club-shaped diverticula placed in a double row (fig. 8). The ovotestis is buried in the cell-mass of the liver (fig. 9). The ovisperm duct (SO) is divided into two external parts separated by the seminal vesicle, through which it passes. One portion, about 5 mm. long, extends back of the sperm duct at its junction with the oviduct and gradually enlarges as it enters the seminal vesicle. A smaller tube, about 3 mm. in length, passes from the seminal vesicle to the ovotestis.

The genitalia of *Planorbis planorbis* have been figured by several European conchologists. Germain's figure (1931, p. 523, fig. 533) is in general like the figures in this work, but there is lack of detail. The spermatheca is shown in a more elongated form, but this organ is subject to more or less variation. The large seminal vesicle is indicated by a swelling in the ovisperm duct. L. Soos's figure (1917, p. 41) agrees in general with that shown in this work. The prostate shows relatively the same number of diverticula. The spermatheca is shown on a long duct and the spermatheca is pear-shaped, not rounded as was observed in all specimens personally examined. Germain's figure is like Soos's in this respect. There appears to be some variation in this organ perhaps due to seasonal or sex condition.

The penial complex in Soos's figure is not shown in sufficient detail, but the position of the retractor muscle indicates a short vergic sac. The seminal vesicle shows an enlargement. A. Soos's figure (1935, p. 25) appears more nearly correct, showing for the first time the separate prostate duct. The spermatheca, however, is shown of a pyriform shape and on a long duct. The figure of the related species *carinatus* Müller (p. 24) given by Soos is more like the Poland specimens of *planorbis* personally examined. The duct of the prostate is shown as very short while in the Poland material the free portion of this duct is much longer before entering the vas deferens. The lower portion of the female complex is shown very much longer in Soos's figure than was observed in the Poland specimens.

Respiratory and Renal Systems. The pseudobranch (P, fig. 3) is leaf-shaped, flattened, about 2.5 mm. long and 2 mm. wide. The rectum (R) pierces it after bordering the columella muscle and the anus has its exit at the lower edge (A). The respiratory tube or pneumostome (PS) forms a short V-shaped lobe to the right of the pseudobranch. It is large and can be greatly expanded.

The kidney (plate 46, fig. 9) is very long and narrow (10 mm. long, 1 mm. wide), the glandular portion occupying only about one-eighth of the length. The ureter is short (1 mm. long), narrowly tubular and turns sharply to the left into the mantle cavity. A cross section of the kidney at about midway of its length shows the lumen to be flattened and widened with a vein at each end (fig. 10). There is no ridge on the lower side. The pericardium is long-oval in shape, 2.5 mm. long and 1.2 mm. wide.

Digestive System. The stomach (plate 48, figs. 6, 7) is elongated and pyriform in shape, the blind sac about as long as the stomach. The intestine runs directly forward and does not make a backward loop as in *Helisoma* and some other groups. The stomach does not show distinct divisions into crop and gizzard. The buccal sac is elongated and shortly pyriform in shape, the fore part near the mouth somewhat tubular. The radula sac is distinct and rounded. The salivary glands are much elongated, cylindrical, and joined behind.

The jaw (plate 50, fig. 21) is horseshoe-shaped and is composed of many small plates, about thirty on the upper or horizontal part, the lower or cutting edges V-shaped.

The radula (plate 67, fig. 7) formula is 24-1-24, 25-1-25, or 26-1-26 and the number of rows of teeth varied as follows: 175, 176, 205, and 209. The central tooth is bicuspid with a wide base of attachment, the cusps long and spade-shaped; lateral teeth (1-10) tricuspid, the cusps large and spade-shaped, the mesocone largest and longest, the reflection reaching nearly to the lower edge of the base of attachment. Intermediate teeth (11-13) with the reflection reaching only about half way to the lower edge of the base of attachment, with four cusps, the ectocone split into two cusps. Marginal teeth (14-20) very narrow with the reflection placed high up on the tooth, with four cusps which become subequal toward the outer margin of the radula membrane. The outer marginals are very narrow, the width being about one-fourth of the height and there are four short, subequal cusps. In one membrane some of the marginal teeth (20) had the entocone split into two sharp cusps. This was rare and occurred only in atypical rows.

The central teeth varied somewhat in width in the same membrane. For example, in rows 1 to 156 the upper part of the central tooth measured 6 microns and the lower part of the base of attachment measured 12 microns in width. In rows 157 to 176 these measurements were 5 and 12 microns respectively. In most membranes the central teeth were very uniform in width.

For the above anatomical data eight specimens were examined, collected by Mr. A. Jankowski from a pond in Swidry-Mate, 25 km. southeast of Warsaw, Poland. No parasitic worms (cercariae) were observed in any of the specimens examined.

Geographical Distribution. The genus *Planorbis,* as herein understood, is distributed throughout Europe from Sweden southward to the Mediterranean and from Great Britain eastward to western Russia. It is also found in northern Asia (Siberia), Asia Minor, and northern Africa.

Species Considered as Valid. Although many species now assigned to other genera were originally placed in the genus *Planorbis* there are now but relatively few species which belong in this genus as now restricted. The best recognized of these are:

Planorbis planorbis (Linn.)
Planorbis carinatus Müller
Planorbis arnouldi Germain
Planorbis marmoratus Michaud
Planorbis atticus Bgt.
Planorbis sieversi Mouss.
Planorbis antiochianus Locard

Geological Distribution. Oligocene to Recent time, according to Wenz. It is probable that some of the species included in this genus by paleontologists really belong to other groups.

Remarks. The genus *Planorbis* is peculiar anatomically in the form of the prostate with many single diverticula and in the comparatively small size of the vergic sac as compared with the preputium. The verge, also, is very small, short, and wide, differing markedly in this respect (as far as known) from any other group of planorbes in Europe. The nature of the genitalia and the form of the shell set this group apart as a distinct genus of the family Planorbidae.

For many years, the author for this genus and the species for its type have been in dispute. Some authors (Tryon 1872, 1884, Fischer 1883, Baker 1902, Binney 1865, Dall 1870, Fischer and Crosse 1879) quote Guettard as authority (Mem. Acad. Sci., p. 151, 1756). Other authors have cited the genus as of Müller (Verm. Hist., p. 152, 1774) with *Helix corneus* Linn. as type (Dall 1905, Pilsbry and Bequaert 1927, Baker 1931). A few have used Guettard 1756 and Müller 1774 in combination with *Helix corneus* as genotype (Germain 1921, 1931). Another group of authors have cited Geoffroy (Traité Coq., Paris, p. 12, 1767) with *Helix planorbis* Linn. as genotype (Kennard and Woodward, 1924, 1926).

Guettard 1756 is pre-Linnean and also non-binomial and would appear to be ruled out on these accounts. Geoffroy 1767 is post-Linnean but this author was not in all cases binomial and is rejected by some students for this reason. Kennard and Woodward (1924, p. 9), however, have presented very convincing arguments in favor of retaining the *Planorbis* of this author. The *Planorbis* of Müller (1774) is preferred by some late writers (Dall 1905, Pilsbry and Bequaert 1927), who cite the *Helix corneus* of Linnaeus as genotype, giving Montfort 1810 (Conch. Syst., II, p. 270) as the first author to select a genotype.

However, whether Geoffroy or Müller is selected, the genotype for both is *Helix planorbis* Linn., the selection of which is governed by the rules of tautonomy (see H. B. Baker, 1930). After reviewing the evidence very carefully there seems to be no valid reason why *Planorbis* Geoffroy, 1767, should not be used, as advocated by Kennard and Woodward (1924). The *Helix corneus* Linn. is the genotype of *Planorbarius* Froriep, 1806. The name *Tropidiscus* Stein (1850) is in use by several European authors (Germain 1921, L. Soos 1917, A. Soos 1935, Thiele 1931) but this name is a synonym of *Planorbis*, having the same genotype, *Helix planorbis* Linn.

Genus ANISUS Studer, 1820 (Gray, 1847)

Type *Helix spirorbis* Linn. selected by Gray in 1847

1820. *Anisus* Studer, Naturwis. Anzeiger Allg. Schweiz. Ges. Gesammt. Naturwiss., 3te Jahrg., Nr. 12, p. 91.

1840. *Spirorbis* Swainson, Treat. Malac., p. 337. Type *Planorbis vulgaris* Swain. Not *Spirorbis* Daudin, 1800 (Vermes).

1840. *Spiralina* HARTMANN, Erd-und Süssw.-Gasterop., 'Syst. Uebersicht.' Nude name.

1843. *Planorbina* HALDEMAN, Mon. Freshwater Univalve Moll., Physidae, p. 14. Type designated by Pilsbry 1934, *Planorbis spirorbis* Linn. Not *Planorbina* Dall, 1905.

1847. *Anisus* Studer, GRAY, Proc. Zool. Soc., p. 180. Type *Helix spirorbis* Linn.

1847. *Spirorbis* HERRMANNSEN, Ind. Gen. Mal., II, p. 492. Type *Planorbis spirorbis* (Linn.).

1850. *Tropidiscus* STEIN (part), Lebend. Schneck. und Musch. Berlins, p. 76.

1855. *Gyrorbis* MOQUIN-TANDON, Moll. Ter. Fluv. France, II, pp. 423, 428. Type designated by Lindholm, 1926, *Planorbis rotundatus* Poir. = *Planorbis leucostoma* Millet. Not *Gyrorbis* Fitz., 1833. As genus.

1870. *Anisus* Fitz. DALL, An. Lyc. Nat. Hist., N.Y., IX, p. 352. Type *Anisus vortex* (Linn.). As section of *Planorbis*.

1883. *Gyrorbis* FISCHER, Man. de Conch., p. 507. Type *Planorbis rotundatus* Poir. As section of *Planorbis*.

1885. *Gyrorbis* WESTERLUND, Fauna Palaearc. Reg., V, p. 64. No type cited. As subgenus of *Planorbis*.

1886. *Gyrorbis* CLESSIN, Syst. Conch. Cab., XVII, p. 34. Type *Planorbis rotundatus* Poir. As subgenus.

1897. *Diplodiscus* WESTERLUND, Act. Soc. Fauna Flora Fennica, XIII, p. 115. First species *Planorbis vortex* (Linn.). Not *Diplodiscus* Dies., 1836, Trematodes.

1899. *Spiralina* Hartmann, VON MARTENS, Biol. Cent. Amer., Moll., p. 395. Type designated *Planorbis vortex* (Linn.), by Lindholm in 1922 and Kennard and Woodward in 1924.

1902. *Diplodiscus* WESTERLUND, Rad. Jugoslav. Akad., 151, p. 120. First species, *Helix vortex* Linn. As subgenus of *Planorbis*.

1905. *Paraspira* DALL, Alaska Moll., pp. 82, 86. Type by original designation *Planorbis rotundatus* Poir. = *Planorbis leucostoma* Millet. As section of *Planorbis*.

1909. *Wüstia* HONIGMANN, Zeitsch. f. Naturw., 81, p. 296. Type designated by Lindholm, 1926, *Planorbis rotundatus* Poir. As synonym of subgenus *Anisus*.

1917. *Gyrorbis* L. SOOS, Ann. Musei Nat. Hungarici, XV, pp. 49, 143. *Gyrorbis spirorbis* first species (Anatomy). As genus.

1921. *Diplodiscus* Westerlund, GERMAIN, Rec. Ind. Mus., XXI, p. 7. Type *Planorbis vortex* (Linn.). Non Dies. 1836. As subgenus.

1921. *Paraspira* GERMAIN, op. cit., p. 7. Type *Planorbis rotundatus* Poir. As subgenus.

1922. *Spiralina* (Hartmann) von Martens, LINDHOLM, Ann. Musee Zool. L'Acad. Sci., Russia, Tome XXIII, p. 320. Type designated by Lindholm *Planorbis vortex* (Linn.). As subgenus.

1923. *Gyrostoma* HAAS, Archiv. f. Molluskund., LV, pp. 43, 45. Type designated *Gyrostoma rotundatum* Poir. = *Planorbis leucostoma* Millet. Not *Gyrostoma* Kirby and Spence 1828, Knietniewski 1897, or Hesse 1909.

1923. *Spiralina* von Martens 1899, WENZ, Fossil. Cat., pars. 22, p. 1529. Genotype *Spiralina vortex* (Linn.). As genus.

1923. *Paraspira* WENZ, op. cit., p. 1530. Genotype *Paraspira rotundata* Poiret. As genus and subgenus.

1926. *Spiralina* (Hartmann MS) von Martens, KENNARD and WOODWARD, Syn. Brit. non-marine Moll., p. 68. Type *Helix vortex* Linn. As subgenus.

1926. *Spiralina* (Hartmann MS) von Martens, 1899, LINDHOLM, Archiv. f. Mollusk. 58 year, Heft 6, p. 252. Ideogenotype *Helix vortex* Linn. As genus.

1926. *Anisus* (Studer, 1820) LINDHOLM, op. cit., p. 253. Ideogenotype *Planorbis spirorbis* (Linn.). As genus.

1926. *Anisus* (S. Str.) LINDHOLM, op. cit., p. 253. Monogenotype *Spirorbis vulgaris*(= *Planorbis vortex* var. of Drap.). As subgenus.

1929. *Anisus* (Studer, 1820) HAAS, Trab. Mus. Cien. Nat. Barcelona, XIII, p. 281. Type evidently *Planorbis spirorbis* (Linn.). As genus.

1929. *Spiralina* (von Martens, 1899) HAAS, op. cit., p. 381. Type evidently *Helix vortex* Linn. As genus.

1931. *Spiralina* (Hartmann, von Martens), Germain, Moll. Ter. Fluv. France, II, p. 526. Type probably intended to be *Planorbis vortex* (Linn.). As subgenus.

1931. *Anisus* (Studer, 1820) Thiele, Handbuch, iv teil, p. 480. As genus.

1931. *Anisus* (SS) Thiele, op. cit., p. 481. Type *Planorbis leucostoma* Millet. As subgenus of *Anisus*.

1931. *Spiralina* (Hartmann) Thiele, op. cit., p. 481. Type *Planorbis vortex* (Linn.). As subgenus of *Anisus*.

1934. *Anisus* Studer, 1820, Pilsbry, Proc. Acad. Nat. Sci., LXXXVI, p. 62. Type *Helix planorbis* Linn. designated by Gray in 1847. As genus.

1935. *Spiralina* (Hartmann) von Martens, 1899, Soos, Allat. Kozlem., XXXII, p. 29. As subgenus of genus *Anisus*.

1935. *Anisus* Studer, 1820, Soos, op. cit., p. 29. As genus.

Subgenus ANISUS SS.

Type *Helix spirorbis* Linn.

Shell (plate 77, figs. 20-22, *Anisus spirorbis* (Linn.), figs. 16-18, *Anisus leucostomus* (Millet), fig. 19, *Anisus vortex* (Linn.)) discoidal with many tightly coiled whorls very slowly increasing in diameter, all of the whorls visible on both sides of the shell; whorls rounded or with a sharp carina at the periphery; aperture small, rounded or ovate, modified in carinate species by the peripheral carina.

Animal. Externally resembling that of *Planorbis*.

ANATOMICAL CHARACTERISTICS

PLATES 6-7

GENITALIA. Male Organs (plate 6, fig. 12, *spirorbis;* plate 7, fig. 2, *leucostomus;* plate 7, fig. 6, *septemgyratus*). Seminal vesicle (SV) long, cylindrical, convoluted, about three times the diameter of the ovisperm duct. Sperm duct (SPD) very long and slender (5 mm. in *spirorbis,* 7 mm. in *septemgyratus,* 3 mm. in *leucostomus,* and 4 mm. in *vortex*). The prostate is long in *vortex* and *septemgyratus* and short in *spirorbis* and *leucostomus*. The number of diverticula vary correspondingly, in *vortex* being about sixty, in *septemgyratus* fifty-seven, in *spirorbis* about twenty, and in *leucostomus* over twenty. The diverticula are sac-like, cylindrical, and are placed on a duct separated from the sperm duct which joins the latter some distance above the vagina to form the vas deferens. Cross sections through the oviduct and prostate show the separation of the two ducts (plate 6, fig. 3 *vortex,* fig. 8 *spirorbis*). The prostate duct varies in length in the different species. It is about 1 mm. long in *spirorbis,* but only about 0.2 mm. long in *vortex, septemgyratus,* and *leucostomus*. The diverticula of the prostate vary in length and diameter as shown in the figures (plate 6, fig. 12; plate 7, figs. 2, 6). The vas deferens is shorter than the sperm duct by about half its length, and, as usual, is a narrow tube.

The penial complex is greatly elongated in all species of the genus *Anisus*. It is about 3.5 mm. long in *vortex,* 2 mm. long in *spirorbis* and *leucostomus*. The preputium is always shorter than the vergic sac, which may be nearly twice as long in *vortex* as in *spirorbis* (figs. 1 and 13 on plate 6). The preputium is cylindrical, usually swollen at the upper part. The vergic sac is elongated, pyriform or club-shaped, narrowing greatly in diameter where it joins the preputium. There is one long, narrow retractor muscle and apparently no supporting muscles.

Internally the penial complex has certain distinctive features, as shown in fig. 10 on plate 6 (*spirorbis*). The preputium has two vertical ridges or pilasters. Between the preputium and the vergic sac there is a thick muscular ring which shows as a swelling on the exterior surface of the upper part of the preputium. A large papilla (PP) is suspended between the walls of the muscular ring, the walls of which are very thick.

Below the large muscular swelling there is a second smaller ring which is here called the diaphragm (D). It is relatively thin and is capable of considerable contraction and expansion, which causes the hole or foramen in the middle, as viewed from above, to be small or large. Buchner shows this ring (Ringwulst) in his fig. 1 on plate 5, but it is there shown in section as almost closed and is placed below the thick papilla. In those specimens of the four species examined the ring has been widely open and the papilla has been extended below the area of the ring (plate 6, fig. 4, *vortex*, fig. 10, *spirorbis*). The papilla is larger and somewhat differently shaped in the figures on plate 6, varying in this respect from Buchner's figure. Possibly changes due to breeding condition may be the reason for this difference.

The verge is long, cylindrically pyriform in shape above and tapering rapidly below the middle of its length to form a slender tube, at the end of which is a small, horny stylet. The sperm canal turns to the side just above the stylet where it has its exit on the side of the verge (plate 6, figs. 4, 5). The stylet is sharp and needle-like, bulbous at the upper part where it is attached to the verge. There is a fine groove extending along one face of the stylet (plate 6, figs. 2, 5; plate 7, fig. 5). The verge of *vortex* is much narrower than that of any other species examined. With the exception of the 'Ringwulst' the penial complex of the four species of the genus *Anisus* agrees with the description and figure of Buchner.

Female Organs. The spermatheca is much elongated and cylindrical in *vortex*, *spirorbis*, and *septemgyratus* with a spermathecal duct about as long as the spermatheca (plate 6, fig. 12). In *leucostomus*, however, the spermatheca is short and bulbous with a short, thick spermathecal duct (plate 7, fig. 2). In several specimens of *septemgyratus* the spermatheca was cylindrical and acutely pointed at the summit. One specimen contained a large spermatophore (plate 7, fig. 6). The spermatheca and its duct are over 1 mm. long in *spirorbis*, but less than a millimeter in *leucostomus*.

The vagina (V) is very short (less than 0.3 mm.) in all species. The uterus (U) is long and cylindrical in *vortex*, *septemgyratus*, and *spirorbis*, but rather short and wide in *leucostomus*. The nidamental gland is long and cylindrical in *vortex*, *spirorbis*, and *septemgyratus* but large and swollen in *leucostomus*. The oviduct shows the same differences, being long and cylindrical in *vortex*, *spirorbis* (3 mm. long), and *septemgyratus*, but is short (about 2 mm. long) and of larger diameter in *leucostomus*. The oviduct is always of greater diameter than the sperm duct (see figs. 2 and 6, plate 7, fig. 12, plate 6). The albumen gland is elongated, narrow, and somewhat arched (plate 6, fig. 9; plate 7, figs. 2, 6, AL).

Hermaphrodite Organs. The ovotestis is made up of many club-shaped diverticula arranged in a double row on the ovisperm duct (plate 6, fig. 12; plate 7, fig. 2, OT, *spirorbis* and *leucostomus*). Two diverticula of *leucostomus* are shown on plate 6, fig. 7. Several diverticula of *vortex* had ripe ova. The ovisperm duct is divided into two parts separated by the seminal vesicle, as in the genus *Planorbis*. The portion between the seminal vesicle and the ovotestis is enlarged in *septemgyratus* and *leucostomus* (plate 7, figs. 2, 6) but is of small diameter in *spirorbis* and *vortex*. In the first two species the enlargement is of the same diameter as the seminal vesicle, of which it may be a part. The portion of the ovisperm duct between the seminal vesicle and the oviduct is a long, slender, smooth tube in *leucostomus*, but in *vortex, septemgyratus,* and *spirorbis* there are small pustule-like bulgings which appear to be glandular extensions of the seminal vesicle.

The genitalia of the four species here recorded are in the main similar to Buchner's fig. 11, tafel 4, which is copied by Simroth. Germain's figure of *rotundatus* (=*leucostomus*) is similar but lacks detail (1931, pp. 527, 539). The prostate is shown too long as compared with the Poland specimens personally examined. Soos's figure (1917, p. 50) is like those in this work, as is also the figure of *vortex* (p. 53).

Respiratory and Renal Systems. The pseudobranch is large, narrow, and flattened in all species examined. It is pierced by the rectum which is long and narrow. The pneumostome is cylindrical and in the specimens examined is rolled into a cylindrical tube with a large cleft extending its whole length. It varies in length in the different species (plate 6, fig. 6 *vortex*, fig. 11 *spirorbis*, and plate 7, fig. 1 *leucostomus*).

The kidney (plate 47) is very long and narrow, the glandular portion occupying only a small part of the entire length. In *spirorbis* (fig. 13) it is 5 mm. long and about 0.3 mm. wide but in *vortex* it is 12 mm. long and over 0.3 mm. wide. The ureter is very short and is sharply bent upward into the mantle cavity. The pericardium is very short as compared with total length of the kidney. Cross sections show no evidence of a ridge. In *vortex* (fig. 14) the kidney is as thick as wide and the veins are placed at the base of the rounded lumen. In *leucostomus* (fig. 15) the kidney is wider than high with the veins lower on the lumen. In these species the kidney is somewhat triangular in shape to fit the sharp angle caused by the peripheral carina of the shell. In a cross section of *spirorbis* (fig. 16) the kidney is seen to be very wide and much flattened with the veins near the middle of the lumen. The kidney of *Anisus* does not differ in any essential way from that of *Planorbis*.

Digestive System. The stomach, buccal sac, and general digestive system are similar to these organs in *Planorbis*. The jaw (plate 50, fig. 25) is similar to that of *Planorbis* with about twenty plates on the upper part. The side jaws are also fragmented.

The radula (plate 67, fig. 6, *spirorbis*) formula is 15-1-15 or 16-1-16. The numbers of rows of teeth vary from 185 to 195. Central tooth with two spade-shaped cusps reaching nearly to the lower edge of the base of attachment. Lateral teeth (1-10) tricuspid, about as wide as high at first but becoming narrower toward the marginal teeth. There is but one intermediate tooth (11), four-cuspid, with the reflection short and wide. Marginal teeth (12-15) narrow, four-cuspid, the reflections very short and wide. The fourth cusp appears as a splitting of the ectocone. The formulae for the other species examined are as follows:

septemgyratus	16-1-16	with 130 rows
vortex	16-1-16	with 142 rows
leucostomus	16-1-16	with 130 rows

The teeth are all very uniform in form. *Anisus* has fewer teeth in a row than *Planorbis*, the formula of which is 25-1-25, but the teeth are similar in form and number of cusps.

For the anatomical information herein presented the following material has been available, all received from Mr. A. Jankowski, of Warsaw, Poland:

vortex, Eight examples from stream in meadow at Jab-Tonna, 18 km. northeast of Warsaw, Poland.

spirorbis, Eight specimens from a trench in Struga, 12 km. northeast of Warsaw, Poland.

septemgyratus, Three examples from turfy meadow in Drewnica, 4 km. northeast of Warsaw, Poland.

leucostomus, Three specimens from small ponds in Bielany Park, Warsaw, Poland.

Geographical Distribution. The genus *Anisus* is distributed throughout Europe from Great Britain to Russia and Siberia and southward to Italy and Algeria. Thus the distribution is about the same as that of *Planorbis*. One species is reported from China (*paravortex*). This distribution may be enlarged when other species are examined anatomically.

Species Considered as Valid. The following species are understood to conform to the concept of *Anisus*.

Anisus spirorbis (Linn.)
Anisus vortex (Linn.)
Anisus septemgyratus (Ziegler)
Anisus leucostomus (Millet)
Anisus vorticulus (Troschel)
Anisus villai (Adami)
Anisus ressmannianus (West.)
Anisus compressus (Michaud)
Anisus johanseni (Mozley)
Anisus perezi (Dupuy)
Anisus fragilis (Millet)
Anisus paravortex (Ping and Yen)
Anisus milleti (Germain)
Anisus charteus (Held.)
Anisus centrogyratus (West.)

Geological Distribution. This genus begins about the middle of the Miocene period.

Remarks. The group of European planorbids under the name *Anisus* differs from the genus *Planorbis* notably in the form of the penial complex (compare fig. 4, plate 1, *Planorbis*, with fig. 10, plate 6, *Anisus*). In *Planorbis* the vergic sac is only one-fourth as long as the preputium while in *Anisus* this organ is always longer than the preputium and the verge is long and narrow and bears a stylet at the end, which is absent in *Planorbis*. The presence of the muscular ring and papilla in *Anisus* is also another striking difference. The seminal vesicle also differs markedly in the two genera. The shell is always flattened and many-whorled but from the shell alone the two groups could scarcely be separated generically.

The proper name for the group of European planorbids typified by *Planorbis spirorbis*, *vortex*, and *leucostomus* has been in considerable doubt. The name most commonly found in the literature, used by Germain, Lindholm, Soos, Kennard and Woodward, and others, is *Spiralina*, a nude name published by Hartmann in 1840. In 1899, von Martens used the name for the European *Planorbis vortex* and the American *Planorbis cultratus* and *sumichrasti*. The last two species are now members of the genus *Drepanotrema*. Thus the type of *Spiralina* becomes *Planorbis vortex* and this species was formally designated the type by Lindholm in 1922 (p. 320), and by Kennard and Woodward in 1924 (p. 68). But in 1847 Herrmannsen (Ind. Gen. Mal. II, p. 286) listed *Spiralina* Hartmann in the synonymy of typical *Planorbis* without comment or question, thus, as

H. B. Baker remarks (1930, p. 49) 'effectually clothing and simultaneously killing the name *Spiralina.*' Thus no subsequent use of this name is permissible. Dall (1905) used the name *Diplodiscus* Westerlund and cited *Planorbis vortex* as type, this being the first species listed. But this name is preoccupied by Diesing in Trematodes.

In 1934 (Proc. Phil. Acad. Sci., p. 62), Pilsbry revived the early name *Anisus* Studer, 1820 and gave some very good reasons for accepting this name for the group typified by *Planorbis vortex* and *spirorbis,* accepting Gray's subsequent designation of *Helix spirorbis* Linn. as type. In this connection he remarks

> Gray's type designation of '*H. spirorbis*' is valid for *Anisus* only if the identity of *spirorbis* Studer and *spirorbis* Linn. is admitted. I see no sufficient reason for doubting it. A more serious question relating to *Anisus* is whether a generic name is valid when admitted by its author to be for a group formed by the union of two prior genera, and containing nothing else. Unfortunately Opinion 9 of the International Commission on Nomenclature is not explicit on this point, but as *Anisus* has been widely used it had better be retained.

Other names have been proposed for this European group and would be available but for previous use in other groups. *Spirorbis* Swainson, *Gyrorbis, Diplodiscus, Wuestia,* and *Gyrostoma* are thus affected, as noted in the list of synonyms of *Anisus.*

The writer agrees with Pilsbry that, since the name *Anisus* has had wide use in the literature it had better be retained for this group, since it was properly clothed as a genus by Gray in 1847. *Anisus* is used by Thiele in his Handbuch, 1931. The best interest of nomenclature is served by the use of *Anisus* rather than by coining a new name.

Subgenus COSTORBIS Lindholm, 1926

Type by original designation *Planorbis strauchianus* Clessin

1926. *Costorbis* LINDHOLM, Archiv. für Mollusk., 58 year, Heft 6, pp. 253, 257. Monogenotype *Planorbis strauchianus* Clessin. As subgenus of *Anisus.*

1931. *Costorbis* THIELE, Handbuch, V, Teil 2, p. 481. Type *A. (C.) strauchianus* Clessin. As subgenus of *Anisus.*

Shell (plate 76, fig. 3). Differing from *Anisus* in being heavily transversely costate, the body whorl angulated above and below, the aperture quadrate.

Animal. The group is anatomically unknown but the shape of the shell would indicate that it should be grouped with *Anisus.*

Geographical Distribution. Russia.

Species Considered as Valid. The only species definitely referable to this subgenus is *Anisus (Costorbis) strauchianus* (Clessin).

Remarks. It is a question whether this group should be separated from *Anisus.* The shell of *strauchianus* is similar in form to that of *Anisus septemgyratus,* differing principally in the costate sculpture. Clessin's figure (copied from Conch. Cab., XVII, plate 31, fig. 5) is reproduced on plate 76, fig. 3. The original description of the shell appears on page 204 of Clessin's work.

Subgenus BATHYOMPHALUS (Agassiz MS) Charpentier, 1837

Type *Helix contorta* Linn. designated by Herrmannsen in 1852

1837. *Bathyomphalus* Agassiz (MS) CHARPENTIER, Neue Denkschr. Allg. Schweiz. Gesell., I, no. 2, p. 20.

1847. *Polygyrus* GRAY, Proc. Zool. Soc., p. 181. Type *Planorbis contortus* (Linn.) (not of Say, 1818, or Beck, 1837).

1850. *Discoidina* STEIN, Leben. Schneck. und Musch. Berlins, p. 82. Type *Planorbis contortus* (Linn.).

1852. *Bathyomphalus* HERRMANNSEN, Ind. Gen. Mal., II, Suppl., p. 16. Type *Planorbis contortus* (Linn.).

1855. *Bathyomphalus* MOQUIN-TANDON, Hist. Nat. Moll. France, II, p. 443. As subgenus.

1870. *Bathyomphalus* DALL, Ann. N.Y. Lyc. Nat. Hist., IX, p. 352. Type *Planorbis contortus* (Linn.). As subgenus.

1883. *Bathyomphalus* FISCHER, Man. Conch., p. 507. Type *Helix contorta* Linn. As section of *Planorbis*.

1885. *Bathyomphalus* WESTERLUND, Fauna Palaearc. Reg., V, p. 65. No type cited.

1886. *Bathyomphalus* CLESSIN, Conch. Cab., XVII, p. 34. Type *Planorbis contortus* (Linn.). As subgenus.

1902. *Bathyomphalus* WESTERLUND, Rad. Jugoslav. Akad., 151, p. 120. Type *Helix contortus* Linn. As genus of *Planorbis*.

1905. *Bathyomphalus* DALL, Alaska Moll., pp. 83, 86. Type *Planorbus contortus* (Linn.). As section of *Planorbis*.

1917. *Bathyomphalus* SOOS, Ann. Musei Nat. Hungarici, XV, pp. 45, 142. Type *Bathyomphalus contortus* (Linn.). As subgenus.

1921. *Bathyomphalus* GERMAIN, Rec. Ind. Mus., XXI, p. 7. Type *Planorbis contortus* (Linn.). As subgenus of *Planorbis*.

1923. *Bathyomphalus* WENZ, Fossil. Cat., Pars 22, p. 1633. Genotype *Bathyomphalus contortus* (Linn.). As genus.

1926. *Bathyomphalus* LINDHOLM, Archiv. für Mollusk., 58 year, Heft 6, p. 253. Monogenotype *Planorbis contortus* (Linn.). As genus.

1926. *Bathyomphalus* KENNARD and WOODWARD, Syn. British Non-marine Moll., p. 68. Type *Helix contorta* Linn. As subgenus of *Planorbis*.

1929. *Bathyomphalus* HAAS, Trab. Museo Cien. Nat. Barcelona, XII, p. 383. Type evidently *Planorbis contortus* (Linn.). As genus.

1931. *Bathyomphalus* GERMAIN, Moll. Terr. Fluv. France, II, p. 520. Type evidently *Planorbis contortus* (Linn.). As subgenus of *Planorbis*.

1931. *Bathyomphalus* THIELE, Handbuch, IV, Teil 2, p. 481. Type *Anisus (B.) contortus* (Linn.). As subgenus of *Anisus*.

1935. *Bathyomphalus* SOOS, Allat. Kozlem., XXXII, p. 30. *Planorbis contortus* (Linn.) cited. As genus.

Shell (plate 77, figs. 23-25). Small, ultradextral with the whorls more numerous and more closely coiled than in *Anisus*, increasing very slowly in diameter, equally visible above and below, but the spire whorls (left side) forming a wide depression, a false umbilicus, not present in *Anisus*.

Animal. Not differing in general characteristics from *Anisus*.

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PLATE 3

GENITALIA. Male Organs (fig. 10). Seminal vesicle (SV) very long (3.5 mm.), of larger diameter than the ovisperm duct with many small tuberculous glands protruding from the surface. Prostate long (about 3 mm.) and composed of forty-eight to fifty relatively short and wide diverticula (fig. 10, PRS, fig. 8). The prostate duct is a narrow tube about 1.5 mm. long from the prostate to its junction with the sperm duct to form the vas deferens (fig. 10, PD, SPD). In the natural position the prostate lies over the sperm duct and until separated from this organ the prostate diverticula appear to be directly attached to the sperm duct (see fig. 8, PD). This junction is placed higher up on the uterus than in *Planorbis* or *Anisus*. The vas deferens is a long (4.5 mm.) narrow tube which enters the vergic sac without enlargement.

The penial complex (fig. 9) is very long and narrow, the preputium (PR) being a little more than half the length of the vergic sac (preputium 1.3 mm. vergic sac 2 mm.). The narrow and cylindrical vergic sac is greatly contracted for about a third of its length near its connection with the preputium. There is one long and narrow retractor muscle attached to the summit of the preputium. Internally, the anatomy of the penial complex is the same as in *Anisus*.

Female Organs. The spermatheca is cylindrical, 1 mm. long, attached to the vagina by a narrow spermathecal duct a little more than 1 mm. long. The vagina (V) is very short (0.3 mm.) and wide. The uterus (U) is long (2 mm. long, 0.2 mm. wide) and narrowly cylindrical. The nidamental gland (NG) is long (about 3 mm.) and of larger diameter than the uterus (about 0.3 mm.). The oviduct (OD) is long (about 4 mm.) and narrowly cylindrical. The albumen gland is about the shape of that organ in *Anisus* (see plate 7, fig. 2).

Hermaphrodite Organs. The ovotestis is like that organ in *Planorbis* and *Anisus*. The diverticula are long and cylindrical and packed closely on the ovisperm duct (plate 3, OT, fig. 7). The ovisperm duct lies at each end of the seminal vesicle, of about the same length in each division, (about 2 mm.) and is a small, smooth tube (SO).

The figure in Germain (1931, pp. 521, 532) does not agree with the Poland specimens in all respects. The penial complex (p) shows the vergic sac as much swollen, while in the specimens examined it was long and narrowly cylindrical. The relative lengths of the female and male systems is shown much shorter than was observed in the Poland specimens. Details of the prostate and ovotestis are not shown. The spermatheca in both figures is the same.

Soos's figure (1917, p. 47) is similar to the ones here presented and is somewhat clearer than those of Germain. The prostate shows the great number of short diverticula, the spermatheca is on a long duct, and the penial complex is like the Poland specimens here figured.

Respiratory and Renal Systems. The pseudobranch (plate 3, fig. 5, P) is about as in *Anisus*, but is smaller and narrower. The pneumostome (PS) is larger than in *Anisus* but is otherwise similar.

The kidney (plate 46, fig. 19) is long and narrow (7 mm. long, 0.5 mm. wide) with a sharply reflected ureter. A cross section of the kidney (fig. 20) shows a laterally pyriform lumen with the veins at about the center of the section at each end. There is no ridge on the ventral side of the kidney but there is a rounded bulging on the left side that does not appear on the right side.

Digestive System. The stomach (plate 48, fig. 8) is greatly elongated, pear-shaped, with a large blind sac, two-thirds as long as the stomach.

The intestine crosses over the oesophagus and extends toward the forward part of the body, but there is no bending backward with a posterior loop as in the Helisomatinae. As in *Anisus*, there is no sharp division into crop, gizzard, and pyloris. The pyloric portion of the stomach appears to merge with the intestine. Germain states that it is absent. The buccal sac is as in *Anisus*.

The jaw is like that of *Planorbis planorbis*, the superior portion having about twenty plates.

The radula (plate 68, fig. 1) formula is 15-1-15 with 140-145 rows of teeth. Central tooth bicuspid, nearly reaches to the lower margin of the base of attachment. Lateral teeth (1-8) are tricuspid with a small additional cusp above the ectocone, placed high up on the reflection. The intermediate teeth (9-11) differ by having the reflection placed higher on the tooth, with four cusps, the ectocone split into three cusps. Marginals (12-15) with five cusps are like the intermediate teeth, the reflection very high on the tooth. The outer marginal (15) is very narrow.

For the anatomical data herein presented, four specimens were dissected, collected by A. Jankowski, at Drewnica, a turfy ground 4 km. northeast of Warsaw, Poland.

Geographical Distribution. This group extends throughout Europe from the British Isles and Portugal eastward to Russia and Siberia, as far east as Kamchatka (Eyerdam, 1928). Southward the distribution includes the countries bordering the Mediterranean Sea and the Caspian Sea.

Species Considered as Valid. Apparently but two species are included in this group: *Anisus (Bathyomphalus) contortus* (Linn.) of Europe and Asia, and *Anisus (Bathyomphalus) dispar* (Westr.) of Sweden and Russia.

Geological Distribution. From the Miocene period to the Recent period.

Remarks. In anatomical features *Bathyomphalus* so nearly resembles *Anisus* that there seems little reason for recognizing the group as distinct. The genitalia strongly resemble those of *Anisus septemgyratus*. The internal structure of the penial complex is similar. The kidney shows some differences in cross section (compare plate 46, fig. 20, with plate 47, figs. 14-16). However, the shell is distinctive and the name has been in use for so long a period that it should be retained as a subgenus of the old group *Spiralina* (=*Anisus*). It should be noted that the radula formula is the same as in *Anisus* and different from that of *Planorbis*.

Genus ODONTOGYRORBIS Lörenthey, 1906

Type by original designation *Planorbis krambergeri* Halaváts

1906. *Odontogyrorbis* Lörenthey, Beiträge zur Fauna und stratigraphischen Lage der pannonischen Schichten in der Umgebung des Balaton-Sees. Resultate d. wissenschaftl. Erforschung des Balatonsees, I, 1, Art. 3, p. 121. Genotype *Planorbis krambergeri* Halaváts.

1923. *Odontogyrorbis* Wenz, Fossil. Cat., Pars. 22, p. 1538. Genotype *Paraspira (Odontogyrorbis) krambergeri* Halaváts. As subgenus of *Paraspira*.

Shell (plate 76, figs. 1, 2). Very small, discoidal, flattened, whorls relatively few, closely coiled, increasing very slowly in diameter, each side showing all of the volutions, right side slightly concave, left side almost flat; the aperture contains three lamellae, one on the base of the lip and two on the upper part of the aperture. The whole edge of the aperture is thickened.

Geological Distribution. Lower Pliocene, Fonyod, Kenese, and Nagyvazsong, Hungary.

Remarks. This group is noteworthy for the presence in the aperture of three folds or plicae, whence the generic name *Odontogyrorbis*. In general form the shell is related to *Anisus vortex* (Linn.), but is very much smaller. Halaváts original specimens (plate 76, fig. 1) were broken and did not have the folds in the aperture. Lörenthey obtained specimens with the lip entire (plate 76, fig. 2). Wenz (1923, p. 1538) made *Odontogyrorbis* a subgenus of *Paraspira* (=*Anisus*). While the shell does resemble the type of *Paraspira* (*Planorbis leucostomus* Millet) no member of the genus *Anisus* has as yet been recorded from the recent fauna with a dentate aperture. For the present *Odontogyrorbis* should be treated as an extinct genus related to *Anisus*.

Species Considered as Valid. *Odontogyrorbis krambergeri* (Halaváts) is the only species here ascribed to the genus *Odontogyrorbis*.

It is of interest to note that the Pliocene planorbid fauna of the Lake Balaton region consist of sixteen species, all but one of which are extinct, the Pleistocene fauna contains fifteen species and races all of which belong to the recent fauna. Some of the supposed extinct species are closely related to their recent allies and might be considered geologic variations of the recent forms, in fact, ancestral species.

Genus GYRAULUS (Agassiz MS) Charpentier, 1837

Type *Planorbis albus* Müller (=*Planorbis hispidus* Drap.)
Designated by Dall in 1870. The first species originally included.

1827. *Planaria* (part) Brown, Illust. Conch. Britain, ed. 1, explan. plate LI, figs. 48, 49. Non Müller 1886 and Golze 1782 (Vermes).

1837. *Gyraulus* (Agassiz MS) Charpentier, Neue Denkschr. Allg. Schweiz. Gesell. I, no. 2, p. 21.

1840. *Gyraulus* Hartmann, Syst. Uebers. Europ. Gattun. (Tableau).

1841. *Trochlea* Haldeman, Amer. Jour. Sci., XLII, p. 216. New name for *Planaria*. Brown.

1844. *Gyraulus* Hartmann, Erd und Süssw. Gaster. der Schweiz. V, p. 89.

1850. *Nautilina* Stein, Leb. Schneck. und Muschl. Berlins, p. 80. Type fixed by Clessin (1886) *Planorbis albus* Müller. As synonym of *Gyraulus*.

1855. *Gyraulus* Moquin-Tandon, Hist. Nat. Moll. France, II, p. 438. No type cited. As genus.

1855. *Giraulus* Moquin-Tandon, op. cit., p. 423. Typographical error for *Gyraulus*.

1857. *Gyraulus* Gray, Turton's Manual, 2nd Ed., p. 234. In synonymy.

1857. *Gyrulus* Gray, op. cit., p. 234. Error for *Gyraulus*.

1865. *Gyraulus* W. G. Binney, L. & F-W Sh. N. A., II, p. 128. No type cited. As subgenus of *Planorbis*.

1870. *Gyraulus* Dall, Ann. N. Y. Lyc. Nat. Hist., IX, p. 351. Type *Planorbis albus* Müller. As subgenus of *Planorbis*.

1883. *Gyraulus* Fischer, Man. Conch., p. 507. Type *Planorbis albus* Müller. As section of *Planorbis*.

1883. *Caillaudia* Bourguignat, Ann. Soc. Nat. Zool., (6), XV, p. 99. Monotype *Caillaudia angulata* Bourg.=*Planorbis costulatus* Krauss. (vide Pilsbry and Bequaert, 1927, p. 124).

1884. *Gyraulus* Tryon, S. & S. Conch., III, p. 106. Example *Planorbis deflectus* Say. As subgenus or *Planorbis*.

1885. *Gyraulus* Westerlund, Fauna Palaearc. Reg., V, p. 75. Type *Planorbis albus* Müll. As subgenus of *Planorbis*.

1886. *Gyraulus* Clessin, Conch. Cab., XVII, p. 33. Type *Planorbis albus* Müller. As subgenus of *Planorbis*.

1899. *Gyraulus* Martens, Biol. Cent. Amer. Moll., p. 392. Type *Planorbis albus* Müller. As subgenus of *Planorbis*.

1902. *Gyraulus* F. C. Baker, Moll. Chi. Area, II, p. 297. No type cited. As subgenus of *Planorbis*.

1902. *Gyraulus* Westerlund, Rad. Jugoslav. Akad., 151, p. 121. Type *Planorbis albus* Müller. As subgenus of *Planorbis*.

1905. *Gyraulus* Dall, Alaska Moll., pp. 83, 86. Type *Planorbis albus* Müller. As subgenus of *Planorbis*.

1912. *Gyraulus* Hannibal, Proc. Mal. Soc. London, X, p. 154. Type *Planorbis albus* Müller. As subgenus of *Planorbis*.

1915. *Gyraulus* Preston, Fauna Brit. India, Moll., p. 118. Type *Planorbis albus* Müller. As section of *Planorbis*.

1917. *Gyraulus* Soos, Ann. Musei Nat. Hungarici, XV, pp. 54, 144. Type *Planorbis albus* Müller. As genus.

1918. *Gyraulus* Walker, Miscel. Pub., Mus. Zool., Univ. Mich., No. 6, pp. 12, 94. Type *Planorbis albus* Müller. As subgenus of *Planorbis*.

1919. *Gyraulus* Annandale and Prashad, Rec. Ind. Mus., XVIII, p. 52. Type *Planorbis albus* Müller. As genus (genitalia and radula).

1921. *Gyraulus* Germain, Rec. Ind. Mus., XXI, pp. 8, 98. Type *Planorbis albus* Müller. As subgenus of *Planorbis*.

1922. *Gyraulus* Annandale, Rec. Ind. Mus., XXIV, p. 361. Type *Planorbis albus* Müller. As genus.

1923. *Gyraulus* Wenz, Fossil. Cat., Pars 22, p. 1540. Genotype *Gyraulus hispidus* Drap. = *G. albus* Müller. As genus.

1926. *Gyraulus* Kennard and Woodward, Syn. British Non-Marine Moll., p. 67. Type *Planorbis albus* Müller. As subgenus of *Planorbis*.

1926. *Gyraulus* F. C. Baker, Trans. Wis. Acad. Sci. Arts, XXII, p. 204. Type *Planorbis albus* Müller. As genus.

1927. *Gyraulus* Pilsbry and Bequaert, Bull. Amer. Mus. Nat. Hist., LIII, p. 124. Type *Planorbis albus* Müller. As subgenus of *Planorbis*.

1928. *Gyraulus* F. C. Baker, F. W. Moll. Wis., I, p. 364. Type *Planorbis albus* Müller. As genus.

1929. *Gyraulus* Haas, Trab. Museo Cien. Nat. Barcelona, XIII, p. 384. Type evidently *Planorbis albus* Müller. As genus.

1931. *Caillaudia* Thiele, Handbuch, IV, 2nd Teil, p. 481. Type wrongly given as *Anisus (C.) letourneuxi* Bourg. (see Pilsbry and Bequaert, 1927, p. 124). As section under subgenus *Armiger* which is a subgenus of *Anisus*.

1931. *Gyraulus* Thiele, Handbuch, IV, 2nd Teil, p. 481. Type *Planorbis albus* Müller. As section under genus *Anisus*.

1931. *Gyraulus* Germain, Moll. Terr. et Fluv. France, II, p. 533. No type cited. As subgenus of *Planorbis*.

1935. *Gyraulus* Soos, Allat. Kozlem., XXXII, p. 30. No type cited. As genus.

Subgenus GYRAULUS SS.

Type *Planorbis albus* Müll.

Shell (plate 77, figs. 1-3). Small, ultradextral, of comparatively few flattened whorls, equally visible above and below, usually rapidly enlarging in diameter; body whorl at aperture usually somewhat deflected, the aperture oblique; the periphery is usually median and in some species carinate; the shell in several species is covered with short, hair-like projections of the periostracum (hirsute).

Animal. External appearance (plate 70, fig. 5). The head bears the long, filiform tentacles characteristic of the Planorbinae with the eyes at the inner base. In general form the animal does not differ greatly from the figures of *Tropicorbis* on plate 78. No pigmentation, however, shows through the shell.

ANATOMICAL CHARACTERISTICS

PLATE 14 (*Gyraulus albus*)

GENITALIA. Male Organs (fig. 7). Seminal vesicle (SV) less than 1 mm. long, composed of a few large diverticula or glands three or four times the diameter of the ovisperm duct. Sperm duct about 2 mm. long, of small diameter. Prostate (PRS) relatively long (1.5 mm.) consisting of about 22 long (less than 0.5 mm.) diverticula attached to a separate prostate duct which is more than twice the diameter of the sperm duct. The free portion of the prostate duct is very short (0.2 mm.) and is of the same diameter as the sperm duct which it joins to form the rather short (1.2 mm.) vas deferens. A cross section through the prostate near the anterior end shows the sperm duct behind the prostate (fig. 9, SPD).

The penial complex (fig. 2) is cylindrically elongated, a trifle more than 1 mm. long, the vergic sac (VS) somewhat shorter than the preputium (PR). There is one long retractor muscle (RM). The vas deferens is not enlarged as it enters the vergic sac. Internally (fig. 1) the preputium has thick walls, two pilasters, a muscular ring or diaphragm (D), and a dependent papilla (PP). The vergic sac has thin walls which increase in thickness toward the preputium. The verge (V) is elongate-pyriform, narrowed at the lower end where there is a stylet (ST). The stylet (fig. 8, ST) is dark brown, dagger-like with a ridge extending down the center. The opening of the sperm canal (SC) turns to one side above the stylet and has its exit on the side of the verge.

Female Organs. The spermatheca (fig. 7, S) is elongate-pyriform, about 0.5 mm. long. It is joined to the vagina by a short, narrow duct about half as long as the spermatheca (SD). The vagina (VG) is very short and wide. The uterus (U) is wider than the vagina and the nidamental gland is wide and made up of many large diverticula (fig. 6, NG). The uterus and gland are hidden in the figure by the large prostate. The free oviduct (fig. 6, OD) is a short and narrow tube, looped beneath the prostate. Figure 6 shows the relationship of the nidamental gland diverticula, the oviduct, the prostate, the sperm duct, which forms a loop, and the method of junction to form the ovisperm duct. The narrow duct of the albumen gland and its connection with the oviduct is shown. The albumen gland is squarish or oval in shape and is composed of large gland cells. It contains cavities for the loop of the intestine, over which it lies (fig. 5).

Hermaphrodite Organs. The ovotestis (OT) consists of a double row of pyriform diverticula attached to a large ovisperm duct (fig. 10). At the posterior end of the ovotestis the diverticula are crowded together (fig. 11). Several diverticula had developing egg cells. The ovisperm duct (SO) is divided into two parts, one at each end of the seminal vesicle (fig. 7, SO).

The figures on plate 14 agree with that of Germain (1931, p. 533, fig. 545). His figure, however, is not very clear. Soos's figure (1917, p. 55) is similar in general form. The prostate shows fewer diverticula, however, and the spermatheca is on a longer duct than in the specimens from Poland examined, and they are figured more irregularly than was observed in the specimens personally examined. A. Soos's figure of *Gyraulus laevis* (Ald.) (1935, p. 27) shows a smaller number of prostate diverticula than appears normal for the genus. The spermatheca is also on a longer duct than in those species of the genus personally examined. No separate prostate duct is indicated.

American species examined differ but little from the European *Gyraulus albus*. *Gyraulus hirsutus* (Gould), the nearest relative to *albus*, has from twenty to twenty-two diverticula on the prostate as in *albus* (plate 15, fig. 2). The seminal vesicle is practically the same. The penial complex has a much shorter preputium with a vergic sac one and one-half times as long as the preputium. This difference in form of the penial complex easily separates *albus* from *hirsutus* (compare fig. 2, plate 14, with fig. 2, plate 15). In *Gyraulus deflectus obliquus* (DeKay) there are forty diverticula on the prostate which is much longer than either *albus* or *hirsutus*. The prostate diverticula are also longer and club-shaped toward the end (plate 16, figs. 11, 12). Plate 16 fully illustrates the genitalia of *obliquus*. *Gyraulus latestomus* F. C. Baker (plate 19, fig. 9) has thirty-two diverticula on the prostate and the penial complex resembles that of *obliquus*. *Gyraulus convexiusculus* (Hutton) (plate 19, fig. 2) of India has about twenty-five prostate diverticula. The penial complex is very long and narrow but generally resembles that of *hirsutus*. The figures on plate 19 agree with those by Annandale and Prashad (Rec. Ind. Mus., XVIII, p. 40) except that the spermatheca in the specimens examined is on a much longer duct than is shown in their figure.

Respiratory and Renal Systems. The pseudobranch of *Gyraulus albus* (plate 14, figs. 3, 4) is broad, somewhat triangular, and flattened. The pneumostome is broad (fig. 3, PS). Figure 4 shows the pseudobranch cut open to indicate the vascular network of blood vessels. The rectum passes through the pseudobranch, as in other genera of Planorbinae. In *Gyraulus hirsutus* (plate 15, fig. 3) the pseudobranch is as broad as in *albus*. In *Gyraulus deflectus obliquus* the pseudobranch was observed to be of several forms (plate 16, figs. 13, 14, 15). It is in each case a broad, flattened organ. Figure 15 is an unusual form, possibly pathologic. In *Gyraulus latestomus* (plate 19, fig. 8) it is broad and flattened. In *Gyraulus convexiusculus*, from India (plate 19, fig. 3) it is flat and very thin and the pneumostome is very large. The pseudobranch appears to be similar in form in species from Europe, America, and India.

The kidney (plate 48) is long and narrow in *obliquus* (fig. 4, 9 mm. long) and *convexiusculus* (fig. 17, 8.5 mm. long). In *hirsutus* (fig. 18, 2.5 mm. long) and *albus* (which has the same form as *hirsutus*) the kidney is short and wide, quite unlike the kidney of the two species previously mentioned. It is similar to that of *vermicularis* (fig. 3). Sections through the kidneys at about the middle show this organ to be flattened, the lumen much wider than high, and the veins to be placed at each end at about the center. *Convexiusculus* (fig. 8), *hirsutus* (fig. 19), and *latestomus* (fig. 11) are similar in form, but *obliquus* (fig. 10) is higher in proportion to width showing that the kidney is thicker than in the other species. There is no ridge. The ureter is short in *convexiusculus* and *obliquus* but longer and more tube-like in *hirsutus* and *albus*.

Digestive System. The stomach (plate 48, fig. 13) is cylindrical with the crop, gizzard, and pyloris plainly indicated. The intestine, after leaving the pyloris, makes a loop over the oesophagus which extends backward, around the liver, and then loops forward to the rectum which has its exit on the pseudobranch. All species of typical *Gyraulus* examined have the same type of stomach and intestine. The buccal sac (of *Gyraulus albus* plate 70, fig. 13) is pyriform with the radula sac greatly developed and protruding behind (RL). The salivary glands (SG) are elongated, cylindrical, and almost as long as the buccal sac. The ducts of these glands are long.

The jaw (plate 50) is horseshoe-shaped and fragmented as in *Planorbis* and *Anisus*. *Gyraulus hirsutus* (fig. 17) has large plates, about forty on the entire jaw. *Gyraulus albus* has the same number. In *Gyraulus deflectus obliquus* (fig. 18) the jaw is arched and consists of over fifty plates which are narrower than those of *albus* and *hirsutus*. In *latestomus* the jaw is similar to that of *obliquus* and has over forty plates.

The radula formula of *Gyraulus albus* (plate 68, fig. 9) is 18-1-18 with 103 to 114 rows of teeth. The center tooth is bicuspid, the cusps long and narrow and reaching only about half way to the lower margin of the base of attachment. The laterals (1-9) are tricuspid with long, narrow cusps. The cusps of intermediate teeth (10-11) are short, placed high up on the reflection, and the ectocone is split into two sharp cusps. The marginal teeth (12-18) have the reflection high up on the tooth, are wide and low and 6-cuspid. The entocone is split into two small cusps, the mesocone is larger, and the ectocone cusps, three in number, are very small and sharp. In several membranes examined a very small 4th cusp appears on the 6th tooth and continues to the intermediate teeth. The center tooth varies in size in the 43rd to 62nd rows being a trifle wider at the top than in the first forty-two rows. The 86th to 103rd rows have a central tooth a little more than half the width of those in the 43rd to 62nd rows.

The radula of *Gyraulus hirsutus* (plate 69, fig. 1) is similar to that of *albus*. The formula is 19-1-19, with 1-9 lateral teeth, 10-11 intermediate teeth, and 12-19 marginal teeth. There are 130 rows of teeth. The radula of *Gyraulus deflectus obliquus* (plate 69, fig. 2) has a formula of 22-1-22, with 1-9 lateral teeth, 10-13 intermediate teeth, and 14-22 marginal teeth. There are 175 to 183 rows. *Gyraulus latestomus* has the formula 20-1-20, with 1-10 marginal teeth, 11-14 intermediate teeth, and 15-20 marginal teeth. There are 155 rows of teeth.

Gyraulus convexiusculus has the formula 20-1-20, with 1-9 lateral teeth, 10-13 intermediate teeth, and 14-20 marginal teeth. The specimens examined differ from the figure by Annandale and Prashad (Rec. Ind. Mus., XVIII, p. 55, fig. 8, B) where the inner laterals are shown as bicuspid, an unusual condition in the genus. Probably the entocones were not observed, for they were present in all of the laterals of the teeth personally examined. The figure of the radula of *Gyraulus euphraticus* (C) by Annandale and Prashad is more correct in the tricuspid character of the lateral teeth. The radulae of all of the typical *Gyraulus* examined have been similar in character.

For the above anatomical data the following material has been available:

G. albus, 25 specimens from park in Krolikarnia, a suburb of Warsaw, Poland. Collected by Mr. A. Jankowski.

G. hirsutus, 9 specimens from mouth of Bass Creek, Lake Nipissing, Ontario. Collected by Mr. A. LaRocque.

G. deflectus obliquus, 13 specimens from Lake Chetek, Wisconsin. Collected by F. C. Baker; 6 specimens from Taylors Lake, near Quebec, Canada. Collected by Mr. A. LaRocque.

G. latistomus, 3 specimens from Cedar Lake, Algonquin Park, Ontario. Collected by Mr. A. LaRocque.

G. convexiusculus, 3 specimens from Calcutta, India, collected by Dr. B. Prashad.

Geographical Distribution. The genus *Gyraulus* is practically worldwide in distribution, differing in this respect from all other genera of Planorbidae. Specific regions include North America, parts of the West Indies and northern South America, Europe, Asia, Africa, Australia, Malaysia, Fiji, New Caledonia, Philippines, and other islands of the Pacific Ocean.

Below is given a list of some of the species of Planorbids believed to belong in the genus *Gyraulus*.* Some of these species may be found, on anatomical examination, to belong to other subgenera or genera. The list is probably not complete.

Species of Europe and Western Asia

albus Müller
acronicus Ferussac
ancylus West.
arcticus Möller
albopersicus Germain
borealis Loven
bourguignati Moitessier
brondeli Raym.
capocestianus V. Brus.
crossei Bgt.
devians Porro
drapanauldi Jeff.
gredleri Bietz
hebraicus Bgt.
infraliratus West.
intermixtus Mouss.
janinensis Mouss.
laevis Alder
limnophilus West.
numidicus Bgt.
piscinarum Bgt.
polaris West.
regulosus Lindholm
socius West.
tetragyrus West.

Species of Australia and Tasmania

essingtonensis Smith
gilberti Dunker
meridionalis Brazier
planissimus Mousson

Species of Africa

abyssinicus Jickeli
adansonii J. E. Gray
aethiopicus Bourg.
agraulus Bourg.
andersoni Ancey
avakubiensis Pils. and Beq.
chedeaui Germain
cockbruni Godwin-Austen
costulatus Krauss
crawfordi Melville and Ponsonby
fouladougouensis Germain
gardei Germain
gibbonsi Nelson
kigeziensis Preston
kisumiensis Preston
lamyi Germain
leucochilus Melville and Ponsonby
misellus Morelet
natalensis Krauss
sperabilis Preston
schweinfurthi Clessin
tilhoi Germain
toukotoensis Germain

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*In this faunal list, which Mr. Baker had never fully edited, the author's name follows each specific name with disregard for use of parentheses to indicate change from original generic assignment.—H.J.V-C.

Species of Fiji Group

singularis Mousson

Species of New Caledonia

montrouzieri Gassies
rossiteri Crosse

Species of India and Asia

associatus Westerlund
acutus Clessin
barrakporensis Clessin
cantori Benson
cherraensis Godwin-Austen
compressus Hutton
convexiusculus Hutton
demissus Westerlund
elegantulus Dohrn
euphraticus Mousson
himalayaensis Hutton
hohenackeri Clessin
huttoni Benson
hyptiocyclos Benson
infralineatus Martens
intermixtus Mousson
issykulensis Clessin
labiatus Benson
laidocensis Nevill
liratus Westerlund
malacaensis Germain
pangongensis Nevill
proclivis Martens
rotula Benson
saigonensis Crosse and Fischer
saltensis Germain
sivalensis Hutton
stelzneri Dohrn
stewarti Germain
sumatranus Martens
tondanensis Quoy and Gaimard
velifer Annandale
yeni Ping and Yen

Species of Japan

amplificatus Mori
biwaensis Preston
hiemantium Westerlund
infirmus Mori
iwaotakii Mori
japonicus Martens
noziriensis Mori
pulcher Mori
tokyoensis Mori

Species of the Philippines

mindanensis Bartsch
quadrasi Mollendorff

Species of America

arcticus (Beck in Möller)
boetzkesi (Miller)
borealis Lovén
cyclostomus F. C. Baker
deflectus (Say)
deflectus obliquus (De Kay)
hirsutus (Gould)
hornensis F. C. Baker
latistomus F. C. Baker

Geological Distribution. According to Wenz the genus *Gyraulus* dates geologically from the Middle Eocene period.

Remarks. The genus *Gyraulus* is closely related to *Anisus* in its anatomical features, especially the genitalia. In fact, *Gyraulus*, *Anisus*, and *Bathyomphalus* form a natural group, based on their anatomy, particularly in the presence of a horny stylet on the verge. The shells of *Anisus* and *Gyraulus*, however, are quite unlike and the genera should undoubtedly be separated on conchological grounds alone.

More than ninety species of *Gyraulus* are listed on the previous pages (excluding those from America). Some of these may be found to belong in other genera, when examined anatomically. Also, it is probable that several additional species should be added to those listed. Completeness is not claimed. All of those listed have been included in the genus *Gyraulus* by competent conchologists.

Subgenus TORQUIS Dall, 1905

Type by original designation *Planorbis parvus* Say

1899. *Gyraulus* (part) Martens, Biol. Cent. Amer., Moll., p. 392. Includes *Planorbis parvus* Say.

1905. *Torquis* Dall, Alaska Moll., pp. 83, 86. Type *Planorbis parvus* Say. As section of subgenus *Gyraulus*.

1918. *Torquis* Walker, Miscel. Contr., Mus. Zool., Univ. Mich., No. 6, pp. 34, 94. Type *Planorbis parvus* Say. As section of subgenus *Gyraulus*.

1921. *Torquis* Germain, Rec. Ind. Mus., XXI, pp. 8, 150. Type *Planorbis parvus* Say. As subgenus of *Planorbis*.

1923. *Torquis* Wenz, Fossil. Cat., Pars 22, p. 1627. Genotype *Gyraulus (Torquis)* Say. As subgenus of *Gyraulus*.

1926. *Torquis* Kennard and Woodward, British Non-Marine Moll., p. 67. As section of *Gyraulus* in synonymy.

1926. *Torquis* F. C. Baker, Trans. Wis. Acad. Sci. and Arts, XXII, p. 204. Type *Planorbis parvus* Say. As subgenus of *Gyraulus*.

1928. *Torquis* F. C. Baker, Fresh-water Moll. Wis., I, p. 373. Type *Planorbis parvus* Say. As subgenus of *Gyraulus*.

Shell (plate 77, figs. 4-6). Ultradextral, smaller than *Gyraulus*, SS, with the whorls less distinctly spirally striated, not hirsute, the base (left side) more or less concave, or excavated (appearing as though reamed out), the lip often slightly thickened within.

Animal. Not differing from *Gyraulus* in general form.

ANATOMICAL CHARACTERISTICS

PLATE 17 (*Gyraulus parvus*)

GENITALIA. Male Organs (fig. 6). Seminal vesicle (SV) short (0.5 mm.) of the same diameter as the sperm duct. There are a number of small glands which stand out like pustules. Sperm duct a trifle more than 1 mm. in length. Prostate (PRS) more than half as long as the sperm duct with eleven long and cylindrical diverticula. The free portion of the prostate duct is very short (PD), joining with the sperm duct to form the vas deferens. A cross section through the prostate shows the cylindrical or pear-shaped diverticula on a separate duct which has a greater diameter than the sperm duct (fig. 10). The vas deferens is at first a large duct but becomes smaller in diameter toward the penial complex (VD). It is about 1 mm. in length.

The penial complex (fig. 6, VS, PR) is very long (about 1.3 mm.) and narrow, and cylindrical. The vergic sac is longer than the preputium. There is one large retractor muscle attached near the junction of the vergic sac with the preputium (fig. 12, RM). The vas deferens is not enlarged as it enters the vergic sac. Internally (fig. 12) the preputium has two vertical pilasters. The vergic sac is long and cylindrical and is enlarged at the upper end (VS). The verge (V) is long and narrow, enlarged at the upper end, very narrow below where there is a horny stylet (ST). The opening of the sperm canal is on the side as in typical *Gyraulus*. Between the vergic sac and the preputium there is a large papilla and below this a swelling of the wall of the preputium representing the better-developed muscular ring or diaphragm of typical *Gyraulus* (not shown in the figure).

Female Organs. The spermatheca (fig. 6, S) is small, pyriform, and connected with the vagina by a duct about as long as the spermatheca

(SD). The vagina is narrow and about as long as the spermatheca and its duct. The uterus and nidamental gland are relatively short and wide (U). The oviduct is short (about 0.5 mm.). The junction of the oviduct and sperm duct to form the ovisperm duct is shown in fig. 7. The albumen gland is squarish in form, longer than wide (about 1 mm. long), and is composed of large diverticula. Its duct is long and looped (fig. 9, DA).

Hermaphrodite Organs. The ovotestis is rather short and is composed of but few club-shaped diverticula arranged in a double row (fig. 6, OT; fig. 11). The ovisperm duct is small and tube-like and is longer between the seminal vesicle and the ovotestis than between the seminal vesicle and the oviduct (fig. 6, SO). Several of the diverticula of the ovotestis were filled with ova ready for extrusion (fig. 11).

Several other species of the subgenus *Torquis* have been dissected and may be compared with *parvus*. *Gyraulus circumstriatus* (Tryon) (plate 17, fig. 1, also fig. 4) is similar in form. The prostate has twelve diverticula. The spermatheca is the same. The duct to the albumen gland is not so long (fig. 2). The penial complex is the same in both species which are of about the same size. In *Gyraulus vermicularis* (Gould) there are sixteen diverticula in the prostate and ten diverticula in the ovotestis (plate 15, fig. 10). The penial complex is somewhat different, the preputium being long and cylindrical and the vergic sac very short, only about half as long as the preputium. In *Gyraulus similaris* (F. C. Baker) (plate 18, fig. 1) there are nineteen diverticula on the prostate and the ovotestis diverticula are few in number. In the penial complex the vergic sac is shorter than the preputium. There is a heavy swelling at the upper part of the preputium where the papilla and muscular ring are located. A section through the penial complex (fig. 3) shows the relationship between the several organs. The verge is very long and slender and has a large stylet (fig. 4). The junction of oviduct, sperm duct, and ovisperm duct is shown in fig. 2.

The genitalia of the subgenus *Torquis* differ from those of typical *Gyraulus* in the form of the seminal vesicle, the fewer diverticula of the prostate, and the rounder spermatheca on a shorter duct. In general, however, the two groups are very similar in the form and position of the genital organs. No figures of the genitalia of the *Torquis* group have been published previously; hence no comparisons can be made.

Respiratory and Renal Systems. The pseudobranch of *Gyraulus parvus* (plate 17, fig. 8) is flattened, wide, leaf-like, and is pierced by the rectum. The pneumostome is very large. In *Gyraulus circumstriatus* (fig. 3) the pseudobranch is much narrower (the animal was much contracted). In *Gyraulus vermicularis* (plate 15, fig. 8) it is flattened and somewhat triangular. In *Gyraulus similaris* (plate 18, fig. 5) it is like that of *vermicularis* but the rectum has a slight ridge which was not observed in any of the other species examined. In the four species of this group studied there was a large, flattened, muscular pad extending backward from the free portion of the pseudobranch to the place where the rectum begins on the intestine. Figure 5 on plate 18 and fig. 8 on plate 15 show the form of this pad. The rectum pierces this pad as well as the pseudobranch and has its exit (A) above the leaf-like pseudobranch.

The kidney (plate 47, fig. 1, *parvus*) is very long and narrow (4 mm. long, 0.5 mm. wide), the ureter short and recurved. In *Gyraulus circum-*

striatus (fig. 2) the kidney is much shorter and wider (less than 2 mm. long). In *vermicularis* it is short and wide as is also the case in *similaris*. Cross sections through the kidney of the four species show a similarity of conditions (fig. 5 *parvus;* fig. 6 *circumstriatus;* fig. 7 *vermicularis;* fig. 9 *similaris*). The kidneys in *Gyraulus* and *Torquis* differ little in structure.

Digestive System. The digestive tract shows division into crop, gizzard, and pyloris and there is a large blind sac. The intestine does not form a posterior loop, as in typical *Gyraulus*, but crosses over the oesophagus and extends forward as in the genus *Planorbis*. The buccal sac is like this organ in typical *Gyraulus*.

The jaw (plate 50, fig. 16, *parvus*) is horseshoe-shaped with many small plates as in *Gyraulus* typical. There are approximately thirty-six to forty plates on the jaw of *parvus* and *Gyraulus vermicularis* has about forty-seven plates (fig. 19). *Gyraulus circumstriatus* (fig. 22) has a small, narrow jaw with about thirty-seven plates. The jaws of *Gyraulus* (figs. 17-18) are not as typically horseshoe-shaped as in the subgenus *Torquis*.

The radula formula of *Gyraulus parvus* (Say) is 14-1-14 with 105 rows of teeth (plate 69, fig. 3). The center tooth is bicuspid, the cusps not reaching the lower margin of the base of attachment. There are 1-6 lateral teeth, tricuspid, with spade-shaped cusps. Intermediate teeth (7-8) with the ectocone split into two small cusps. The 9th tooth is also transitional with the ectocone split into three small cusps. Typical marginal teeth (10-13) have the entocone split into two small cusps, the mesocone large and spade-shaped, and the ectocone split into three small cusps.

In *Gyraulus vermicularis* (Gould) (fig. 5) the formula is 15-1-15, with 1-6 laterals, 7-10 intermediates and 11-15 marginals. There are 120-125 rows of teeth. In *Gyraulus similaris* (F. C. Baker) (fig. 4) the formula is 22-1-22 with 1-7 laterals, 8-10 intermediates, and 11-22 marginals. There are 130 rows of teeth. *Gyraulus circumstriatus* (Tryon) has the formula 14-1-14 with the same number and position of teeth as in *parvus*. The radula teeth of the subgenus *Torquis* do not differ in general characteristics from those of typical *Gyraulus*. Compare figs. 1, 2 with figs. 3, 4, 5 on plate 69.

For the above anatomical data the following specimens were studied:

Gyraulus parvus (Say), 14 specimens from Winnebago Lake, Wisconsin, Henry Co., Illinois, and Meach Lake, Canada, collected by F. C. Baker and A. LaRocque.

Gyraulus circumstriatus (Tryon), 17 specimens from Wainwright Park, Alberta, collected by Dr. Swales, and North Star Lake, Wisconsin, collected by F. C. Baker.

Gyraulus vermicularis (Gould), 10 specimens from Mt. Lake, San Francisco, California, and Hat Creek, Bishop, California, both lots collected by Dr. G. D. Hanna.

Gyraulus similaris (F. C. Baker), 17 specimens from Smartweed Lake, Toland, Colorado, collected by Dr. Frank Smith.

Geographical Distribution. The subgenus *Torquis* is found throughout North America from Mexico northward. It is also apparently represented by *Gyraulus santacruzensis* Germain from the Island of St. Croix, West Indies. *Gyraulus laevis* Alder, a common species of Europe, also belongs to this subgenus. Some of the other species listed under the distribution of typical *Gyraulus* may belong to *Torquis*, but not enough material is available for study to confirm this suggestion.

Species Considered as Valid. The American species included in this subgenus are:

Gyraulus (Torquis) aeruginosus Morelet
Gyraulus (Torquis) arizonensis Pilsbry and Ferriss
Gyraulus (Torquis) altissimus (F. C. Baker)
Gyraulus (Torquis) carus Pilsbry and Ferriss
Gyraulus (Torquis) circumstriatus (Tryon)
Gyraulus (Torquis) circumstriatus walkeri Vanatta
Gyraulus (Torquis) parvus (Say)
Gyraulus (Torquis) santacruzensis (Germain)
Gyraulus (Torquis) similaris (F. C. Baker)
Gyraulus (Torquis) vermicularis (Gould)
Gyraulus (Torquis) vermicularis hendersoni Walker

Geological Distribution. *Torquis* apparently dates geologically from the Oligocene period. *Torquis siliceus* Pilsbry and Brown, Oligocene of Dry Hill, Antigua.

Remarks. Except for some small details in genitalia, referred to on a previous page, the subgenus *Torquis* is similar in anatomical details to typical *Gyraulus*. It is, however, a convenient name for the smaller species with 'reamed out' left side, like *parvus* and *vermicularis*, which have narrower and smoother whorls than the species of typical *Gyraulus*, like *albus* and *deflectus*.

Genus ARMIGER Hartmann, 1840

Type by designation of Hartmann in 1842, *Nautilus crista* Linn.

1840. *Armiger* Hartmann, Syst. ubers. Europ. Gatt., table.

1842. *Armiger* Hartmann, Erd-und Süss. Gasterop., V, pp. 172, 219. Type *Armiger cristatus* Drap. = *Nautilus crista* Linn.

1847. *Nautilus* Gray, Proc. Zool. Soc., p. 181. Type *Turbo nautilus* Linn.

1850. *Nautilina* Stein, Leben. Schneck. und Musch. Berlins, p. 81. Ideogenotype *Planorbis nautilus* Stein = *Planorbis cristata* Drap. Type designation by Lindholm in 1926.

1885. *Armiger* Westerlund, Fauna Palaearc. Reg., V, p. 65. No type cited. As subgenus of *Planorbis*.

1902. *Armiger* Westerlund, Rad. Jugoslav. Akad., 151, p. 121. Type *Turbo nautilus* Linn. As subgenus of *Planorbis*.

1903. *Spiniformis* Germain, Bull. Soc. Sci. Nat. Ouest France, ii, III, p. 204. Vide Germain, 1931.

1905. *Armiger* Dall, Alaska Moll., pp. 83, 86. Type *Planorbis crista* (Linn.). As section of subgenus *Gyraulus*.

1918. *Armiger* Walker, Miscel. Contr., Mus. Zool., Univ. Mich., No. 6, pp. 13, 94. Type *Planorbis crista* (Linn.). As section of subgenus *Gyraulus*.

1923. *Armiger* Germain, Rec. Ind. Mus., XXI, pp. 8, 153 Type *Planorbis crista* (Linn.). As subgenus of *Planorbis*.

1923. *Armiger* Wenz, Fossil. Cat., Pars 22, p. 1625. Genotype *Gyraulus (Armiger) crista* (Linn.). As subgenus of *Gyraulus*.

1926. *Armiger* Lindholm, Archiv. für Mollusk., 58 year, Heft 6, p. 253. Monogenotype *Armiger cristatus* Drap. = *Planorbis crista* (Linn.). As genus on conchological grounds.

1928. *Armiger* F. C. Baker, Fresh-water Moll. of Wisconsin, I, p. 385. Type *Nautilus crista* Linn. As subgenus of *Gyraulus*.

1929. *Armiger* Haas, Trab. Museo Cien. Nat. Barcelona, XIII, p. 386. Type evidently *Nautilus crista* Linn. As genus.

1929. *Armiger* Odhner, Die Mollusk. Fauna Takern, p. 22. Type *Armiger crista* (Linn.). As genus on anatomical grounds.

1931. *Armiger*, Germain, Moll. terr. fluv. de France, II, p. 540. Type *Planorbis crista* (Linn.). As subgenus of *Planorbis*.

1931. *Armiger* Thiele, Handbuch, IV, Teil 2, p. 481. Type *Anisus (Armiger) crista* (Linn.). As subgenus under *Anisus*.

1935. *Armiger* A. Soos, Allat. Kozlem., XXXII, p. 30. As subgenus of *Gyraulus*. No type indicated.

Shell (plate 76, fig. 6). Ultradextral, small, with few rapidly increasing, costate whorls, the costae usually projecting at the periphery. The general form is like that of *Gyraulus*.

Animal. External form like that of *Gyraulus*.

ANATOMICAL CHARACTERISTICS

PLATE 18

GENITALIA. Male Organs (plate 18, fig. 7). Seminal vesicle (SV) with very few large glands or diverticula. Sperm duct 1.5 mm. long, bent upon itself in a loop posterior to the prostate. Prostate 0.5 mm. long, consisting of thirteen long, cylindrical diverticula placed on a separate prostate duct. The free portion of the prostate duct is very short. Vas deferens a long (1 mm.), small duct.

Penial complex (fig. 7) with a vergic sac one and one-half times as long as the preputium. The vergic sac is enlarged at the end where the vas deferens enters it as an enlarged tube. There is one retractor muscle (RM). The preputium is of larger diameter than the greater part of the length of the vergic sac.

Internally (fig. 9) the penial complex is formed like that of *Gyraulus*. There are two pilasters, a dependent papilla (D), and also a muscular ring or diaphragm (not shown in figure). The verge (V) is elongated, cylindrical, tapering gradually to the end, which does not bear a horny stylet, as in *Gyraulus*, but a small, pointed fleshy papilla (fig. 10, PA, fig. 11, PA). The opening of the sperm canal is just above this papilla at the end of the verge, in the center and not at the side as in *Gyraulus* (figs. 10, 11, SC).

Female Organs. The spermatheca (S) is long and pyriform in shape, tapering gradually to the short, wide vagina (VG), the duct being very short. The uterus (U) and nidamental gland are wide, the uterus short and the gland rather long. The oviduct (OD) is short and greatly swollen below the junction with the sperm duct to form the ovisperm duct. The albumen gland (fig. 8) is large (1 mm.), elongated and composed of large gland cells. It is joined to the large, bulbous carrefour (CF) by a long, very fine duct (DA). The carrefour connects with the oviduct. The intestine extends the whole length of the albumen gland which covers the greater part of the intestine. The space occupied by this organ is shown in the figure (AL).

Hermaphrodite Organs. The ovotestis (OT) consists of many club-shaped diverticula placed in a double row. The ovisperm duct (SO) is twice as long between the oviduct and the seminal vesicle as between that organ and the ovotestis.

No figure of the whole genitalia of *Armiger* was available before the publication of A. Soos's paper in 1935. His figure (1935, p. 28) differs in several respects from the ones here presented. The prostate has nine diverticula which appear widely spaced while there were thirteen crowded diverticula in the specimens personally examined. The separate prostate duct is not shown in Soos's figure. The spermatheca in Soos's figure is also on a longer duct. The penial complex differs in several respects.

In 1929 (pp. 22, 30) Odhner called attention to the absence of a stylet in *Armiger,* figured the verge of *Armiger crista* to show the absence of the stylet and the presence of a small penial papilla. This is, apparently, the first indication of this anatomical difference between *Armiger* and *Gyraulus.* Odhner noted a difference in the size of the teeth and formula of *crista,* those from the Täkern having much smaller teeth than specimens from near Stockholm. The formula, also, was only 11-1-11 while the larger form has a formula of 14-1-14.

Germain (1931, p. 540) says 'Appareil génital comme chez les espèces du sous-genre *Gyraulus.*' But this is not the case. There is no stylet at the end of the verge and the opening of the sperm canal is at the center beside a small papilla and not at the side above a stylet as in *Gyraulus.* The seminal vesicle is also different in form of glands. These differences in anatomy are sufficient to remove *Armiger* as a subgenus of *Gyraulus* and indicate its right to full generic rank. The genitalia of *Armiger* and *Torquis* may be compared on plate 18, where the difference in the structure of the termination of the verge is plainly indicated.

Respiratory and Renal Systems. The pseudobranch (plate 18, fig. 6) is broadly triangular, leaf-like. The rectum is a large tube bordering the upper side of the pseudobranch and the anus is above the pseudobranch.

The kidney (plate 47, fig. 20) is short and wide, somewhat resembling the kidney of *Gyraulus vermicularis* (fig. 3). A section through the kidney near the middle (fig. 21) shows it to be flattened, convex above, with the veins near the center of each side of the oval lumen. The section is also similar to that of *Gyraulus vermicularis* (fig. 7).

Digestive System. In the region of the stomach (plate 48, fig. 15) there is a distinct division into crop, gizzard, and pyloris. The intestine makes a loop forward and then backward *under* the oesophagus. It bends around the liver and turns forward, ending in the rectum on the pseudobranch. The stomach region resembles that of *Gyraulus* (fig. 13). The buccal sac is like that of *Gyraulus.*

The jaw (plate 50, fig. 20) is narrow and characteristically horseshoe-shaped with the lateral processes elongated. There are twenty-two plates in the upper or superior jaw and fourteen to sixteen plates in each of the side jaws. The jaw most nearly resembles that of *Gyraulus circumstriatus* (fig. 22) except that it bears a larger number of plates.

The radula formula is 16-1-16 with 150 rows of teeth. The center tooth is bicuspid and resembles that of *Gyraulus vermicularis* (fig. 5). The laterals are four-cuspid (1-9), the intermediate teeth (10-11) five-cuspid, and the marginals (12-13) six-cuspid. The outer marginals are vestigial. The teeth resemble those of *Gyraulus* except that there is always an accessory cusp above the ectocone, even in the lateral teeth.

For the above anatomical data ten specimens were dissected, collected from a swamp on University Bay, Lake Mendota, near Madison, Wisconsin, by Dr. J. P. E. Morrison. These represent the variety *imbricatus.* Typical *crista* from a pond in Krolikarnia, a suburb of Warsaw, Poland, collected by A. Jankowski, provided most of the anatomical data.

Geographical Distribution. *Armiger* is Palearctic in distribution, occurring in the northern United States and Canada, northern Europe and Asia. *Armiger crista* is reported from the trans-Mediterranean region, from Algeria, Tunis, etc. A species (*Armiger annandalei* Germain) has been described from eastern Asia. The genus contains several forms which should probably rank as species.

Geological Distribution. According to Wenz (pp. 1632-1633) *Armiger* is first known from the Middle Miocene period.

Species Considered as Valid. The only species definitely assigned to this genus in the present volume are:

Armiger crista (Linn.)
Armiger crista spinulosum (Clessin)
Armiger imbricatus (Müller)
Armiger annandalei (Germain)

Remarks. By the form of the penial complex this group is distinct from *Gyraulus* and should be considered as of full generic rank. L. Soos (1917) and A. Soos (1935) list it as a subgenus of *Gyraulus*, but the lack of a penial stylet removes it from that group. Lindholm (1926) considers it a genus. Thiele (1931) considers it a subgenus of *Anisus*. Odhner (1929, p. 30) gives the group full generic rank on the basis of the lack of a stylet on the verge which is characteristic of *Gyraulus*. A good figure of the verge of *Armiger crista*, showing the small penial papilla at one side of the sperm outlet, is shown (fig. 10). Haas (1929, p. 386) considers *Armiger* a distinct genus.

Odhner (1929, pp. 20, 21, 30) states his belief that *Armiger* represents a stage in the evolution of *Gyraulus*. He found young *Gyraulus borealis* of two whorls without a stylet on the verge while those of three and one-half whorls had a well-developed stylet. Specimens of *Gyraulus laevis* of three whorls had a stylet. From these observations he concludes that the development of the stylet (penisstachel) may be checked in the later fall, possibly through some unfavorable climatic condition. Haas, in a review of this work (1930, p. 20) does not fully agree with Odhner, believing that more study should be given the subject before conclusions are made. This is undoubtedly true, but the subject is one of great interest and dissections should be made of many species at different ages to determine whether the stylet is absent in young and immature *Gyraulus*. It has been present in all specimens personally examined, but these were either full grown or nearly full grown.

This group of small snails is highly variable specifically and a number of names have been bestowed upon the variations. Two forms appear distinct enough to rank as species, *crista* (Linn.), with strong ribs projecting from the shell, and *imbricatus* (Müller), in which no ribs project from the shell. *Armiger spinulosus* (Clessin) is probably a race of *crista* Linn. Another species in eastern Asia has been named *annandalei* by Germain.

The value of recognizing subgenera for these variations may be questioned seriously. In 1922, Dybowski and Grochmalachi erected three subgenera based on spiny variation in *Armiger: Nautiloarmiger*, *Cristoarmiger*, and *Atropoarmiger* (vide Lindholm, 1926, p. 24).

There appears to be some variation in the genitalia and also in the radula. Odhner found the formula to be 11-1-11 and 14-1-14 in *crista* from two localities and the writer obtained the formula 16-1-16 from *crista* collected in Poland. These differences may all be individual. The group merits additional anatomical study.

Genus TAPHIUS H. and A. Adams, 1855

Type by original designation *Planorbis andecolus* Orb.

1855. *Taphius* H. and A. ADAMS, Genera, II, p. 262. Type *Planorbis andecolus* Orb.
1870. *Taphius* DALL, Ann. N. Y. Lyc. Nat. Hist., IX, p. 351. Type *Planorbis andecolus* (H. and A. Adams, error for Orb.). As subgenus of *Planorbis*
1883. *Taphius* FISCHER, Man. de Conch., p. 507. Type *Planorbis andecolus* Orb. As section of *Planorbis*
1884. *Taphius* TRYON, S. and S. Conch., III, p. 106. Type *Planorbis andecolus* Orb. As subgenus of *Planorbis*
1886. *Taphius* CLESSIN, Syst. Conch. Cab., XVII, p. 33. Type *Planorbis andecolus* Orb. As subgenus of *Planorbis*
1899. *Taphius* MARTENS, Biol. Cent. Amer., Moll., p. 396. Mentions *Planorbis subpronus* Martens. As subgenus of *Planorbis*
1905. *Taphius* DALL, Alaska Moll., p. 81. Type *Planorbis andecolus* Orb. As synonym of *Helisoma*
1921. *Taphius* Germain, Rec. Ind. Mus., XXI, pp. 7, 62. Type *Planorbis andecolus* Orb. As subgenus of *Planorbis*
1924. *Taphius* PILSBRY, Proc. Acad. Nat. Sci. Phil., 86, p. 49, plate 4. Variation of *Planorbis andecolus* Orb.
1930. *Taphius* H. B. Baker, Oc. Papers, Mus. Zool. Univ. Mich., 210, p. 43. Monotype *Planorbis andecolus* Orb. As genus
1931. *Taphius* THIELE, Handbuch, Part 2, p. 479. Type *Planorbis andecolus* Orb. As section of *Planorbis*

Shell (plate 77, figs. 13-15). Sinistral, whorls few, rapidly increasing in diameter, the body whorl wide and much enlarged; spire greatly depressed below the level of the body whorl, the spire whorls bluntly angulate; umbilical side flattened; all the whorls visible and nearly in the same plane; aperture large, expanded; no lamellae within the aperture.

Animal. The characteristic of the animal and its anatomy have not been described.

Geographical Distribution. South and Central America from southern Mexico to Peru and Bolivia.

Species Considered as Valid. Only five species are here referred to *Taphius*.

Taphius andecolus (Orb.) Lake Titicaca, Peru
Taphius montanus (Orb.) Lake Titicaca, Peru
Taphius titicacensis (Clessin) Lake Titicaca, Peru
Taphius pronus (Martens) Venezuela
Taphius subpronus (Martens) Mexico

Geological Distribution. Not definitely known. *Taphius pronus* has been found fossil in Lake Valencia, Venezuela, probably of Pleistocene age.

Remarks. The systematic position of the genus *Taphius* is greatly in doubt because its anatomy is unknown. Some of the species, as *pronus* and *subpronus*, resemble certain species of *Tropicorbis* and *Taphius* may be another genus of Planorbidae peculiar to both Central and South America. Typical *andecolus* bears a striking resemblance to the typical group of *Helisoma* and Dall (1905) made *Taphius* a synonym of that group. Germain (1921) makes it a subgenus of *Planorbis* allied to *Helisoma*.

Pilsbry (1934, p. 47) associates *Taphius* with *Helisoma* and refers *Taphius pronus* to *Helisoma* together with *calodcrma*, but *pronus* certainly does not resemble any form of *Helisoma*, rather is it allied to *Tropicorbis*. What the group may be and where it may be placed can only be determined by an anatomical study. With our present limited knowledge, it seems best to regard *Taphius* as a genus related to *Tropicorbis*. An excellent account of the shell variation of *Taphius andecolus*, accompanied by a good plate, is given by Pilsbry (1924, p. 49, plate 4).

Genus TROPICORBIS Pilsbry and Brown, 1914

Type by original designation, *Planorbis liebmanni*
Dunker (= *Planorbis orbiculus* Morelet)

1880. *Gyrorbis* Fischer and Crosse, Études Moll. terr-fluv. Mex. et Guat., II, p. 70 (non *Gyrorbis* Fitz., 1833). Example *Planorbis orbiculus* Morelet.

1884. *Menetus* Tryon (non H. and A. Adams), S. and S. Conch., iii, p. 106. Example *Planorbis heloicus* Orb.

1899. *Planorbula* Martens (part), Biol. Cent. Amer., Moll., p. 398. Includes *Planorbis obstructus* Morelet and *Planorbis dentiens* Morelet, now referred to *Tropicorbis*.

1899. *Menetus* Martens (part) (non H. and A. Adams), op. cit., p. 390. Includes species now referred to *Tropicorbis*.

1914. *Tropicorbis* Pilsbry and Brown, Proc. Acad. Nat. Sci. Phil., 66, p. 212. Type *Planorbis liebmanni* Dunker. As section of *Planorbis*.

1921. *Tropicorbis* Germain, Rec. Ind. Mus., XXI, p. 91. Type incorrectly given as *Planorbis maya* Morelet. As subgenus of *Planorbis*.

1923. *Tropicorbis* Wenz, Fossil. Cat., Pars 22, p. 1627. Genotype *Gyraulus (Tropicorbis) liebmanni* (Dunker). As subgenus of *Gyraulus*.

1930. *Tropicorbis* H. B. Baker, Oc. Papers Mus. Zool. Univ. Mich., No. 210, p. 43. Type *Planorbis liebmanni* Dkr. As genus.

1931. *Tropicorbis* Thiele, Handbuch, IV, Teil 2, p. 480. Type wrongly stated to be *Planorbis maya* Morelet. As section of *Planorbis*.

1934. *Tropicorbis* Pilsbry, Proc. Acad. Nat. Sci. Phil., 86, p. 52. Type *Planorbis liebmanni* Dunker. As genus. Anatomy described.

1936. *Tropicorbis* F. C. Baker, Nautilus, 49, p. 104. Anatomy of *Planorbis obstructus* Morelet and *Planorbis havanensis* Orb. described. As genus.

1939. *Obstructio* Haas, Zool. Ser. Field Mus. Nat. Hist. XXIV, p. 99. Type by original designation *Planorbis janeirensis* Clessin. As subgenus of *Planorbis*.

1940. *Tropicorbis* F. C. Baker, Nautilus, LIII, p. 106. As genus.

1941. *Obstructio* Haas, Nautilus, 55, p. 31.

Shell. Of medium size, ultradextral, orbicular, of few whorls which may increase regularly in diameter (plate 77, figs. 7-9 *orbiculus*) or the body whorl may increase rapidly in diameter (plate 77, figs. 10-12, *pallidus*); whorls in view equally on both sides, somewhat overlapping on the left (spire) side; aperture unarmed or with one large parietal lamella with a small infraparietal below it, and four lamellae within the outer lip. The labial lamellae differ principally from those of the genus *Planorbula* in having the lower palatal lamella pointing slightly downward on the left side while in *Planorbula* this lamella always points upward, in the group *Haldemanina* the upward end forming a vertical and transverse lamella combined. The basal lamella in *Planorbula* is normally more massive and is, in some species, distinctly curved (plate 76, figs. 7, 8, 9).

Animal. When in locomotion the foot is rather long and narrow, rounded before and tapering to a point behind. The tentacles are very long and filiform and the eyes are large, black, and conspicuously placed at the inner base of the tentacles (plate 78, figs. 3, 4). The velar area is well developed. When at rest (plate 70, fig. 4, *Tropicorbis havanensis*) the foot may be hunched up, rounded, and even the tentacles may be drawn backward. The *Tropicorbis* group is noteworthy for the peculiar pigmentation observed in some species, this consisting of dark, blackish or brownish, markings which show plainly through the shell (plate 78, figs. 3, 4, *Tropicorbis nigrilabris* (Lutz)), and are particularly plain when the animal is removed from the shell (plate 12, fig. 5, *T. havanensis* (Pfr.)). These sometimes show on the base, through the shell, as dot-like markings (plate 70, fig. 4, *T. havanensis*).

ANATOMICAL CHARACTERISTICS

PLATE 12 (*Tropicorbis havanensis*)

GENITALIA. Male Organs (fig. 11). Seminal vesicle (SV) of greater diameter than the ovisperm duct. It is beset with numerous protuberances or glands many of which have the form of club-shaped diverticula. They vary in size anteriorly, the larger vesicles being nearer the ovotestis. The whole seminal vesicle is about 2 mm. long. The sperm duct is over 5 mm. long and is very narrow. It is peculiarly enlarged at the junction of the oviduct and sperm canal and might be considered a carrefour, but that feature is attached to the female system and is a small swelling into which the albumen duct enters (fig. 11, CF). See figs. 7, 8, CF.

The prostate (PRS) is very long (3.5 mm.) and bears about fifty short, sac-like diverticula. These are placed on a separate duct, the prostate duct, the free portion of which is very short and quickly joins the vas deferens. A cross section through the prostate (fig. 9, PD, SPD) shows the relationship between these two separate ducts. The vas deferens (VD) is moderately long (3.5 mm.) and is a small tube throughout its length except that it is slightly enlarged where it enters the vergic sac (fig. 1, VD).

The penial complex (fig. 11) is much elongated; the preputium (PR) is cylindrical and slightly longer than the vergic sac (VS). In another specimen (fig. 10) the preputium and vergic sac were more nearly equal in length and the upper part of the vergic sac was slightly enlarged. The vergic sac is always of less diameter than the preputium. The retractor muscles (RM) are somewhat complicated, there being three branches all connected by cross muscles. There are also several small muscles below the retractor muscles which are attached to the mantle and not to the columella muscle. These may be what we have called supporting muscles. There are several series of muscles on the opposite side of the penial complex which we have called supporting muscles (SM). These are attached to the upper part of the neck. The upper set, which have small branches, may also help in retracting the penial complex following coitus.

Internally (fig. 1) the preputium has two or more pilasters. There is a heavy muscular ring or diaphragm which separates the preputial cavity from the vergic space (fig. 1, D, fig. 2). This apparently takes the place of the papilla in *Gyraulus*, but there is no second ring below this ring, as there is in *Gyraulus*. The verge (V), very long and cylindrical, ends in a small papilla and the sperm canal has a central outlet (fig. 3). The walls of the vergic sac are thin but those of the preputium are rather thick.

Female Organs. The spermatheca (S) is pear-shaped and less than 1 mm. long. The spermathecal duct is longer than the spermatheca, very narrow, and enters the short vagina (VG) near the female opening. The uterus (U) is narrow and slightly longer than the spermatheca and its duct. The nidamental gland (NG) is long and narrow (about 3 mm. long) and of larger diameter than the uterus. The oviduct (OD) is about 2 mm. long and smaller in diameter than the nidamental gland but much wider than the sperm duct. The albumen gland is short, somewhat pear-shaped with large gland cells (fig. 6). It lies over the intestine, one loop of which passes through a trough-like space on the under side of the albumen gland. The junction between the oviduct, sperm duct, and ovisperm duct, together with the albumen gland connections, are shown in figs. 7 and 8.

Hermaphrodite Organs. The ovotestis (OT) consists of many club-shaped diverticula placed in a double row. The ovisperm duct is very short between the seminal vesicle and ovotestis but three times this length between the seminal vesicle and the oviduct. The duct is a narrow tube.

Two other species of *Tropicorbis* have been dissected by the writer. *Tropicorbis riisei* (Dunker) (plate 13, fig. 9) has twenty-four diverticula on the prostate and *Tropicorbis obstructus* (Morelet) has eighteen diverticula on its prostate. The penial complex is about the same in the three species. Some of the diverticula of the prostate are folded over at the end in *riisei* (figs. 4, 5). The retractor muscle complex is complicated in *riisei* but quite simple in *obstructus*. The spermatheca is rounder and less pyriform in *riisei* and *obstructus* and the ducts are longer than in *havanensis* (compare the figures). In *obstructus* a number of the diverticula of the ovotestis contained eggs almost ready to be discharged (plate 13, fig. 3). The junction of the prostate duct and the sperm duct to form the vas deferens is shown in fig. 8 (*riisei*).

Pilsbry (1934, p. 53) has figured the genitalia of *Tropicorbis pallidus* (C. B. Adams), from Bolivar, near Santa Marta, Colombia. This figure differs in a few respects from the genitalia of *riisei*, *havanensis* and *obstructus* as figured in this volume. There are twelve long and somewhat irregular diverticula on the prostate. The penial complex shows a very long and narrow vergic sac, considerably longer than the preputium. The verge appears as in the other species studied. There is one retractor muscle as in *obstructus*.

It is evident from the knowledge afforded by the four species of which the anatomy is known that there is considerable variation in the details of structure of the genus *Tropicorbis*. The prostate, particularly, may bear as many as fifty diverticula (*havanensis*) or as few as twelve diverticula (*pallidus*). The penial complex may have the vergic sac shorter than the preputium (*havanensis*) or much longer than the preputium (*pallidus*). There is complete agreement, however, in the long, narrow verge with terminal opening, the lobulate seminal vesicle, the long and narrow oviduct, nidamental gland, and sperm duct, and the rounded or pear-shaped spermatheca on a long duct. It is desirable that the genitalia of the type species (*orbiculus*=*liebmanni*) be known. It is believed to be like *havanensis*, a related species. Hundreds of shells of *orbiculus* have been seen but no material containing the animal has been available.

Respiratory and Renal Systems. The pseudobranch (of *havanensis*, plate 12, fig. 4) is a thin, leaf-shaped, fleshy organ doubled or folded upon itself. The rectum (R) lies above the pseudobranch and has a conspicuous crested ridge extending nearly its whole length, ending some distance above the anus. There is a large pneumostome (PS). In *riisei* (plate 13, fig. 10) the folded nature of the pseudobranch is better shown as is also the crested ridge. The crest is present in all species examined. Pilsbry's figure of the pseudobranch of *pallidus* (1934, p. 53, B) shows a simple folded pouch. In his figure C, the pseudobranch is figured as much elongated. This appears to be a pathologic condition.

The kidney (plate 46, fig. 11, *riisei*) is rather long (about 2.5 mm.), the ureter sharply reflected. A cross section near the middle (fig. 12) shows the kidney to be rounded with the lumen rounded, the two veins being at the lower corners of the section. There is no ridge on the kidney but there is a distinct vertical ridge in the mantle to the left of the kidney. A cross section of the kidney of *havanensis* (fig. 13) shows that in this species this organ is much more compressed and much wider than in *riisei;* the central lumen is irregularly oval with the two veins placed below the lumen at the outer ends of the section. Of *pallidus*, Pilsbry says 'The kidney is long, band-like, and flat, with no trace of a superposed ridge' (p. 52).

Digestive System. Stomach region with distinct division into crop, gizzard, and pyloris. There is a large blind sac. The intestine makes a backward loop around the liver and extends forward, the rectum ending near the pseudobranch. The digestive organs are alike in all species examined. The buccal sac is pyriform with a large and conspicuous radula sac which protrudes from the posterior end of the buccal sac as a rounded projection. This sac is longer in *obstructus* than it is in *riisei*. The salivary glands are cylindrical, longer than the buccal sac, and joined behind, as in other groups of the Planorbinae.

The jaw of *riisei* (plate 50, fig. 12) is composed of three pieces, a wide and low superior part, finely striated along the face, and two lateral pieces which assume the form of a question mark. These are enlarged at their junction with the superior jaw and taper to a point at the lower end. The jaw of *obstructus* is similar to that of *riisei* (fig. 11). H. B. Baker has described the jaws of *pallidus* and *kühnianus* (1930, pp. 47, 48). The jaws of *Tropicorbis* are unlike those of the other genera of Planorbinae (excepting *Australorbis*) and resemble those of the subfamily Helisomatinae.

The radula formula of *havanensis* (plate 68, fig. 8) is 19-1-19 or 20-1-20 with 109 to 112 rows of teeth. The central tooth has a broad base of attachment and is bicuspid, the cusps spade-shaped and reaching to the lower margin of the base of attachment. Laterals (1-6) squarish with three cusps, the entocone larger than the mesocone and ectocone. The 6th tooth has a small interstitial cusp on the entocone and two very small cusps above the ectocone. The 7th tooth is an intermediate, the entocone broken up into four small cusps and the ectocone with two small cusps on the outer edge above. The 8th to the 16th or 17th teeth are marginals (8, 10, 12), the reflections becoming very long and narrow, with an entocone of four or five small cusps, a single spade-shaped mesocone, and four to six or seven small cusps on the outer edge representing the ectocone. The marginal teeth become narrower toward the edge of the membrane. The outer three marginals are vestigial and are without denticulations. The central teeth of the different rows vary in width at the upper part of the tooth. The first thirty-four rows measure 5.4 microns, rows 35 to 89 measure 6 microns and rows 90 to 109 measure 5.4 microns. All central teeth examined exhibited this variation in width.

In *rüsei* (plate 68, fig. 6) the formula is 18-1-18 with 105 rows of teeth. The center tooth is like that of *havanensis* but the cusps do not reach the base of attachment. There are four lateral teeth. The 5th and 6th teeth are intermediate with interstitial cusps between the entocone and ectocone and small cusps above the ectocone (figs. 7, 5, 6). Seven to twelve are typical marginals with a variable number of small cusps, as in *havanensis*. The 15th to 18th teeth are vestigial. The center teeth vary in width as in *havanensis*, but the teeth are somewhat smaller.

In *obstructus* (plate 68, fig. 7) the formula is 19-1-19 and there are 124 rows of teeth. There are seven tricuspid laterals, the 8th tooth is intermediate, modified only on the entocone, and there are nine marginals becoming narrower toward the edge of the membrane. The outer marginals are vestigial. The center tooth varies in width as in the other species.

H. B. Baker (1930, plate 28, fig. 8) figures the radula of *pallidus* from Bolivar, Colombia. The formula is 18-1-18 with five laterals and there are 106 rows of teeth. The radula of *kühnerianus* is described on page 47 of the same paper. The formula is 19-1-19, with six laterals and 106 rows of teeth. Thus the radulae of five species of *Tropicorbis* are known; *havanensis*, which is nearest to *orbiculus* (=*liebmanni*), the type of the genus, *obstructus*, *rüsei*, *pallidus*, and *kühnerianus*. These cover fairly well the different variations of the species of the genus.

The material personally examined is as follows:

havanensis. New Orleans. Collected by Dr. E. C. Faust; 10 specimens
rüsei. Barceloneta, Puerto Rico. Collected by Dr. W. A. Hoffman; 12 specimens
obstructus. New Orleans. Collected by Dr. E. C. Faust; 10 specimens.

Geographical Distribution. The genus *Tropicorbis* is one of the most widespread of any group of American Planorbidae. From Louisiana and Texas in the United States, it extends southward through Mexico and Central America into South America as far south as the Argentine Republic, a distance of about 7,000 miles. The group is also found in many of the islands of the West Indies. In number of species represented, it outranks any other group of the family found in America except *Helisoma*, upward of thirty-three species and races being now recognized (see a later page for the list of species).

Geological Distribution. Oligocene or Lower Miocene to Recent time.

Remarks. The genus *Tropicorbis* presents some puzzling features of its anatomy which render its systematic position debatable. The nature of the prostate, with many diverticula in a single row, on a separate prostate duct, places the genus in the subfamily Planorbinae. The kidney is also like other members of this subfamily. The penial complex differs from that of *Anisus* and *Gyraulus* in lacking a penial stylet. The jaw is quite different and resembles this organ in Helisomatinae and Planorbulinae. The teeth of the radula also differ in having interstitial cusps on the intermediate and marginal teeth. Pilsbry (1934, p. 53) remarks that the group resembles *Gyraulus* but differs in the unarmed verge and the different jaw and marginal teeth. All points considered, it would seem that its place is with the Planorbinae, the largest number of characteristics agreeing with those of this subfamily.

Some of the species of *Tropicorbis* have been heretofore placed in the genus *Planorbula* because of the presence of lamellae within the aperture. These lamellae have the same general position in the two groups but the lower palatal lamella in *Planorbula* points upward while in *Tropicorbis* it points slightly downward. The basal lamella is also usually more massive in *Planorbula* than in *Tropicorbis* (plate 76, figs. 7, 8, 9). *Planorbula*, however, has a very different form of genitalia which removes it from the Planorbinae and places it, with *Menetus*, in a separate subfamily, Planorbulinae.

The relationship between the South American *Tropicorbis* and certain species in Africa is quite remarkable and has been emphasized by Pilsbry (1934, p. 54). Two African species (*adowensis* and *pfeifferi*) have been dissected and the genitalia are very similar to the same organs in *Tropicorbis*. The African forms may be placed in *Afroplanorbis* of Thiele, at least, until more is known about other species of the African fauna. This relationship is discussed at greater length under the description of the genus *Afroplanorbis*.

While the anatomy of the several group forms is similar, there are variations in the shell which seem to warrant a division of the genus into three subgenera or sections. These are indicated below.

Subgenus TROPICORBIS SS.

Type *Planorbis orbiculus* Morelet

Shell orbicular, the whorls increasing gradually in diameter, the last whorl not notably expanded. Apertural lamellae never present at any stage of growth.

Subgenus OBSTRUCTIO Haas, 1939

Type by original designation, *Planorbis janeirensis* Clessin

Shell orbicular, whorls increasing slowly in diameter. Aperture with lamellae during some stage of the growth of the shell (plate 76, fig. 7).

Subgenus LATEORBIS F. C. Baker, New Subgenus

Type *Planorbis pallidus* C. B. Adams

Shell with whorls rapidly increasing in diameter, the body whorl notably enlarged. Aperture never with lamellae.

Species Considered as Valid. The species and races believed to group under the three subgenera of *Tropicorbis* are tabulated below.

TROPICORBIS

orbiculus (Morelet)
maya (Morelet)
havanensis (Pfeiffer)
philippianus (Dunker)
heloicus (Orbigny)
tepicensis (Martens)
gracilentus (Gould)
peregrinus (Orbigny)
chilensis (Clessin)
meridaensis (Preston)
bourcardianus (Preston)
centimetralis (Lutz)
fieldi (Tryon)

OBSTRUCTIO

janeirensis (Clessin)
dentiens (Morelet)
dentiens cannarum (Morelet)
obstructus (Morelet)
obstructus donbilli (Tristram)
obstructus anodontus (Pilsbry)
dentiferus (C. B. Adams)
declivis (Tate)
paparyensis (F. Baker)
nigrilabris (Lutz)
albicans (Pfeiffer)

LATEORBIS

pallidus (C. B. Adams)
riisei (Dunker)
stramineus (Dunker)
petenensis (Morelet)
isthmicus (Pilsbry)
decipiens (C. B. Adams)
pedrinus (Miller)
canonicus (Cousin)
trigyrus (Philippi)

Genus AFROPLANORBIS Thiele, 1931

Type by original designation *Planorbis sudanicus* Martens

1885. *Menetus* Westerlund (non H. and A. Adams, 1855), Fauna Palaearc. Reg., V, p. 64. No type cited. As subgenus of *Planorbis*.

1902. *Menetus* Westerlund, Rad. Jugoslav. Akad., 151, p. 120. Type *Planorbis boissyi* P. and M. (non Adams, 1855).

1923. *Planorbulina* Germain, Rec. Ind. Mus., XXI, p. 179. Citation for *Planorbulina* Jickeli (1874) Fauna der Land und Süsswasser Mollusk Nord-ost-Afrika. Dresden, p. 221 ('pour la *Planorbis alexandrinus* Ehrenberg (*Segmentina* sous-genre *Planorbulina*)').

1925. *Planorbula* Connolly, Trans. Royal Soc. S. Africa, XII, p. 195 (non Haldeman). Anatomy of *Planorbis pfeifferi* Krauss.

1931. *Afroplanorbis* Thiele, Handbuch, Teil 2, p. 480. Type *Planorbis sudanicus* von Martens. As section of *Planorbis*.

1934. *Afroplanorbis* Pilsbry, Proc. Phil. Acad. Nat. Sci., 86, p. 55. Type *Planorbis sudanicus* von Martens.

1936. *Afroplanorbis* Haas, Abh. Sencken. Natur. Gesell., No. 431, p. 25. Type *Planorbis sudanicus* von Martens. As genus.

1939. *Planorbulina* Haas, Malac. Notes, Field Mus. N. H., Zool., XXIV, p. 100. Citation from Jickeli 1874, Nova Acta Acad. Leop. Carol., XXXVII, p. 221.

1939. *Biomphalaria* Connolly (part), Ann. South African Mus., XXXIII, part 1, p. 483.

1940. *Planorbulina* Haas, Nautilus, p. 33. States that citations from Jickeli's paper (1874) are erroneous, there being no reference to this name in the work mentioned, the name used being *Planorbula*. *Planorbulina* was used by d'Orbigny in 1826 in Foraminifera.

Shell (plate 81, figs. 2, 3). Small to medium size, orbicular, of few or many whorls which may be closely coiled or rapidly increase in diameter; usually flattened on both sides; aperture rounded, usually in the same plane as the last whorl, lips sharp, the aperture with or without lamellae.

Animal. Not observed.

ANATOMICAL CHARACTERISTICS

PLATE 71

GENITALIA. Male Organs (fig. 9, *Afroplanorbis pfeifferi* (Krauss)). Seminal vesicle occupying about half the length of the ovisperm duct, the glandular follicles short and projecting from the side of the duct. Sperm duct a narrow tube about as long as the ovisperm duct and seminal vesicle combined. Prostate short, composed of five main branches each of which branch again two to four times, thirteen diverticula showing at the upper or outer end of the prostate. From the figure the diverticula appear to be arranged in fan-like manner. There is but one series of diverticula but there is no indication of a separate prostate duct. The vas deferens is a long, fine duct, apparently as long as the sperm duct and ovisperm duct combined.

The penial complex has a sac-like preputium with a narrow retractor muscle attached to the summit near the junction of preputium and vergic sac. The vergic sac is a narrow tube, not much greater in diameter than the vas deferens. It is about as long as the preputium and appears from the figure to be slightly enlarged at the end. The features of the interior of the penial complex are neither figured nor described.

Female Organs. The spermatheca is an elongated pouch connected with the rather long vagina by a duct half as long as the spermatheca. The uterus swells behind the vagina to more than twice the diameter of the vagina. The nidamental gland is about as long as the uterus and is swollen to twice the diameter of the uterus. The oviduct is shorter than the uterus and rapidly narrows to meet the sperm duct. The albumen gland is a large, elongate-ovate organ, half as high as long.

Hermaphrodite Organs. Ovotestis apparently a double series of club-shaped diverticula. The ovisperm duct is very narrow and its free portion is about as long as the sperm duct. The seminal vesicle is placed nearer the ovotestis than observed in the species of *Tropicorbis* examined.

Pilsbry's figures of *Planorbis adowensis* Bourguignat (plate 71, figs. 10-12) are essentially the same in general generic characters as in *pfeifferi* described above. The prostate (fig. 10) shows about sixteen short diverticula which are unbranched. The penial complex (fig. 11) shows a wide, sac-like preputium and a slender vergic sac equal in length to the preputium. The retractor muscle is inserted at the junction of vergic sac and preputium. Internally (fig. 12) the preputium has three vertical pilasters and the verge is very long and slender. The spermatheca (fig. 10) is more pyriform than that of *pfeifferi* and the duct is longer.

The pseudobranch of *Planorbis pfeifferi* (fig. 7) appears to be folded as it is in *Tropicorbis*. The figure of the digestive system (fig. 8) shows a wide gizzard, a narrow and elongated pyloris, a narrow blind sac, and the intestine looped about the stomach. The salivary glands form a short loop behind the buccal sac.

The above anatomical notes are drawn from the papers of Connolly (1925) and Pilsbry (1934).

Geographical Distribution. *Afroplanorbis* appears to be distributed over northern and central Africa and to include a number of species.

Species Considered as Valid. The following are the species believed to be referable to *Afroplanorbis*. Other species may be added when their anatomy becomes known.

Afroplanorbis sudanicus (von Martens)
Afroplanorbis pfeifferi (Krauss)
Afroplanorbis alexandriensis (Ehrenb.)
Afroplanorbis boissyi (Pot. and Mich.)
Afroplanorbis salinarum (Morelet)
Afroplanorbis sudanicus tanganikanus (Bourg.)
Afroplanorbis bridouxianus (Bourg.)
Afroplanorbis adowensis (Bourg.)
Afroplanorbis ruppelli (Jickeli)

Geological Distribution. Not ascertained. The group is probably as old as *Tropicorbis*.

Remarks. The anatomy of *Afroplanorbis sudanicus* (von Martens) is unknown, but the shell so closely resembles that of *Afroplanorbis adowensis* (Bourg.) that they appear to be congeneric. Pilsbry (1934, p. 54) calls attention to the similarity of the shells. He also dissected *Planorbis adowensis* (his figures are copied on my plate 71) and found the anatomy to be very much like that of *Tropicorbis*. Connolly (1925, plate 8) figures the genitalia of *Planorbis pfeifferi* Krauss and his figure differs little from that of Pilsbry except in specific details. The branched diverticula of the prostate are believed to be attributed to faulty drawing rather than to real differences in structure. The chief difference between *Tropicorbis* and *Afroplanorbis* appears to be in the longer seminal vesicle of the latter, the smaller number of prostate diverticula, the greater size of the uterus and nidamental gland, and the greater difference in diameter between the preputium and vergic sac.

The African group would appear properly to take the name *Afroplanorbis* proposed by Thiele, preferably as a genus closely related to *Tropicorbis*. It has no relationship with *Planorbula* Haldeman which is purely an American genus belonging to a different subfamily. The close relationship between *Tropicorbis* of Central and South America and the African species here referred to *Afroplanorbis* is, as pointed out by Pilsbry (1934, p. 55), an interesting parallel in zoogeography. A similar relationship is found in the Ancylidae and in some groups of land shells.

In a recent work (1939, p. 483) Connolly uses the generic name *Biomphalaria* Preston for all of the African species once referred to *Planorbula*. However, the anatomy of the type of this genus, *smithi* Preston, is unknown and until that species has been examined anatomically it would seem unwise to use this name so inclusively. Should the anatomy prove to be like that of the two species here referred to the genus *Afroplanorbis*, *Planorbis adowensis* and *P. pfeifferi*, it would then take precedence over *Afroplanorbis* which would become a synonym of *Biomphalaria*. *Tropicorbis* appears to be generically distinct from the African species and can not be included in either *Afroplanorbis* or *Biomphalaria*, as suggested by Connolly (p. 484).

Genus SYRIOPLANORBIS F. C. Baker

New name for HETERODISCUS Westerlund, preoccupied. Type
Planorbis libanicus Westerlund, originally designated for HETERODISCUS

1902. *Heterodiscus* Westerlund, Rad. Jugoslav. Akad., 151, p. 120. Type *Planorbis libanicus* Westerlund. As subgenus of *Planorbis*. Non *Heterodiscus* Sharp, Insecta, 1886.

1905. *Heterodiscus* Dall, Alaska Moll., p. 83. Type *Planorbis libanicus* Westerlund. As section of *Planorbis*.

1931. *Heterodiscus* Thiele, Handbuch, Teil 2, p. 479. Type *Planorbis libanicus* Westerlund. As section of *Planorbis*.

'**Shell** n: t. media (d. 14 mm.), supra late profundeque concavo-umbilicata, subtus subplana, sub lente distincte spiraliter lineata, spira magna, utrinque orbiter subaequa, anfr. 5-6, primi lenti, ultimus subcylindraceus (typ. *Pl. libanicus* W.).' Westerlund, p. 120.

Original description of *Planorbis libanicus* Westerlund: 'Testa magnitudine mediocris, supra late profundeque concavo-umbilicata, infra subplana, nitida, cornea (subtus paullo pallidior), firma, laevigata, sub lente forti densissime at distincte spiraliter lineata; anfr. 5½-6, convexi, interiores utrinque perlente accrescentes, spiram magnum, subaequalem formantes, ultimus major, rotundatus, subcylindraceus, supra convexus, subtus pone suturam impressam obtusissime angulatus, extrorsum paullo planulatus; apertura oblique rotundato-lunaris, marginibus distantibus, disjunctis, basali oblique surrecto. Diam. 14, alt. ad apert. 5 mm.

'Hab. Mons Libanon (legit beat. Evers, Havniensis).

'Haec species forte typum novi subgeneris format, quod a subgen. Meneto differre videtur; Testa supra late concavo-umbilicata, infra subplana, sub lente tenue distincte spiraliter lineata, spira magna, utrinque subaeque lata.' Westerlund, Nach. Deutsch. Malak. Gesell., 1899, pp. 170-171.

Remarks. All of the information concerning this group name and its type species is given above. No specimens for figuring have been obtainable and no figure has been published, as far as known to the writer. Westerlund mentions in the description of the species (*libanicus*) that it differs from the subgenus *Menetus* and that it should become the type of a new subgenus, which he later calls *Heterodiscus*, which is unfortunately preoccupied.

In Westerlund's list of the subgenera of *Planorbis* (1902, p. 120), the type of *Menetus* is given as *Planorbis boissyi* P. and M., which is now placed in the genus *Afroplanorbis*, the type of *Menetus* being *Planorbis opercularis* Gould. The comparison of *Heterodiscus* with *Menetus* would indicate that the latter group was somewhat related to the African species and the Latin description would fit, in a measure, some species, as *adowensis* and *sudanicus*. The habitat of *Planorbis libanicus* is not so far removed from the African region as to preclude the possibility that this species might group with *Afroplanorbis*, hence the new name *Syrioplanorbis* (*Heterodiscus*) would become a synonym of *Afroplanorbis*. Only an examination of the animal of *libanicus* would positively settle this question.

Species Considered as Valid. *Syrioplanorbis libanicus* (Westerlund) is the only species attributable to this genus and, as indicated above, the validity of the generic concept is not wholly certain.

Genus BIOMPHALARIA Preston, 1910

Type by original designation *Biomphalaria smithi* Preston

1901. *Planorbia* J. E. S. MOORE, To the Mountains of the Moon, p. 260. Monotype *Planaria albertensis* J. E. S. Moore (non *Planaria* Brown, 1827, or Müller, 1776).

1910. *Biomphalaria* PRESTON, Ann. Mag. N. H. (8), VI, p. 535, plate ix, figs. 26, 26a. Type *Biomphalaria smithi* Preston. As genus.

1927. *Planaria* PILSBRY and BEQUAERT, Bull. Amer. Mus. N. H., LIII, p. 121. Monotype *Planaria albertensis* J. E. S. Moore.

1927. *Biomphalaria* PILSBRY and BEQUAERT, op. cit., p. 115. Monotype *Biomphalaria smithi* Preston. As synonym of *Planorbis* Müller.

1931. *Biomphalaria* THIELE, Handbuch, Teil 2, p. 479. As section of genus *Planorbis*. Type wrongly given as *Planorbis choanomphalus* von Martens.

1934. *Biomphalaria* PILSBRY, Proc. Phil. Acad. Nat. Sci., 86, p. 55. Type *Biomphalaria smithi* Preston.

1936. *Biomphalaria* HAAS, Abh. Secken. Natur. Gesell., No. 431, p. 25. Type *Biomphalaria smithi* Preston. As genus.

Shell (plate 81, fig. 4). Subdiscoidal, planulate with concave spire, last whorl very large; umbilicus open, but shallow; aperture gaping; labrum greatly receding below (Preston). The shell is ultradextral. Of this species Pilsbry says (1927, p. 120) 'The prominent character of this species is the deviation towards the left of the last half-whorl.' Viewed as a dextral species, the last part of the whorl drops below the periphery as in some specimens of *Gyraulus deflectus*.

Animal. The anatomy of the group is at present unknown.

Geographical Distribution. Lake Albert Edward, Belgian Congo, Africa. Only the type species is known. *Planorbis ruppelli* Dunker, *Planorbis choanomphalus* Martens and *Planorbis katangae* Haas, included in this genus by Haas (1936) appear to belong elsewhere. They do not have the characteristics assigned to *Biomphalaria*.

Species Considered as Valid. *Biomphalaria smithi* Preston is the sole representative of the genus here recognized.

Remarks. This genus is unknown anatomically and its true position in planorbid nomenclature can not be definitely assigned until the animal has been dissected. Pilsbry (1927, p. 120) suggests that it is a modification of the *Planorbis adowensis* type and might be placed in the same section of the genus *Planorbis*. In a later publication (1934, p. 55) this relationship is again emphasized. In both references by Pilsbry the suggestion is made that the shell might have been modified somewhat after the manner of *Taphius*. The shells as figured by Pilsbry (1927, p. 121, reproduced on plate 81 of this work) are strongly suggestive of *Taphius*, and *Biomphalaria* might bear the same relationship to *Afroplanorbis* that *Taphius* bears to *Tropicorbis*. Its best place in classification at present appears to be near *Afroplanorbis* as a distinct genus.

Genus AUSTRALORBIS Pilsbry, 1934

Type by original designation *Planorbis guadaloupensis*
Sowb. = *Planorbis glabratus* Say

1883. *Menetus* Fischer, Man. de Conch., p. 509. Type *Pl. guadaloupensis* Sowb. (non H. and A. Adams, 1855). As section of *Planorbis*

1899. *Menetus* Martens, Biol. Cent. Amer., Moll., p. 390 (non H. and A. Adams, 1855). Martens gives no type but says subgenus is peculiar to South America and mentions *Planorbis cumingianus* Dkr., and *Planorbis guadaloupensis* Sowb. as examples

1905. *Planorbina* Dall, Alaska Moll., pp. 81, 84. Type by original designation *Planorbis olivaceus* Spix (non *Planorbina* Haldeman, 1843). As section of *Planorbis*

1918. *Planorbina* Walker, Miscel. Pub. Mus. Zool., Univ. Mich., No. 6, pp. 11, 94. Type *Planorbis olivaceus* Spix (non *Planorbina* Hald, 1843). As section of *Planorbis*

1921. *Planorbina* Germain, Rec. Ind. Mus., XXI, pp. 6, 41. Type *Planorbis guadaloupensis* Sowb. (non *Planorbina* Haldeman, 1843). As subgenus of *Planorbis*

1923. *Planorbina* Wenz, Fossil. Cat., pars 22, p. 1482. Genotype *Planorbis guadaloupensis* Sowb. (non *Planorbina* Haldeman, 1843). As genus and subgenus

1930. *Planorbina* H. B. Baker, Oc. Papers, Mus. Zool., Univ. Mich., No. 210, p. 43. Type *Planorbis olivaceus* Spix (non *Planorbina* Haldeman, 1843). As genus

1931. *Planorbina* Thiele, Handbuch, Teil 2, p. 480. Type *Planorbis olivaceus* Spix (non *Planorbina* Haldeman, 1843). As section of *Planorbis*

1934. *Australorbis* Pilsbry, Proc. Acad. Nat. Sci. Phil., 86, p. 55. Type *Planorbis guadaloupensis* Sowb.(= *Planorbis glabratus* Say). As genus

1938. *Australorbis* Martins, Contribuição ao estudo do genero *Australorbis* Pilsbry, 1934. On p. 47 lists Brazilian species of this and other genera. Some of the species listed belong to *Tropicorbis*

1940. *Australorbis* Scott, Notulae Naturae, No. 54, p. 9. As genus.

Shell (plate 77, figs. 29-31, *Australorbis glabratus* (Say)). Large, biconcave, smoothish, of slowly widening whorls which are rounded or angular laterally (Pilsbry, p. 55). The shell is sinistral.

Animal. Resembling *Tropicorbis* in general form. The color is grayish or blackish, the mantle mottled with brown or cinnamon.

ANATOMICAL CHARACTERISTICS

PLATE 9 (*Australorbis glabratus*)

GENITALIA. Male Organs (fig. 10). The seminal vesicle (SV) is 3 mm. long and is an enlargement of the ovisperm duct on which there are many elongated follicles placed laterally. For a distance of 2 mm. behind and 4 mm. in front of the seminal vesicle there are numerous nodes which are probably continuations of the seminal vesicle. The sperm duct (SPD) is a very long and narrow tube (29 mm. long) of the same caliber throughout. The prostate is 8 mm. long and is composed of twenty-three or twenty-four diverticula, the two or three anterior diverticula single and unbranched and the three posterior diverticula bifurcate. The others, eighteen in number, have three main branches from a single stem, each branch again dividing two or three times, the secondary diverticula being of unequal length. All diverticula arise from the sperm duct in a single series, not in multiple series, as in *Helisoma*. A single branched diverticulum is shown in fig. 6. The diverticulum enters the sperm duct directly and is not placed on a separate duct as in *Tropicorbis*. The vas deferens (VD) is a narrow tube about 10 mm. long, of less diameter than the sperm duct.

The penial complex (fig. 10) consists of an elongated, cylindrical, sac-like preputium (PR), about 4 mm. long and 0.7 mm. wide and of about the same diameter throughout its length. The very narrow vergic sac (VS) is 3 mm. long or slightly shorter than the preputium. It is not much greater in diameter than the vas deferens. There is a rounded enlargement of the vergic sac at the end receiving the vas deferens. There are several sets of muscles. A wide retractor muscle (RM) composed of several smaller branches, is attached to the upper part of the preputium and to the columellar muscle. On the same side of the preputium there is a wide muscle about midway of its length and two smaller muscles near the male opening which appear to be supporting muscles since they are attached to the mantle above the penial complex. On the opposite side of the preputium there is a narrow muscle attached to the upper part near the insertion of the vergic sac, and a very wide muscle or set of small muscles which are attached to the roof of the mantle cavity and are presumed to be supporting muscles (SM). Some of these may aid in retracting the penial complex after coitus.

Internally (fig. 9) there are two wide, heavy pilasters in the preputium tapering to a point at the upper part of the preputial space. The space between the pilasters is marked by many cross muscles forming a reticulated pattern (PL). There is a flattened muscular ring or diaphragm (D). The verge (V) is long and very narrow. It tapers to a point and the sperm canal is placed at the center (fig. 5). There is no penial papilla.

Female Organs. The spermatheca is pear-shaped (S) and the duct (SD) is narrow and as long as the spermatheca. Both gland and duct measure a trifle more than 3 mm. in length. The vagina (VG) is very short and wide. The uterus is the same width as the vagina and gradually enlarges in diameter to meet the nidamental gland (NG) which is very long and wide (about 8 mm. long, 1.5 mm. wide). A part of the uterus projects behind the nidamental gland for several millimeters. The oviduct (OD) is a narrow tube extending from the ovisperm duct backward. It is about twice the diameter of the sperm duct and is about 18 mm. in length. There is a rounded carrefour (CF) extending from the oviduct to which the duct of the albumen gland is attached. The albumen gland (fig. 8) is rectangular in form and is composed of large follicles. The space for the passage of the intestine (IN) is quite conspicuous.

Hermaphrodite Organs. The ovisperm duct (SO) is very long (17 mm.) and is a simple tube except for the portion occupied by the seminal vesicle. The ovotestis is composed of multiple diverticula as seen in situ (fig. 10, OT). In cross section (fig. 4) the ovotestis appears to consist of a main diverticulum (fig. 1) upon which a number of short diverticula are attached (2). The organ is not multiple in the same sense that *Helisoma* is, which is observed to be fan-shaped in section. Several of the diverticula contained one large ovum ready for expulsion.

The above description agrees substantially with that of Pilsbry (1934, p. 55). The spermathecal duct in the specimens examined was not short, as Pilsbry found it, and, therefore, the spermatheca was not really adnate. The vergic sac, also, is almost as long as the preputium in the specimens examined. With these exceptions the genitalia of *glabratus* (*guadaloupensis*) here figured are like the figures of the race *christopherensis* given by Pilsbry on page 57. The figure by Scott (1940, p. 10) agrees with the specimens personally dissected, especially in the form of the spermatheca.

Respiratory and Renal Systems. The pseudobranch is rather long and rounded. A frilled crest or ridge extends down the center of the rectum (R) which it crosses as a simple ridge to the anal opening (A) and extends across the pseudobranch to the lower edge. There is a large pneumostome (PS).

The kidney (plate 45, fig. 1) is long and narrow (16 mm. long, 2.5 mm. wide). The ureter is nearly 2 mm. long and is a narrow tube directed upward at a right angle from the kidney. The veins are very large. The pericardium is 3 mm. long and 2 mm. wide. A low, wide ridge extends from below the pericardium to the lower end of the kidney.

Cross sections show several interesting features. The position of each section is shown at A, B, C, D, E, in fig. 1. Section E (fig. 7) through the pericardium shows a large lumen nearly filling the entire section, containing many glandular diverticula. There are no veins. In section D (fig. 8) the lumen is smaller, rather squarish in shape, with the pulmonary vein (AP), large and round, on one side and the renal vein (RA), smaller and oviform, on the other side. The low ridge is seen at the left. In section C (fig. 9) the lumen is somewhat smaller and there is the same disparity in size between the two veins. The ridge (RK), though wide, is higher than in section D. In section B (fig. 10) the lumen is much smaller, the veins still disproportionate in size and the ridge very wide, but low, and projecting over the left margin. In section A (fig. 11) near the base of the kidney, the whole organ is seen to be flattened, the lumen very small, the veins flattened, more nearly equal, and the ridge wide, flattened, and projecting over the left margin. The form of the long ridge to the left of the kidney is shown at the left in this section (RD). The ridge is a very characteristic feature in the kidney of *Australorbis*.

Digestive System. The stomach region (plate 48, figs. 9, 10) resembles that of *Promenetus*, the gizzard rather rounded, not flattened, the pyloris long and the blind sac rather short and placed as in *Helisoma*. The intestine makes a loop around the stomach and another loop around the liver, then runs forward to the rectum which bears a plaited crest or ridge (plate 48, fig. 9).

The buccal sac is short and high, not much elongated. The radula sac or pouch is large and rounded, somewhat as in *Tropicorbis*. The salivary glands are narrow and nearly three times as long as the buccal sac. They are joined behind as in *Helisoma*.

Jaws three in number as in *Tropicorbis* (plate 50, fig. 13). The superior jaw is very high, the length being about three times the height. It is finely striated on its anterior face. The side jaws are much shorter than the width of the superior jaw and are very narrow. The side jaws are shorter in comparison with the length of the superior jaw than in most species of Planorbidae. The figure on plate 50 agrees with that by Pilsbry (1934, p. 57).

The radula formula is 31-1-31 to 33-1-33 with 182 rows of teeth (plate 68, fig. 5). The center tooth (60) is wider than high, the lower outer corners of the base of attachment expanded to the extent that the base is twice as wide as the summit of the tooth. There are two sharp, spade-shaped cusps which extend below the lower margin of the base of attachment. Lateral teeth (1-13) asymmetrical, tricuspid, the cusps sharp, subequal, and extending below the base of attachment. The intermediate teeth (14-15) differ from the lateral teeth in having either an extra interstitial cusp between the ectocone and mesocone (14) or an interstitial cusp as in 14 and an extra cusp above the ectocone. Marginal teeth (16-26) elongated, oblique, the mesocone remaining a large sharp cusp, but the entocone splitting into three to five small, subequal cusps arranged obliquely. The ectocone continues as a large cusp but above it, on the margin of the tooth, there are three to six very small cusps in addition. The ectocone is always separated from the mesocone by a distinct gap. The small cusps above the ectocone are placed higher up on the tooth than in other genera. The outer marginals are very narrow and oblique and the cusps appear as minute serrations. Even here, however, the two groups of cusps, mesocone and ectocone, are separated by a considerable space.

Pilsbry (1934, p. 55) figures the radula of the race *christopherensis* which agrees in all essential details with the figures on plate 68. He gives the formula as 30-1-30 with seventeen laterals. In specimens personally dissected the marginals began on the 16th tooth in two specimens and on the 18th tooth in one specimen, the 15th to 17th teeth being intermediate in character. These differences are unimportant.

Scott (1940, pp. 10-12) figures the radula of specimens from Caracas, Venezuela, and Puerto Rico, showing great variation in the form of the cusps. The Venezuela form with a formula of 45-1-45 may be representative of the race *olivaceus*.

The material used for this anatomical study was received from Dr. Wm. A. Hoffman and was collected at Lares, Puerto Rico.

Geographical Distribution. Except for its occurrence in Haiti, Puerto Rico, and the Caribbean islands, *Australorbis* is a South American group (Pilsbry). It is known in South America from Venezuela southward to Argentine Republic.

Species Considered as Valid. Many names have been given to variations within this genus and consequently there are many synonyms. The following species and races appear to be recognizable:

Australorbis glabratus (Say) (= *guadaloupensis* Sowb.)
Australorbis glabratus christopherensis Pilsbry
Australorbis glabratus olivaceus (Spix and Wagner)
Australorbis glabratus refulgens (Dunker)
Australorbis glabratus lugubris (Wagner)
Australorbis glabratus blauneri (Germain)
Australorbis antiguensis (Sowerby)
Australorbis immunis (Lutz)
Australorbis bahiensis (Dunker)
Australorbis tenagophilus (Orbigny)

Geological Distribution. This genus probably dates from the Oligocene or Miocene period of the West Indies and South America.

Remarks. *Australorbis* is so peculiar in certain of its anatomical characteristics as to puzzle the systematist regarding its proper position in the classification of the family Planorbidae. In its narrow penial complex without penial gland it is related to *Tropicorbis*. The prostate, however, is very different from any member of the Planorbinae and superficially resembles some of the Helisomatinae in the presence of multiform diverticula. The ovotestis is also of a multiform nature. The prostate diverticula are also attached directly to the sperm duct instead of to a separate prostate duct as is the case in *Tropicorbis*. In this respect, the prostate of *Australorbis* resembles that of the genus *Drepanotrema*, the few diverticula in this group being attached directly to the sperm duct. The kidney is of the *Helisoma* type, with a distinct ridge.

In spite of the multiple nature of the diverticula of the prostate and ovotestis, the group appears to be related to *Tropicorbis* and to be correctly placed in the subfamily Planorbinae. The absence of a penial gland removes it from Helisomatinae and Planorbulinae and the absence of a flagellum, and also the form of the shell (with overlapping whorls), excludes it from the subfamily Segmentininae. When the characteristics of the prostate are closely examined it is seen to be uniserial in form in spite of the branched nature of the diverticula. Each diverticulum arises from the sperm duct as a single tube, the branching taking place after the diverticula are above the sperm duct. So also in the ovotestis, each diverticulum arises from the ovisperm duct as a single tube, the branching being on one side only.

In the Helisomatinae, both the prostate and the ovotestis have the diverticula radiating from the ducts like the spokes of a wheel, in fan-formation. The ridged kidney is an exception in the Planorbinae. This characteristic, as well as the apparent multiple appearance of the prostate and ovotestis, may show ancient affinities with the Helisomatinae. *Australorbis* is apparently an aberrent genus of the family.

Pilsbry has suggested (1934, p. 56) that it might be considered a subgenus of *Tropicorbis* but this procedure would appear untenable because of the peculiar prostate and ovotestis as well as the ridge on the kidney. Pilsbry did not examine the ovotestis or the kidney.

The name *Planorbina* Haldeman was used for this group by Dall in 1905, the Brazilian species *Planorbis olivaceus* Spix and Wagner being designated as the type. Germain, in 1921, selected *Planorbis guadaloupensis* Sowb., as type of *Planorbina*. But as Pilsbry states in his description of *Australorbis*, neither *olivaceus* nor *guadaloupensis* answer to Haldeman's description 'whorls numerous, nearly equal,' the whorls in these species increasing in diameter to such an extent that the last whorl is notably wider than the preceding whorl. Haldeman's *Planorbina* is now considered a synonym of *Anisus*. Pilsbry's discussion of the reasons for rejecting the types proposed for *Planorbina*, for which no type was designated by Haldeman, by Dall or Germain are well stated and do not need to be repeated here.

Genus ANISOPSIS Sandberger, 1875

Type herein nominated *Planorbis calculus* Sandberger

1875. *Anisopsis* SANDBERGER, Land und Süssw. Conch. der Vorwelt, p. 958. No type cited

1905. *Anisopsis* DALL, Alaska Moll., p. 81. *Planorbis loryi* Coq., and *Planorbis calculus* Sandb. cited as examples

Shell (of *Anisopsis calculus* (Sandberger), plate 81, fig. 10). 'Testa calculiformis, superne excavata, inferne latissime umbilicata. Anfractus 3½, gracilis, quadrangulates, superne excavati, ad margineum superum necnon ad umbilicum carina cincta, suturis tenuibus profundis disjuncti, costulis transversalibus subtilibus ornati, ultimus permagnus, spiram eminens (Sandberger, p. 14). Taf. 1, fig. 7, 7a (stark vergrössert).'

The shell is ultradextral, with a distinct, sharp carina in the middle of the whorls on the right side. The left side also has carinated whorls. The whorls are few in number, increasing rather rapidly in diameter. From the figures there appears to be a carina at the periphery.

Horizon and Distribution. Middle or brown Jurassic period. Cajac, in layers e and f. Very rare.

Remarks. The name *Anisopsis* appears to be a nude name, no type having been formally designated for it, as far as the writer is aware. It also appears to have been comparatively unnoticed by recent students of the Mollusca. The only American reference observed is that by Dall in 1905, who cites *Planorbis loryi* Coq., and *Planorbis calculus* Sandb. as examples. The original reference is in a stratigraphic table on page 958 of Sandberger's work in which *Anisopsis* appears between *Bathyomphalus* and *Anisus*. The only valid reason for associating the two species mentioned above with *Anisopsis* is the presence of the stars in the Middle (Mittlerer) Jura and the Upper (Oberer) Jura in the table, indicating that these two species are the ones intended for this group name, since no others from these horizons occur in the body of this work.

Planorbis calculus Sandberger occurs first on page 14 and should be taken as the type of *Anisopsis*. On page 15 Sandberger mentions the likeness of this species to the tricarinate Valvatas of North America typified by *Valvata tricarinata*. The figure of this species does look much like *Valvata tricarinata* on the right side but on the left side the figure is too wide, lacking the distinct carina and deep umbilicus of the American *Valvata*. Dall (1905, p. 81) suggests its relationship to *Helisoma* but the left side is different from any species of that genus known. The exact size is not given by Sandberger, who states that the figure is much enlarged.

The second species, *Planorbis loryi* Coquand (Sandberger, p. 41) is more planorboid in form and somewhat different in shape from *calculus* (see plate 81, fig. 11). It is also larger. Sandberger suggests its resemblance to *Planorbis complanatus* (Linn.) (=*fontanus* Lightfoot) and *Planorbis carinatus* Müller, but the figures do not resemble either of these species. Sandberger's description of this species is as follows: 'Testa calculiformis, superne profunde excavata, inferne depressa, latissime umbilicata. Anfractus quinque, gracilis, costulis transversalibus tenuibus muniti et carinis duabus acutis insignes, prima partem superam excavatam, altera basin cingente. Apertura trapezoidea, valde iniquilateralis.'

The horizon and localities for this species are given as follows by Sandberger (p. 41): 'Villers le Lac (physaschicht b), les Rousses, Charix bei Nantuar, Alfermé und Vigneules am Bieler See in den gleichen Schichten.' These localities are in the Upper or White Jura.

The group *Anisopsis*, which may be designated as a genus of the subfamily Planorbinae, may be retained to contain these early fossil species. The two species referred to this genus may not be congeneric, *loryi* appearing more like some of the species of *Planorbis* or *Anisus*. Many of the names of groups of the Planorbidae have been used rather loosely by European writers. Sandberger, for example, lists the subgenera *Menetus, Helisoma*, and *Carinifex* among the European fossils, groups which we now know are confined to America and have no representatives outside the Western Hemisphere. All of the extinct Planorbidae, both American and European, are badly in need of a thorough taxonomic revision.

Species Considered as Valid. *Anisopsis calculus* (Sandberger), the genotype, is the only species unquestionably assigned here. The assignment of *Planorbis loryi* Coquand seems indefensible.

Subfamily SEGMENTININAE F. C. Baker, New

The prostate diverticula are simple sacs placed in a single row along a prostate duct as in the subfamily Planorbinae. The penial complex has one or two flagella placed at the end of the vergic sac and in addition several genera have a penial gland in the preputium. The jaw is fragmented as in Planorbinae. The radula teeth are modified by additional cusps or by the presence of many interstitial cusps. The kidney is without a ridge.

Type genus *Segmentina* Fleming.

The groups included in this subfamily are as follows:

With penial gland but without duct: *Segmentina, Hippeutis, Pingiella*.
With penial gland and an external duct: *Intha*.
Without penial gland: *Polypylis, Drepanotrema, Acrorbis*.
With long flagella: *Pingiella, Polypylis, Intha*.
With short flagella: *Segmentina, Hippeutis, Acrorbis*.
With both long and short flagella: *Drepanotrema*.
With lamellae or barriers within the aperture: *Segmentina, Polypylis, Trochorbis*.
Without lamellae or barriers within the aperture: *Hippeutis, Helicorbis, Pingia, Intha, Drepanotrema, Platytaphius, Acrorbis*.

Several groups have not been examined anatomically and their position is doubtful. Such are *Helicorbis, Trochorbis*, and *Platytaphius*. The fossil group *Paraplanorbis* must, of course, be placed by shell characters alone.

Genus SEGMENTINA Fleming, 1817

Monotype *Nautilus lacustris* Lightfoot = *Planorbis nitidus* O. F. Müller

1817. *Segmentina* Fleming, Edinburgh Encyclopedia, Conchology, ed. VII, Vol. XII. Monotype, *Nautilus lacustris* Lightfoot = *Planorbis nitidus* O. F. Müller

1818. *Segmentina* Fleming, Supplement to 4-6th ed. Encyc. Brit., III, 'Conchology,' p. 309. Type *Nautilus lacustris* Lightfoot

1819. *Hemithalamus* Leach, Moll. Brit. Synop. (proofs), p. 137

1831. *Hemithalamus* 'Leach' Turton, Man. Land Fresh-water Shells Brit. Isl., p. 116. In synonymy of *Segmentina nitida* O. F. Müller

1833. *Hemithalamus* Fitzinger, Syst. Verz. p. 110

1840. *Segmentaria* Swainson, Treat. Malac., p. 337. Lapsus for *Segmentina*. As subgenus of *Planorbis*

1842. *Segmentina* Haldeman, Mon. Fresh-water Univ. Moll., U. S., p. 14. No type cited. As subgenus of *Planorbis*

1847. *Segmentina* Gray, Proc. Zool. Soc., p. 509. Type *Nautilus lacustris* Lightfoot. As genus

1847. *Discus* Gray, Proc. Zool. Soc., p. 509. No type cited. As synonym of *Segmentina*

1850. *Segmentina* (part) Stein, Schnecken u. Musch. Berlins, p. 78. *Segmentina* x *Hippeutis*

1855. *Segmentina* Moquin-Tandon, Hist. Moll. Terr. Fluv. France, II, pp. 423, 424. Type *Planorbis nitidus* Müller. As genus

1865. *Segmentina* Binney, L. and F-W. Shells N. A., II, p. 136. No type cited. As genus

1867. *Appendicularia* (part) Ficinus, Zeits. für gesamm. Naturw., XXX, p. 363

1870. *Segmentina* Dall, Ann. N. Y. Lyc. N. H., IX, p. 352. Type *Planorbis lacustris* Lightfoot. As genus

1883. *Segmentina* Fischer, Man. de Conch., p. 509. Type *Planorbis nitidus* Müll. As subgenus of *Planorbis*

1884. *Segmentina* Tryon, S. and S. Conch., III, p. 107. Type *Segmentina lacustris* Lightfoot. As genus

1885. *Segmentina* Westerlund, Fauna Pal. Reg., V, p. 85. No type cited. As subgenus of *Planorbis*

1886. *Segmentina* Clessin, Syst. Conch. Cab., ed. 2, XVII, p. 34. Type *Planorbis nitidus* Müller. As genus

1902. *Segmentina* Westerlund, Rad. Jugoslav. Akad., 151, p. 121. Type *Planorbis nitidus* Müller. As subgenus of *Planorbis*

1905. *Segmentina* Dall, Alaska Moll., p. 97. Type *Planorbis nitidus* Müller. As genus

1912. *Segmentina* Hannibal, Proc. Mal. Soc. Lond., X, p. 154. Type *Planorbis nitidus* Müller. As subgenus of *Planorbis*

1915. *Segmentina* Preston, Fauna Brit. India, Moll. FW. Gast. and Pelec., p. 124. Type *Planorbis nitidus* Müller. Includes species now referred to *Helicorbis, Trochorbis*, and *Polypylis*

1917. *Segmentina* L. Soos, Ann. Hist. Nat. Musei Hungarici, XV, pp. 140, 142. Type *Planorbis nitida* Müller. As genus

1918. *Segmentina* Walker, Miscel. Pub., Mus. Zool., Univ. Mich., No. 6, p. 13. Type *Nautilus lacustris* Lightfoot. As genus

1919. *Segmentina* Annandale and Prashad, Rec. Ind. Mus., XVIII, p. 56. Type *Planorbis nitidus* Müller. As genus

1921. *Segmentina* Germain, Rec. Ind. Mus., XXI, p. 163. Type *Planorbis nitidus* Müller. As genus

1923. *Segmentina* Wenz, Fossil. Cat., pars 22, p. 1661. Genotype *Segmentina lacustris* (Mantagu). As genus

1926. *Segmentina* Lindholm, Archiv. für Mollusk., 58 year, Heft 6, p. 252. Monogenotype *Nautilus lacustris* Lightfoot (=*Planorbis nitidus* Müller). As genus

1926. *Segmentina* Kennard and Woodward, Syst. Brit. Non-Marine Moll., p. 89. Type *Planorbis nitidus* Müller. As genus

1927. *Segmentina* Pilsbry and Bequaert, Bull. Amer. Mus. N. H., LIII, p. 128. Type *Planorbis nitidus* Müller. As genus

1929. *Segmentina* Haas, Trab. Museo Cien. Nat. Barcelona, XIII, p. 388. Type evidently *Planorbis nitidus* Müller. As genus

1931. *Segmentina* Germain, Moll. Terr. Fluv. France, II, p. 542. Type *Segmentina nitida* (Müller). As genus

1931. *Segmentina* Thiele, Handbuch, Teil 2, p. 481. Type *Anisus (S.) nitidus* (Müller). As subgenus of *Anisus*

1935. *Segmentina* A. Soos, Allat. Kozlem., XXXII, p. 29. As genus

Shell (plate 79, figs. 1-3). Small, ultradextral, smooth, and glossy; whorls few, notably overlapping the body whorl embracing most of the preceding whorls, causing the preceding whorl to project far within the width of the aperture; periphery rounded or carinated. Cavity of the last whorl restricted by several barriers, each set usually composed of three large transverse lamellae, parietal, basal, and palatal. There may be other smaller lamellae (plate 76, fig. 4). The internal lamellae are composed of enamel-like substance. The embryonic whorls have spiral rows of small pits.

Animal. With a short foot, rounded in front, pointed behind; tentacles filiform, enlarged at the base, the eyes sessile at their inner bases. Edge of mantle thickened. The color of the animal is brownish black much paler when immature.

ANATOMICAL CHARACTERISTICS

PLATES 2 and 3

GENITALIA. Male Organs (plate 3, fig. 2). Seminal vesicle sac-like, about three times the diameter of the ovisperm duct with several protuberances near the posterior end. It is about 2 mm. long. Sperm duct long (4.5 mm.) and of small diameter. Prostate moderately long (1.7 mm.) with twenty-two to twenty-five club-shaped diverticula of varying lengths, placed on a separate prostate duct, which joins the sperm duct to form the vas deferens. The free portion of the prostate duct is about 0.7 mm. long and of larger diameter than the sperm duct. In the specimens examined the posterior end of the prostate duct is free of diverticula for about 0.3 mm. The vas deferens is of medium length (about 3 mm.) and of small diameter. A cross section through the prostate and sperm duct shows the relative position of these parts of the animal (plate 3, fig. 3).

The penial complex (plate 3, fig. 1) is very long (about 3 mm.). The preputium (PR) occupies half of the length of the complex and is elongate-pyriform in shape, the upper part swollen. The vergic sac (VS) is very long and narrow, almost tube-like, and is as long as the preputium. There are two short, narrow flagella (FL) at the end of the vergic sac at the point of insertion of the vas deferens. There is a single, rather wide retractor muscle, but no supporting muscles.

Internally (plate 2, fig. 2) the preputium presents some striking features. There is a single heavy ridge on one side (plate 2, fig. 1) which extends vertically up a large portion of the preputium and is in the nature of a pilaster (PL). This ridge merges into a long, sac-like glandular organ which is reflected toward the base or opening of the preputium (SB). This penial gland has a shallow cup, the bottom of which is paved with small protuberances resembling pavement (plate 2, fig. 3), the fleshy sides rolled upward. In cross section this gland presents the appearance shown in fig. 4 of plate 2. On the right side of the preputium there is a long, very narrow pilaster which extends the whole length of the preputium from the external opening upward to the muscular ring (D) separating the preputium from the vergic sac. The large gland is free from attachment to the wall of the preputium and is connected only with the large left pilaster.

The verge (V) is long and very narrow. At its distal end it bears a fleshy papilla (plate 2, figs. 5, 6, PA) which is also long and narrow. This papilla is an extension of the verge only from one side, the sperm canal (SC) being in the center of the verge at the end, as shown in the figures.

Female Organs. The spermatheca (plate 3, fig. 2) is long and sac-like and is attached to the vagina by a long narrow duct which is somewhat longer than the spermatheca. The spermatheca is constricted about midway of its length. The vagina is narrow and about 0.5 mm. in length. The uterus is about twice the diameter of the vagina and is a trifle over 1 mm. in length. The nidamental gland is very long (about 3 mm.), sac-like, and envelops the uterus. The oviduct is about half the diameter of the nidamental gland and about 1.5 mm. long. The albumen gland is rather small and oval in shape.

Hermaphrodite Organs. The ovotestis (plate 3, fig. 2) consists of relatively few (less than twenty) large club-shaped diverticula. They are placed in a double row on the ovisperm duct. The ovisperm duct between seminal vesicle and ovotestis is very short, but anteriorly, between the seminal vesicle and the oviduct, it is a long (2 mm.), narrow tube.

The figures on plates 2 and 3 agree in the main with those already published by European malacologists. L. Soos's figure (1917, p. 44, fig. 17) is the same, showing the few large ovotestis diverticula, the elongated spermatheca and duct, and the few diverticula on the prostate. The flagella are shown somewhat longer than those in the figure on plate 3. Germain's figure (1931, p. 543, fig. 56) is practically the same, the flagella being more like the figure on plate 3.

Respiratory and Renal Systems. The pseudobranch (plate 3, fig. 4) is rather small, smooth, elongate-ovate, and folded. The pneumostome is very large (fig. 4, PS).

The kidney (plate 47, fig. 22) is very long (8 mm.) and narrow, ribbon-like, the short ureter reflected at right angles to the kidney. In cross section (fig. 23, below the middle) it is seen to be rounded, a trifle wider than high, with the veins placed at the upper corners of the lumen, which is oval in shape. There is no superposed ridge.

Digestive System. The stomach region (plate 48, fig. 16) is very narrow, divided into crop, gizzard, and pyloris. There is a short blind sac. The intestine makes a sharp turn about the stomach and another around the liver, then runs forward to the rectum.

The buccal sac is much elongated, the salivary glands short, wide, and looped behind. There is a conspicuous radula sac which projects notably from the rear end of the buccal sac.

The jaw (plate 50, fig. 24) is horseshoe-shaped, and composed of many small plates (about sixty). It is similar in form to that of *Planorbis*.

Radula (plate 69, fig. 7). The formula is 23-1-23 with 164 rows of teeth. The central tooth is wider at the lower edge of the base of attachment than at the upper margin of the tooth. The two short cusps do not reach the lower margin of the base of attachment. Lateral teeth (1-7) long and narrow, the reflection low and wide and placed high up on the tooth. There are seven cusps, dagger-like and subequal in size, the ectoconic cusps a trifle smaller. There are six teeth which may be called intermediate (8-13), since the cusps are a trifle smaller than those of the lateral teeth. Marginal teeth (14-21) with the reflection very low and wide, 7-cuspid, the mesocone a trifle larger than the three cusps on each side. The outer marginals (22, 23) are vestigial. The teeth are all crowded on the membrane, some of them even overlapping. The teeth are very uniform in size and shape.

Twelve specimens of *Segmentina nitida* were dissected, collected from marshes in a meadow in Czerniakow, a suburb of Warsaw, Poland, by A. Jankowski.

Geographical Distribution. Typical *Segmentina* is distributed throughout Europe and northern Asia. A single species, *S. nitida* (Müller), is recognized, with several races, by Westerlund and others. Some small species, as *kempi* Preston and *angusta* Jickeli, may be true *Segmentina*. Species quoted from northern Africa probably belong to other genera, as *Afroplanorbis*. South African species may belong to an undescribed group. The Indian and Chinese species included by authors in *Segmentina* probably all belong to *Polypylis*, *Pingiella*, or *Helicorbis*. Only an anatomical examination can correctly place the many species referred to *segmentina*.

Geological Distribution. Oligocene period to Recent fauna.

Species Considered as Valid. Since the genus *Segmentina* is not found in America, it is extralimital to the scope of the present work. *Segmentina nitida* (Müller), the genotype, is the only species definitely considered.

Remarks. The genus *Segmentina* is distinguished not only by its glossy shell with the embracing body whorl and internal barriers, but also by its genitalia with the two short flagella on the verge, the few large ovotestis diverticula, the ductless penial gland in the preputium, and the papilla at the end of the verge. No mention is made of this peculiar gland in any work consulted. The prostate is on a separate duct as in the Planorbinae. These special features of the anatomy distinguish *Segmentina* from all other genera of Planorbidae.

The generic name has been used in a rather wide sense and has included one group which belongs in another subfamily (*Planorbula*) and several other related groups which are separated generically from *Segmentina* (*Popypylis*, *Pingiella*, *Helicorbis*). As typified by *Planorbis nitidus* Müller it is a well characterized genus.

Segmentina nitida appears to be a favorite host for parasitic worms, all of the twelve specimens examined being more or less heavily infested. The ovotestis appeared to be most affected and in several specimens this organ was almost obliterated. The liver was also affected.

Genus HIPPEUTIS (Agassiz MS) Charpentier, 1837

Type designated by Clessin in 1886, *Planorbis complanatus* Drap. (= *Helix fontana* Lightfoot), one of the two species originally included

1837. *Hippeutis* 'Agassiz' in J. de Charpentier, Neue Denksch. Allg. Schweiz. Naturw., I, No. 2, p. 22. As subgenus of *Planorbis*

1837. *Hippeutis* Gray, in Turton, Man. Land FW. Shells Brit. Isl., Ed. 2, p. 243. As subgenus of *Planorbis*

1844. *Hippeutis* Hartmann, Erd-und Süsswassser-Gast. der Schweiz., V, pp. 51, 87. As subgenus of *Planorbis*

1850. *Hippeutes* M. E. Gray, Fig. Moll. Anim., IV, Syst. Arrang., p. 119. Typographical error for *Hippeutis*

1850. *Segmentina* (part) Stein, Leben. Schneck. Muschl. Berlins, p. 78. Non *Segmentina* Fleming, 1817. (*Segmentina* plus *Hippeutis*)

1855. *Hippeutis* Moquin-Tandon, Hist. Moll., Terr. Fluv. France, II, pp. 423, 426. Type *Planorbis fontanus* (Lightfoot). As genus

1885. *Hippeutis* Westerlund, Fauna Palearc. Reg. Binnen. Conch., V, pp. 65, 84. No type cited. As subgenus of *Planorbis*

1886. *Hippeutis* Clessin, Syst. Conch. Cab., Ed. 2, XVII, p. 34. Type *Planorbis complanatus* Drap. As subgenus of *Planorbis*

1902. *Hippeutis* Westerlund, Rad. Jugoslav. Akad., 151, p. 121. Type *Planorbis fontanus* (Lightfoot). As subgenus of *Planorbis*

1905. *Hippeutis* Dall, Alaska Moll., pp. 82, 86. Type *Planorbis fontanus* (Lightfoot). As subgenus of *Planorbis*

1912. *Hippeutis* Hannibal, Proc. Mal. Soc. London, X, p. 154. Type *Planorbis complanatus* Drap. (= *Helix fontana* Lightfoot). As subgenus of *Planorbis*

1915. *Hippeutis* Preston, Fauna Brit. India, Moll., FW. Gast and Pelec., p. 124. Type *Planorbis fontanus* (Lightfoot). As section of *Planorbis*

1918. *Hippeutis* Walker, Mis. Pub. Zool. Mus., Univ. Mich., No. 6, p. 94. Type *Planorbis fontanus* (Lightfoot). As subgenus of *Planorbis*

1923. *Hippeutis* Wenz, Fossil. Cat., Pars 22, p. 1633. (Genotype *Hippeutis complanatus* (Drap.) = *Helix fontana* Lightfoot. As genus

1923. *Hippeutis* Germain, Rec. Ind. Mus., XXI, pp. 8, 159. Type *Planorbis fontanus* (Lightfoot). As subgenus of *Planorbis*

1926. *Hippeutis* Lindholm, Archiv. für Mollusk., 58 year, Heft 6, p. 253. Ideogenotype *Planorbis complanatus* Drap. As genus

1926. *Hippeutis* Kennard and Woodward, Syn. Brit. Non-Marine Moll., p. 69. Type *Helix complanatus* Linn. As subgenus of *Planorbis*

1927. *Hippeutis* Pilsbry and Bequaert, Bull. Amer. Mus. N. H., LIII, p. 128. Type *Planorbis complanatus* Drap. = *Planorbis fontanus* (Lightfoot). As subgenus of *Planorbis*

1929. *Hippeutis* Haas, Trab. Museo Cien. Nat. Barcelona, XIII, p. 387. Type evidently *Helix fontana* Lightfoot. As genus

1931. *Hippeutis* Germain, Moll. Terr. Fluv. France, II, p. 541. Type not cited but *Planorbis complanatus* (Linn.) described. As subgenus of *Planorbis*

1931. *Hippeutis* Thiele, Handbuch, Teil 2, p. 481. Type *Anisus (H.) complanatus* (Linn.). As subgenus under genus *Anisus*

1935. *Hippeutis* A. Soos, Allat. Kozlem., XXXII, p. 29. As subgenus of *Segmentina*. No type cited

Shell (plate 79, figs. 4-6). Small, ultradextral, lens-shaped, shining, the body whorl very wide and overlapping most of the inner whorls and forming a sharp keel at the periphery, the preceding whorl forming a sharp extended ridge on the parietal side of the aperture. Aperture triangular, outer lip thin. There are no barriers or lamellae within the aperture. The embryonic whorls have spiral punctures as in *Segmentina*.

Animal. Not differing from that of *Segmentina* in general form. The body of the animal is clear and translucent.

ANATOMICAL CHARACTERISTICS

PLATE 2 (*Hippeutis complanatus* (Linn.))

GENITALIA. Male Organs (fig. 15). Seminal vesicle rather short (about 0.7 mm.), placed midway between ovotestis and oviduct, the diameter of the organ about the same as the ovosperm duct, with many pustule-like vesicles. Prostate short (about 0.6 mm.) with ten long and narrow diverticula. Free portion of prostate duct short (fig. 8). Sperm duct (SPD) long (over 1 mm.) and of large diameter. Vas deferens (VD) about as long as sperm duct, but of smaller diameter.

Penial complex (plate 2, fig. 14) less than 1 mm. long. Preputium (PR) strikingly pyriform, tapering to a narrow neck near the outlet. Vergic sac (VS) shorter than the preputium, sac-like, of much smaller diameter than the preputium. There are two short flagella (FL). There is a single wide retractor muscle (RM) attached to the preputium at the lower part of the bulbous swelling.

Internally (fig. 12), the preputium has two large fleshy pilasters (PL), to the left one of which is attached a large, sac-like penial gland, which extends crosswise of the preputial cavity (SB). There is a depression at the end of the gland but apparently no cavity or cup. The square end of the gland is folded backward upon itself. It is shown folded in fig. 12 (SB) and with the end stretched out in fig. 9, where the small depression may be plainly seen. The retractor muscle (RM) is attached to the preputium at the point where the gland joins the pilaster (fig. 12, SB).

The verge is swollen above and tapers to a narrow diameter for about half its length (V). The sperm canal has a central outlet but there is no papilla. There is a narrow muscular ring or diaphragm (D) between vergic sac and preputium. The two short flagella (FL) are hollow and under high power show a minutely punctate surface at the upper rounded end (fig. 11).

Female Organs (fig. 15). The spermatheca (S) is long, ovate, sac-like and is joined to the short, wide vagina (V) by a long, tube-like duct, which is twice the length of the spermatheca. The uterus (U) is twice as wide as the vagina, and shorter than the spermatheca and its duct. The nidamental gland (NG) is longer than the uterus, much swollen and about half as wide as long. The oviduct (OD) is short (about 0.5 mm.) and about the same diameter as the uterus. There is a large, bulbous carrefour (CF) which receives the duct from the long and narrow albumen gland (AL; also fig. 10).

Hermaphrodite Organs. The ovotestis (OT) has about thirty club-shaped diverticula placed for the most part in a double row (fig. 7). The ovisperm duct (SO) is very long (about 2 mm.) and of small diameter.

Odhner (1929, p. 32, fig. 13) figures the genitalia of this species agreeing in most respects with the material personally examined. A few points, however, are figured differently from the position observed in the specimens studied. The prostate is shown as having thirteen diverticula rather widely spaced on the sperm duct, quite different from the long, crowded diverticula personally observed (see plate 2, fig. 15, PRS). The ovotestis diverticula are shown extending in pairs from a short duct which enters the ovisperm duct. In this species, as well as others of this subfamily and of Planorbinae, the ovotestis diverticula arise in pairs directly from the ovisperm duct, each diverticulum entering the duct separately (see plate 2, fig. 7). No mention is made of a separate prostate duct or of a gland in the preputium. An elongated object in the upper part of the preputium is shown in Odhner's figure which might represent this organ.

Odhner's figure of the radula of *Hippeutis complanatus* differs somewhat from the radula as personally examined, there being no interstitial cusps between the larger cusps. The formulas of Odhner's specimens agree exactly with ours.

Respiratory and Renal Systems. The pseudobranch (plate 2, fig. 13) is small, rather narrow, and pierced above by the rectum (P). The pneumostome is very large.

The kidney (plate 46, fig. 17) is rather short (1.5 mm.) and wide, the greatest width being almost one third of the length. The ureter is not sharply reflexed as in *Segmentina*, but extends horizontally into the mantle cavity. A cross section below the middle (fig. 18) shows the kidney to be flattened, the lumen rounded with the veins placed at the upper corners of the lumen. There is no superposed ridge. The kidney of *Hippeutis* is quite different from that of *Segmentina* (compare fig. 17, plate 46, with fig. 22, plate 47).

Digestive System. The stomach (plate 48, fig. 12) is elongated, as in *Segmentina*. The intestine loops around the stomach and liver, and there is a large blind sac. The buccal sac is elongated, narrowed in front with a large radula sac behind. The salivary glands are short and do not extend far beyond the posterior end of the buccal sac. They are joined behind as in *Segmentina.*

The jaw is fragmented as in *Segmentina* and is made up of many small plates.

The radula formula is 16-1-16, with 150 rows of teeth. The center tooth is higher than wide with two wide cusps which do not reach the lower margin of the base of attachment. The laterals (1-9) are squarish and tricuspid, the mesocone large and almost reaching the lower margin of the base of attachment. The entocone is shorter than the mesocone. The ectocone is shorter than the entocone and is placed high on the margin of the tooth. In the marginal teeth the reflection is wide and low and is placed high up on the tooth. The entocone and mesocone are of equal length and the ectocone is shorter with two small cusps above on the outer margin of the tooth. The radula teeth of *Hippeutis* resemble those of *Bathyomphalus contortus* shown on plate 68, fig. 1. They are not like those of *Segmentina nitida* figured on plate 69, fig. 7.

The above anatomical information was obtained from specimens collected in a pool on a meadow in Jabtonna, 16 km. north of Warsaw, Poland. The specimens were obtained by Mr. A. Jankowski.

Geographical Distribution. Europe from Great Britain, Norway, and Sweden south to Portugal, Italy, and Albania. Eastward to northern Siberia. A palearctic group. It has been recorded from northern Africa and the group may be circum-Mediterranean in distribution. As in *Segmentina* a number of species have been described with many varieties. The species cited from South Africa, India, and China probably belong in other genera.

Species Considered as Valid. The following species are apparently referable to *Hippeutis:*

Hippeutis complanatus (Linn.)
Hippeutis riparius (Westerlund)
Hippeutis syracusanus (Cafici)
Hippeutis diaphanellus (Bgt.)
Hippeutis raymondi (Bgt.)
Hippeutis junodi (Connolly)
Hippeutis benguelensis (Dunker)

Geological Distribution. From the Lower Eocene period (Wenz). Eighteen species and races of fossil *Planorbis* are referred to this genus by Wenz.

Remarks. *Hippeutis complanatus* resembles *Segmentina nitida* in its anatomy. The prostate, however, has fewer diverticula. The penial gland differs in shape but both are attached to the right pilaster. The whole genitalia of *Segmentina* are much elongated while these organs in *Hippeutis* are short and heavy. Internally the penial complex of the two groups differs in details. The kidneys of the two genera are quite unlike. The radula resembles *Bathyomphalus* rather than *Segmentina.* The shell is wholly without barriers or lamellae of any kind within the aperture and this characteristic at once marks *Hippeutis* as a separate genus.

Species from northern Africa and eastern Asia have been assigned to *Hippeutis* but until these species have been examined anatomically this reference remains open to doubt. The Asiatic forms probably belong to Benson's genus *Helicorbis.* Parasites were not observed in any of the material examined.

Genus POLYPYLIS Pilsbry, 1906

Type by original designation *Segmentina largillierti* (Dunker) (= *S. hemisphaerula* (Benson))

1906. *Polypylis* Pilsbry, Proc. Acad. Nat. Sci. Phil., LVIII, p. 166. Type *Segmentina largillierti* (Dunker). As subgenus of *Segmentina*

1921. *Segmentina* (part) Prashad (non Fleming), Rec. Ind. Mus., XXII, p. 585. Mentions *Segmentina calathus* (Benson), included in *Polypylis*

1922. *Segmentina* Annandale (non Fleming), Rec. Ind. Mus., XXIV, p. 362. Mentions *Planorbis calathus* Benson and *Planorbis caenosus* Benson, both included in *Polypylis*

1923. *Polypylis* Germain, Rec. Ind. Mus. XXI, p. 164. As synonym of *Segmentina*

1939. *Polypylis* Haas, Field Mus. N. H., Zool., Miscel. Notes, XXIV, p. 96, fig. 8a. Type *Segmentina largillierti* (Dunker)(= *S. hemisphaerula* (Benson)). As subgenus of *Segmentina*

Shell (plate 79, figs. 7-9) less compressed than *Segmentina* (*nitida*) and not carinate, but glossy with deeply clasping whorls. The parietal lamina is obliquely transverse, the others transverse, basal long, a shorter one in the outer wall, and one or two in the upper margin. There are several or many barriers (Pilsbry). The embryonic whorls are punctured.

Animal. Not examined.

ANATOMICAL CHARACTERISTICS

PLATE 5

GENITALIA. Male Organs (fig. 7). Seminal vesicle (SV) almost twice the diameter of the ovisperm duct, rather long (2 mm.) convoluted, with but few pustulose excrescences. The vesicle gradually decreases in diameter to the ovisperm duct which is not sharply distinguished from the vesicle. Sperm duct (SPD) about 3 mm. long, rather narrow. Prostate 1.3 mm. long, on a separate prostate duct (PD), consisting of twenty-eight to thirty-four long and narrow diverticula, the tip of which is bent over in most of the diverticula (fig. 4). Several of the diverticula are bifid at the end. The free prostate duct is very short. The vas deferens (VD) is a small, tube-like duct somewhat shorter than the sperm duct.

The penial complex (plate 8, fig. 10) is long and narrow (0.5 mm. long). The preputium (PR) is sac-like, rather narrow and elongated (1 mm. long). The vergic sac (VS) is two-thirds as long as the preputium and is very narrow. There is a single flagellum (FL) which is long (over 1 mm.) and narrow and has a bulbous enlargement at the end which is almost half as long as the flagellum. The narrow part of the flagellum has about the same diameter as the vergic sac. The vas deferens enters the vergic sac at one side of the flagellum, as shown in the small figure in fig. 10. There is one large retractor muscle (RM) which is attached to the preputium near the junction of this organ with the vergic sac.

In *Polypylis calathus* there are two short flagella and the vergic sac is longer than in *hemisphaerula*. The pilasters, also, are very thick pads in *calathus*. There are over thirty diverticula on the prostate of *calathus* and the seminal vesicle is very large with projecting vesicles.

Internally, in the penial complex of *hemisphaerula* (plate 8, fig. 9) the preputium has two pilasters extending the whole length of the sac. There is a small, narrow muscular ring or diaphragm (D) separating the preputial cavity from the vergic cavity. The verge (V) is long (0.7 mm.) and very narrow, tube-like and at the end there is a fleshy papilla and the sperm canal has its outlet at the side of the verge just above this papilla (plate 5, fig. 6). There is no penial gland in the penial complex.

Female Organs (plate 5, fig. 7). The spermatheca (S) is rather small and is attached to the long and narrow vagina by a narrow duct (SD) about 1 mm. long. The vagina rapidly enlarges from its external opening to the point of juncture of the spermathecal duct (VG). The uterus (U) is not much longer than the vagina. The nidamental gland is long (2 mm.) and much swollen (NG). The oviduct (OD) is short (1 mm. long) and of about the same diameter as the uterus. There is a large carrefour (CF). The albumen gland is large (1.7 mm. long) and ovate in outline (fig. 2).

Hermaphrodite Organs. The ovotestis (fig. 7, OT) consists of many very long and club-shaped diverticula placed in a double series. As many as thirty-eight pairs of diverticula were counted in one specimen. The ovisperm duct (SO) is very short between the ovotestis and seminal vesicle and very long (2.5 mm.) between the seminal vesicle and the oviduct.

Respiratory and Renal Systems. The pseudobranch (plate 5, fig. 3) is long and narrow and somewhat folded, squarely truncated at the lower margin. There is a large pneumostome.

The kidney of *Polypylis hemisphaerula* is very long (7 mm.) and narrow. It resembles the kidney of *Polypylis calathus* (plate 47, fig. 24) which is long and narrow and 9 mm. in length. A cross section is similar to that of *calathus* (plate 47, fig. 25) which shows the kidney to be flattened, without a ridge, the lumen oval, wider than high with the two lateral veins of large diameter. In *hemisphaerula* the lumen is rounder and the veins relatively smaller. In outline the section of *hemisphaerula* more nearly resembles that of *Segmentina nitida* (plate 47, fig. 23) than that of *calathus*.

Digestive System. The stomach resembles that of *Segmentina nitida* (plate 48, fig. 16) but the blind sac is somewhat larger. The buccal sac is pyriform, with a large radula sac behind and two small salivary glands like those in *Segmentina nitida*.

The jaw is like that of *Segmentina nitida*, segmented with many plates (plate 50, fig. 24). *Polypylis calathus* has a similar jaw with many small plates.

The radula formula of *hemisphaerula* is 25-1-25 with over 200 rows of teeth. The teeth are like those of *Polypylis calathus* (plate 69, fig. 8), all 6-cuspid, the cusps short and the reflections wide and low and placed high up on the teeth. In *calathus* the formula is 26-1-1-26 with 205 to 210 rows of teeth. The rows of teeth are all in straight lines, as in *Segmentina*.

The above anatomical details were obtained from the following material:

Polypylis hemisphaerula (Benson) from Peiping, China, sent by the Fan Memorial Institute, Peiping, China. Four specimens.

Polypylis calathus (Benson), from weedy tank near inspection bungalow, Mongyai, N. Shan States, Burma. Collected by Dr. H. S. Rao and Mr. B. H. Chopus. One specimen examined.

Polypylis taia (Annandale and Rao), from below Machligaon, Port Blaie, Andamans. Collected by Dr. H. S. Rao. One specimen examined.

Geographical Distribution. *Polypylis* is found throughout much of eastern China and India and on some of the islands lying off the coast of China and India. Its full distribution and the species belonging to it can not be fully known until more of the species from Asia have been anatomically examined.

Species Considered as Valid. The following species appear to be correctly placed in this genus:

Polypylis hemisphaerula (Benson)
Polypylis calathus (Benson)
Polypylis lucida (Gould)
Polypylis nitidella (Martens)
Polypylis swinhoei (H. Adams)
Polypylis taia (Annandale and Rao)
Polypylis usta (Gould)

Geological Distribution. Not ascertained.

Remarks. *Polypylis* differs generically from *Segmentina* and *Intha* in the absence of a penial gland in the preputium. There is some variation in the form of the flagella in the species examined. In *hemisphaerula* there is but one flagellum on a long duct, while in *calathus* and *taia* there are two short flagella as in *Segmentina.*

The shell of *Segmentina* differs notably from that of *Polypylis*, being flattened with an acute periphery, while the periphery of *Polypylis* is rounded and the shell is high. The lamellae within the aperture in *Segmentina* are three in number, parietal, basal, and upper labial, all transverse to the whorl (plate 76, fig. 4). The space between the lamellae is narrow and three-cornered, quite unlike the wide space in the aperture of *Polypylis* (plate 76, fig. 5).

The difference between the form of flagellum in the type species and the flagella of the other species examined from India and China might indicate a division into two groups, as suggested below.

Group I. With one swollen flagellum on a long duct.
Example: *Polypylis hemisphaerula* (Benson).

Group II. With two short, narrow flagella without swollen end.
Example: *Polypylis calathus* (Benson).
Polypylis taia (Annandale and Rao).

However, too few of the Asiatic species have thus far been examined anatomically to warrant separation into subgenera at the present time.

Genus HELICORBIS Benson, 1855

1855. *Helicorbis* Benson, Jour. Asiatic Soc. Bengal, XXIV, p. 126. Subgenus of *Planorbis.* No type cited. The species *Planorbis (Helicorbis) umbilicalis* Benson, one of the original species listed, is here nominated as type of the genus.

1906. *Helicorbis* Dall, Nautilus, XIX, p. 105. Considers group equal to *Hippeutis* (Ag.) Charp., 1837.

1921. *Hippeutis* Annandale and Prashad (non Charp., 1837), Rec. Ind. Mus., XXII, p. 584. Places *Planorbis umbilicalis* in this genus.

1922. *Hippeutis* Annandale (non Charp., 1837). Rec. Ind. Mus., XXIV, p. 361. Mentions *Planorbis umbilicalis* Benson as belonging in genus *Hippeutis.*

1926. *Helicorbis* Kennard and Woodward, Syn. Brit. Non-Marine Moll., p. 69. Considered synonym of subgenus *Hippeutis.*

1931. *Helicorbis* Thiele, Handbuch, Teil 2, p. 481. Treated as synonym of *Hippeutis.*

Shell (plate 78, figs. 5-7). Ultradextral, the body whorl wide and overlapping or embracing the previous whorl, all whorls visible on upper (right) side, but mostly concealed on lower (left) side, the spire depression forming a false umbilicus. The whorls are rounded or at most only subangulate, not sharply carinate. Lips thin. There are no internal barriers or lamellae within the aperture. The embryonic whorls are marked as in other genera of the family.

The figure of *Planorbis umbilicalis* in Clessin, Conch. Cab., XVII, Taf. 15, fig. 6 does not represent that species but is a good representation of the new genus *Pingiella* F. C. Baker. Germain (1921, p. 177) has called attention to the discrepancy in Clessin's figure and gives good figures of *umbilicalis* on plate II, figs. 19, 20, and 21. The periphery in these figures is rather well-rounded. The figures in Hanley and Theobald, Conchologia Indica (1876), plate 40, figs. 7, 8, and 9 show the periphery as slightly carinated. Clench and Bequaert (1939) give the best figures observed (plate 1, figs. 8, 9, and 10) showing well the slight angulation of the periphery. We can not agree, however, that *Helicorbis mearnsi* Bartsch is a synonym of *umbilicalis* (see plate 2, figs. 10-12); it is too sharply angulated on the periphery. It is evident that the species referred to the subfamily Segmentininae are in need of careful revision.

Animal. 'The external soft parts generally resemble those of *Gyraulus* except that the branchial process and the pulmonary siphon are a little better developed' (Annandale and Prashad, 1921, p. 584).

ANATOMICAL CHARACTERISTICS

GENITALIA. 'The male genitalia generally approximate to Simroth's Typus I, but differ in details. The vas deferens is very long and coiled. The penis sac is a well-developed ovoidal structure with an elongated tubular preputium in continuation of the sac. The penis is massive with a lateral opening and without any stylet' (Annandale and Prashad, 1921, p. 585).

Radula. 'The radula is very minute and the dental formula is approximately 14-12-1-12-14(26-1-26): The central tooth is comparatively large and bicuspid with sharp cusps. The laterals and marginals both have a peculiar twinned structure, and the line of demarcation between the laterals and marginals is not very sharp. The laterals are tricuspid, the central cusp much the largest' (Annandale and Prashad). The radula is figured on page 583 of the work cited (fig. 16B). The teeth are like those of *Bathyomphalus* and *Hippeutis*. The twinned nature noted for some of the teeth was not particularly apparent in the radula of *Hippeutis complanatus* examined.

Geographical Distribution. Not clearly known but including eastern and central China and India, the Philippines, and probably other islands off the east coast of Asia.

Species Considered as Valid. Just what species may be included in this genus is not definitely known. The following are believed to belong here:

Helicorbis umbilicalis (Benson)
Helicorbis caenosus (Benson)
Helicorbis mearnsi (Bartsch)
Helicorbis papyraceus (Benson)

Geological Distribution. Not ascertained.

Remarks. The Segmentina-like shells of India and China referred to *Hippeutis* are apparently not like the type of that genus, *Hippeutis complanatus* (Linn.), at least as far as the shells are concerned. Both agree in lacking internal barriers or lamellae in the aperture. The shell of *complanatus,* however, is lenticular with a sharply angular peripheral keel and the aperture is longitudinally triangular, wider than high. *Helicorbis,* on the contrary, has a higher shell with rounded or subangular whorls and the aperture is oblique and higher than wide.

The published description of the anatomy of this group (the type, *Planorbis umbilicalis*) is insufficient for the purpose of making comparisons with *Hippeutis complanatus*, as no mention is made of flagella, penial gland, or prostate. The penis (verge) is said to have its sperm canal opening on the side, which is like that of *Hippeutis* (see plate 2, figs. 5, 6). Until more is known of the genitalia of *Planorbis umbilicalis,* the group *Helicorbis* had better be considered a separate genus related to *Hippeutis*.

The name *Helicorbis* has been almost unnoticed since its publication in 1855. Dall (1905) overlooked it in his Alaska Mollusks but later (1906) he considered it equal to *Hippeutis* Agassiz, 1837. Germain (1921) omits all reference to it. Kennard and Woodward make it a synonym of *Hippeutis* (1926), as does Thiele (1931). Bartsch, in a paper on Philippine mollusks (1907, p. 84), places a related species in *Helicorbis*, the latter treated as a subgenus of *Planorbis*. Bequaert and Clench in a later paper on Philippine Lymnaeidae and Planorbidae (1939, p. 16) place *Planorbis umbilicalis* in *Hippeutis*, which is recognized as a genus.

In Benson's paper (1855, p. 126) three species are mentioned under *Helicorbis; hemisphaerula* and *nitida* are ruled out by the remark in the paragraph above concerning *Segmentina* (of which *nitida* is the type) which refers to the internal divisions or barriers. *Hemisphaerula*, also, is the type of Pilsbry's *Polypylis*. There remains the species *umbilicalis* which has not previously been used as a type for any group and this is here nominated for the type of *Helicorbis* Benson.

Helicorbis may bear something of the same relationship to *Hippeutis* that *Polypylis* bears to *Segmentina*, although the anatomical differences between the last two groups are greater than appears to be the case of the first two groups.

Genus TROCHORBIS Benson, 1855

Type by original designation *Trochorbis trochoideus* Benson

1855. *Trochorbis* Benson, Jour. Asiatic Soc. Bengal, XXIV, p. 126. Type *Trochorbis trochoideus* (Benson). As subgenus of *Planorbis*.

1906. *Trochorbis* Dall, Nautilus, XIX, p. 105. Type *Planorbis trochoideus* Benson. As subgenus of *Planorbis*.

1927. *Trochorbis* Kennard and Woodward, Syn. Brit. Non-Marine Moll., p. 90. No type cited. Considered a synonym of *Segmentina*.

Description of the type of the genus *Planorbis trochoideus* Benson: 'Testa vix perforata, diaphana, nitida, inconspicue radiato-striata, subtrochiformi, convexa; spira parvula, arcte convoluta, concava; sutura profunde impressa; anfractibus 3½, penultimo valde convexo, ultimo majori, versus suturam obtuse angulato, extus depresso, inferne acute carinato, intus laminis rarissimis pleurumque minuto, subtus plano, medio, versus umbilicum inconspicuum, leviter excavato, versus periphaeriam vix declivi; apertura obliqua subsagittata, margine superiori arcuato, prominente, inferiori recidente. Diam. 3 mm., axis vel 2' (Benson, 1850, p. 352).

'The infrequency and irregularity of the internal laminae in this species, causing them to look more like accidental thickenings of the shell, made me overlook this structure in my original description. The species is singular from the nearly total absence of umbilicus' (Benson, 1850, p. 352). The shell is treated as dextral (ultradextral).

Animal. The anatomy of this species is at present unknown.

Geographical Distribution. Barrackpore, Bengal, India.

Species Considered as Valid. *Trochorbis trochoideus* Benson, the genotype, is the only species assigned to this genus.

Remarks. In 1850 (p. 352) Benson noted the trochoid form and small umbilicus of *Planorbis trochoideus* and in 1855 (p. 126) erected the group *Trochorbis* for it. This name has been overlooked by most writers on Asiatic mollusks. Dall (1906, p. 105) considered *Trochorbis* a synonym of *Segmentina*. In Preston's Fauna of British India (1915, p. 125) the species appears as *Planorbis* (*Segmentina*) *trochoideus* without reference to its use as type of *Trochorbis*. Germain (1921, p. 175) does not mention the group name proposed by Benson and places the species *trochoideus* in the genus *Segmentina*. Kennard and Woodward (1926, p. 90) consider it an absolute synonym of *Segmentina*. *Trochorbis* is not recognized by Annandale and his co-workers in the studies of the mollusk fauna of the Indian Empire.

Typical *Segmentina* is not found in eastern Asia, the species previously referred to that genus now being placed in the genus *Polypylis* of Pilsbry. *Trochorbis trochoideus* greatly resembles *Planorbis calathus* Benson which belongs to the genus *Polypylis* and from the shell characters appears to be only specifically distinct from *calathus*, if one can judge from the very excellent figures of both species in Hanley and Theobald, Conchologia Indica, plate 39, figs. 1-3 (*calathus*) and 4-6 (*trochoideus*).

The species *trochoideus* has a much smaller shell than *calathus* and the periphery is more acute. According to Benson, the apertural lamellae are so weak that he overlooked them in his first description of the species. The Asiatic mollusks allied to *Segmentina* have shown such diversity in anatomical characteristics that until the animal of *trochoideus* is examined it seems best to treat *Trochorbis* as a separate genus. Its place, as far as can be judged at present, is near the group of shells called *Polypylis*, with the internal lamellae far within the aperture.

Genus PINGIELLA F. C. Baker, New Genus

Type *Pyramidula (Patula) peipinensis* Ping and Yen

1932. *Pyramidula (Patula) peipinensis* Ping and Yen, Bull. Fan Memorial Inst. Biol., III, p. 25, figs. 1-3. Wrongly interpreted as a land shell.

1938. *Anisus (Hippeutis) peipinensis* Mori, Mem. Col. Sci., Kyoto Imp. Univ., Ser. B, XIV, No. 2, p. 288, plate 14, fig. 6.

Shell (plate 78, figs. 8-10). Ultradextral, lenticular, flattened, with sharp peripheral carina, the last whorl very large and strongly overlapping or clasping the preceding whorls, the base flattened, with a narrow spire depression exhibiting all of the whorls, the depression about one third of the diameter of the shell. Aperture without internal lamellae. Major diameter of shell 7.8 mm. to 8.6 mm. The embryonic whorls are pitted.

Animal. Foot and pneumostome lead color, body yellowish finely mottled with black. Kidney pigmented (from alcoholic specimens).

ANATOMICAL CHARACTERISTICS

PLATE 4

GENITALIA. Male Organs (plate 4, fig. 9). Seminal vesicle (SV) large, tortuous, more than double the diameter of the ovisperm duct, with several vesicles, but mostly tubular. Sperm duct, long (3.5 mm.), narrow. Prostate (PRS) about 2 mm. long with twenty to twenty-two long diverticula. Free portion of prostate duct very short. Vas deferens long (4 mm.) and tubular.

Penial complex (fig. 5) with a large, sac-like preputium (PR) and small, narrow, short (little more than 0.5 mm.) vergic sac (VS). The vergic sac is placed on the side of the upper part of the preputium. There are two flagella, short and wide, placed on tube-like ducts longer than the whole penial complex. The sac-like flagella (FL) are turned horizontally to the tube-like duct. There is a very long and very fine, tube-like external penial duct (DC), about three times as long as the penial complex when stretched to its fullest extent. There is a single, wide retractor muscle (RM) attached about midway of the preputium at the point where the penial duct has its exit.

Internally (plate 4, fig. 6), there is a short, wide pilaster which bifurcates about midway of the preputial cavity, one branch forming a wide, flat gland (GL) which is doubled backward at the end (fig. 6). The other branch is short and narrow and ends above in a rounded, disc-like organ (G). The very long duct (DC) which appears on the outside of the preputium, enters a canal in this small branch (fig. 2, C, fig. 7, C) which terminates on the underside of the reflexed end of the gland (fig. 7, GL). The other end of the penial duct passes on the outside of the small pilaster and enters the round, turban-like termination of the small pilaster (figs. 2, 6, G and DC). There is a thickened muscular ring or diaphragm between the vergic space and the preputial space (figs. 6, 8, D). The retractor muscle is attached to the preputium near the small branch of the pilaster (fig. 6, RM).

The verge (fig. 8, V) is long and narrow, swollen or pear-shaped at the upper part but narrowed and tubular below. The lower end of the verge is notably flattened and broad, with a small penial papilla at the end, just beside the sperm canal exit, which is in the center of the verge (figs. 3, 4). The sac-like portion of the flagella is large and the cavity is lined with elliptical cells which show on the exterior surface as small, rounded projections (fig. 5, FL). The duct of the flagellum is narrow but is of greater diameter than the vas deferens.

Female Organs. The spermatheca is globe-shaped (S) with a short, narrow duct about as long as the greater diameter of the spermatheca (SD). Another specimen had a spermatheca long and sac-like (fig. 5, plate 5) attached to the vagina by a very short wide duct. This spermatheca contained a spermatophore and the specimen was evidently in gravid condition. The form of the spermatheca evidently varies with the breeding condition of the animal. Vagina rather short but longer than wide (VG). Uterus (U) short and as narrow as the vagina. Nidamental gland (NG) very long (3 mm.) and much swollen. Oviduct (OD) short and narrow. Albumen gland (fig. 1) elongated, about twice as wide as long, placed over the stomach, the intestine looped beneath it.

Hermaphrodite Organs. The ovotestis (OT) consists of many long and narrow diverticula placed in a double series. The ovisperm duct (SO) is of small diameter. The portion between the seminal vesicle and the ovotestis is very short (less than 1 mm.) but the portion between the seminal vesicle and the oviduct is very long (about 3 mm.).

An egg capsule on one of the shells, presumably of this species, contained eight eggs.

Respiratory and Renal Systems. The pseudobranch (plate 5, fig. 1, P) is small and inconspicuous, resembling that of *Hippeutis.*

The kidney is long and narrow, resembling that of *Segmentina,* but not as long. The ureter is directed horizontally into the mantle cavity, not reflected. There is no superposed ridge. A section of the kidney near the middle shows a wide and low lumen about three times as wide as high with the veins at the upper corners. A section below the middle shows a flatter form with the lumen almost as high as wide and somewhat triangular, the veins at the upper part of the triangle. This triangular form is caused by the acute angle of the shell on the periphery.

Digestive System. The stomach is long and narrow as in *Segmentina,* the intestine making a loop around the stomach and another around the liver and then passing forward to the rectum and pseudobranch. The blind sac is very short and pointed below.

The buccal sac is elongated, pear-shaped, the radula sac large and near the middle of the posterior end. The salivary glands extend considerably beyond the rear end of the buccal sac and are united behind; the ducts are small and tube-like.

The jaw is fragmented with about eighty plates. It is horseshoe-shaped as in the other groups of this subfamily.

Radula formula 26-1-26 with 160-170 rows of teeth. The teeth resemble those of *Segmentina* and *Polypylis* (see plate 69, figs. 7, 8). The laterals have six short, spade-shaped cusps and the marginals have seven short cusps.

The anatomical details have been obtained from three specimens from Peiping, China, received from the Fan Memorial Institute of Peiping, through the courtesy of Dr. Chi Ping.

Geographical Distribution. Northern and eastern China and Japan. It is probable that this distribution will be extended when more material has been examined from China and India.

Geological Distribution. Unknown.

Species Considered as Valid. *Pingiella peipinensis* (Ping and Yen), the genotype, is the only representative of this monotypic genus.

Remarks. This genus is remarkable for the peculiar characteristics of the penial complex, the penial gland, bifurcated into a large and a small branch, the latter with a turban-shaped termination, and the very long, tube-like external duct with its peculiar gland terminations. The terminal end of the verge is also peculiar. The flagella are notable in having the long ducts and the small, sac-like glands. These differences are sufficient to stamp the species as belonging to a new and hitherto unknown generic group. It differs from *Segmentina* in the possession of an external duct and from *Polypylis* by having a penial gland which is absent in that genus.

It is quite probable that other species belong in this genus and will be discovered when examined anatomically.

Mori (1938, p. 288) has called attention to the fact that this species is a planorbid and not a land shell. He, however, places the species in the genus *Anisus*, subgenus *Hippeutis*, following the classification of Thiele. The anatomy, especially the genitalia, indicates that this species can not correctly be referred to either *Anisus* or *Hippeutis*, differing widely in its internal organization.

The genus is dedicated to Dr. Chi Ping, research professor in the Fan Memorial Institute of Biology, Peiping, China, an accomplished student of the Asiatic molluscan fauna. Dr. Ping has supplied the author with a number of mollusks for anatomical study from near Peiping.

Genus INTHA Annandale, 1922

Type by original designation *Intha capitis* Annandale

1922. *Intha* Annandale, Rec. Ind. Mus., XXIV, p. 361. Type *Intha capitis* Annandale. As genus.

1931. *Intha* Thiele, Handbuch, Teil 2, p. 482. *Anisus (I.) capitis* (Annandale). As subgenus under genus *Anisus*.

Shell. 'In this genus the body-whorl, though relatively smaller than it is in *Hippeutis*, completely embraces and occludes the rest of the shell in such a way that the spire is entirely concealed, except in so far as it can be detected by transparency. The shell is very minute and has few whorls, which increase in size rapidly. Those of the spire are cylindrical, but the body whorl is flattened below and has the form of a flattened conoid slightly truncate above. The outer lip arises in the middle of the upper surface and forms a small lobe at its point of origin. The aperture is large and very oblique but with a cordate outline. There is a well-developed simple callus on the inner lip, but internal ridges are completely absent. The lower surface is narrowly umbilicate. The external surface is practically smooth' (Annandale, p. 361). The shell is ultradextral. No figure of the shell is available and the single specimen used for dissection had the shell badly broken which made it unfit for illustration.

Animal. 'The animal is remarkable externally for the large upper and lower lobes into which the mantle is divided. The pseudobranch is poorly developed' (Annandale, p. 362). The head of the animal bears short, blunt tentacles (plate 8, fig. 3).

ANATOMICAL CHARACTERISTICS

PLATE 8

GENITALIA. Male Organs (fig. 11). Seminal vesicle (SV) very large, about three times the diameter of the ovisperm duct, with a few irregular, pointed, glandular projections. It is less than 1 mm. long. Sperm duct (SPD) long (slightly more than 1 mm.) and of large diameter. Prostate short, with six large, club-shaped diverticula. Prostate duct (free portion) about as long as the prostate. Vas deferens (VD) of small diameter and very long (about 5 mm. when stretched out).

The penial complex has a large, bulbous preputium (PR) and a small, slender vergic sac (VS), somewhat shorter than the preputium (fig. 6). Together both organs measure 1 mm. in length. There is a short, narrow penial gland duct on the outside of the preputium, emerging from the latter about midway between the outlet and the summit of the preputium. At the upper end of the vergic sac there are two very large flagella (about 1 mm. long) which are sausage-shaped and are attached to the vergic sac by a very short duct, in fact they are almost sessile. Small glands on the interior of the flagella show through as white circles, as shown in the figure (fig. 11, FL). There is a wide retractor muscle which is attached to the upper part of the preputium.

Internally (fig. 8), the preputium has a large penial gland (GL) which is attached to the preputium only at its base, the cup being free. It is more or less circular in shape, depressed, with a wide cup-shaped depression in which the walls are ridged (probably glandular). There is a short duct, external to the preputial cavity, which enters a round, fleshy ring or diaphragm between the vergic and preputial cavities (fig. 8, D). The relationship of the gland and duct to the preputial sac is well shown in fig. 7. The verge (V) is narrow, tapering, with the exit at the end in the center. There is a very small papilla at one side of the opening (fig. 4). The two flagella are joined in one tube before they enter the vergic sac (fig. 11, VS; fig. 8, FL).

Female Organs (fig. 11). The spermatheca (S) is large and almost circular, and is joined to the short, wide vagina (V) by a duct which is shorter than the diameter of the spermatheca. The uterus (U) is wide and shorter than the spermatheca and its duct. The nidamental gland (NG) is very wide, sac-like, and about twice as long as the uterus. The oviduct (OD) is short and wide, about as long as the preputium. There is a large carrefour (CF). The albumen gland (AL) is large, about 1 mm. long, and has a space for the passage of the intestine (fig. 1).

Hermaphrodite Organs. The ovotestis (OT) is large with the diverticula long and club-shaped. They are placed in a double series. The ovisperm duct (OS) is very short between the seminal vesicle and the ovotestis and about 1 mm. long between the seminal vesicle and the oviduct. A spermatophore of peculiar form was found in the spermatheca (fig. 5).

No figure or description has been published of the genitalia of this genus. Annandale says of the genitalia: 'The male organ resembles that of *Planorbis*, except that the penial bulb is relatively very large' (op. cit., p. 362).

Respiratory and Renal Systems. The pseudobranch (fig. 2, P) is a flatly rounded, simple lobe, pierced above by the rectum. The kidney (plate 47, fig. 26) is wide and flattened and not as long as in *Segmentina* or *Polypylis*. There is no superposed ridge. In section (fig. 27) the lumen is long, oval in outline with the veins about in the center on each side.

Digestive System. The stomach is narrow as in *Segmentina*, the intestine making the same loops around the stomach and liver as in the genus *Segmentina*. The buccal sac resembles that of *Segmentina*. The jaw (plate 50, fig. 23) is fragmented as in *Segmentina*. There are more than sixty plates on the jaw.

The radula has the formula 15-1-15 with over 125 rows on a broken membrane (plate 69, fig. 9). Center tooth bicuspid, the cusps not reaching the lower margin of the base of attachment. Lateral teeth (1-5) with two entocone cusps, a single mesocone, and three ectocone cusps, the mesocone a trifle larger than the other cusps. Marginal teeth 7-cuspid (6, 8, 11, 12) with three small cusps on each side of a mesocone cusp. There are no intermediate teeth. The teeth are all in a straight row. They are very uniform in size and shape but become narrower toward the outer edge of the membrane. The teeth are essentially like those of *Segmentina*.

For the above anatomical details a single specimen was dissected, received from Dr. H. S. Rao, collected by Dr. N. Annandale in Inle Lake, southern Shan States, Burma.

Geographical Distribution. Known at present only from the type locality, He-Ho and Inle valleys (3000-3800 ft. alt.) southern Shan States, Burma. Recent and fossil.

Species Considered as Valid. *Intha capitis* Annandale is the only species recognized for this monotypic genus.

Remarks. *Intha* is peculiar in the form of its shell and also in the characteristics of its genitalia, with the few prostate diverticula of large size, the two enormous flagella, and the striking penial complex with a penial gland which has a small, short duct entering the circular ring between the vergic sac and the preputium. In this respect it resembles some of the Helisomatinae (typical *Helisoma*) but differs in the form of the prostate and ovotestis. It appears to be another peculiar variant of the *Segmentina* group of Planorbidae.

Genus DREPANOTREMA Fischer and Crosse, 1880

Monogenotype *Planorbis yzabalensis* C. and F. (= *Planorbis anatinum* d'Orbigny)

1880. *Drepanotrema* Fischer and Crosse, Miss. Scient. Mex., Moll., II, pp. 59, 75. Type *Planorbis yzabalensis* C. and F. As subgenus.

1883. *Drepanotrema* Fischer, Man. de Conch., p. 509. Type *Planorbis yzabalensis* C. and F. As section of *Planorbis*.

1884. *Drepanotrema* Tryon, S. and S. Conch., III, p. 107. Type *Planorbis yzabalensis* C. and F. As subgenus of *Planorbis*.

1884. *Bathyomphalus* Tryon (non Agassiz, 1837), S. and S. Conch., III, p. 106. *Planorbis anatinus* Orb., cited as example.

1884. *Anisus* Tryon (non Studer, 1820), S. and S. Conch., III, p. 106. *Planorbis kermatoides* Orb., cited as example.

1899. *Drepanotrema* Martens, Biol. Cent. Amer., Moll., p. 397. As synonym of *Hippeutis*.

1899. *Spiralina* Martens, (part) op. cit., p. 395. Includes *Drepanotrema cultratum* and *sumichrasti*.

1899. *Hippeutis* Martens (non Agassiz, 1837), op. cit., p. 397. Cites *Planorbis yzabalensis*, type of *Drepanotrema*.

1905. *Drepanotrema* Dall, Alaska Moll., p. 82. Type *Planorbis yzabalensis* C. and F. As section of subgenus *Hippeutis*.

1921. *Drepanotrema* Germain, Rec. Ind. Mus., XXI, p. 8. Type *Planorbis yzabalensis* C. and F. As subgenus of *Planorbis*.

1930. *Drepanotrema* H. B. Baker, Oc. Papers, Mus. Zool., Univ. Mich., No. 210, pp. 43, 38, 51. Type *Planorbis yzabalensis* C. and F. As genus.

1931. *Drepanotrema* Thiele, Handbuch, Teil 2, p. 481. Type *Drepanotrema yzabalensis* C. and F. Section of *Gyraulus*, subgenus of *Planorbis*.

1934. *Drepanotrema* Pilsbry, Proc. Acad. Nat. Sci. Phil., 86, p. 58. Type *Planorbis yzabalensis* C. and F. As genus. Figures genitalia of *D. lucidum* (Pfr.) and *D. cultratum* (Orb.).

Shell (plate 79, figs. 16-18). Small, ultradextral, of few whorls, the body whorl large and expanded, embracing the previous whorl; whorls rounded or carinated; the right side with whorls sunken below the upper surface or showing a wide, slightly concave depression. There are no barriers or lamellae within the aperture. The embryonic shell is punctate.

Animal. The body is long and narrow, rounded before and sharply pointed behind. The tentacles are long and filiform, the eyes large and conspicuous, placed at the inner base of the tentacles. There may be two dark lines of color extending down the neck and top of the head. In some species (as *melleus* Lutz, plate 78, figs. 1, 2) the body is not much pigmented, but in some others (as *hoffmani* F. C. Baker, plate 10, fig. 1) the body is deeply pigmented with black.

ANATOMICAL CHARACTERISTICS

PLATES 9, 10, 11

GENITALIA. Male Organs (plate 9, fig. 2; plate 10, fig. 2; plate 11, fig. 3, respectively *anatinum*, *hoffmani*, and *lucidum*). Seminal vesicle (SV) large, much elongated, swollen, two to three times the diameter of the ovisperm duct, varying in length in the three species examined. It is about half the length of the ovisperm duct region in *hoffmani* but only about a third of this length in *lucidum*. *Anatinum* is much like *hoffmani*. The prostate (PRS) varies greatly in the three species: in *hoffmani* it is 3.5 mm. long and is made up of twenty-three short, club-shaped, widely spaced diverticula; in *lucidum*, there are but eight diverticula on a prostate about 1 mm. long; in *anatinum*, there are seven diverticula still more widely spaced and the prostate is about 1 mm. long. All diverticula arise directly from the sperm duct and are not on a separate duct as in *Segmentina* and other members of the subfamily.

The sperm duct (SPD) also varies in length, being 5 mm. in *hoffmani*, 2.3 mm. in *lucidum* and a little over 1 mm. in *anatinum*. These lengths do not include the sperm duct portion under the prostate diverticula. The vas deferens of the three species is always a long, narrow tube, varying in length in the different species.

The penial complex is much elongated in all species examined. In *hoffmani* (plate 10, fig. 5) the preputium is elongated, cylindrical, and about twice the diameter of the long and narrow vergic sac, which is nearly twice the length of the preputium. In *lucidum*, the preputium is about three times the diameter of the vergic sac, which is considerably longer than the preputium (plate 11, fig. 4). In another specimen, the preputium and the vergic sac were about equal in length (plate 11, fig. 5). In *anatinum* (plate 9, fig. 1), the vergic sac is shorter than the preputium, which forms a reversed cone, becoming smaller in diameter toward the upper part.

The flagella of the three species differ considerably. In *hoffmani* (plate 10, figs. 6, 7, 8), the flagellum is very short and is bifid at the end; in *lucidum* (plate 11, figs. 4, 5), the flagellum is very long (1 mm. or more) and is not bifid at the end; in *anatinum* (plate 9, fig. 1), the flagellum is as long as the preputium (0.6 mm.) and is bifid at the end. A strong retractor muscle is attached to the end of the vergic sac near the insertion of the flagellum (plate 10, fig. 7). There is also a large nerve at this point (N).

Internally, the penial complex is simple in all species studied and resembles the condition observed in *hoffmani* (plate 10, fig. 6). There are three rather heavy pilasters, a small muscular ring or diaphragm between the preputium and the vergic sac, and a very long verge completely filling the vergic sac (V). The verge is narrow at the end with a central sperm outlet (plate 10, fig. 9).

Female Organs. These also differ in the three species. In *hoffmani* (plate 10, fig. 2) the spermatheca is pyriform and is joined to the long and narrow vagina by a duct twice as long as the spermatheca; in *lucidum* the spermatheca (plate 11, fig. 3) is globular, much wider than in *hoffmani*, and is connected with the vagina (which is shorter than in *hoffmani*) by a duct a trifle longer than the spermatheca; in *anatinum* (plate 9, fig. 2) the spermatheca is wider than in *hoffmani* but not as globular as in *lucidum* and is attached to the narrow vagina by a duct almost three times as long as the spermatheca. The uterus (U) is very long and narrow in *hoffmani*, shorter and wider in *lucidum*, and narrow in *anatinum*.

The nidamental gland is long and wider than the uterus in all three species. The oviduct (OD) is very long and narrow in *hoffmani* (about 5 mm. long), much shorter in *lucidum* (about 2 mm.) and very short in *anatinum* (less than 1 mm.). There is a small and inconspicuous carrefour (CF) in all species. The albumen gland is much elongated (plate 10, fig. 4).

Hermaphrodite Organs. The ovotestis (OT) consists of a few club-shaped diverticula placed in a double series. The ovisperm duct is much longer in *lucidum* than in either *hoffmani* or *anatinum* (see plate 9, fig. 2; plate 10, fig. 2; plate 11, fig. 3).

Several specimens of *lucidum* had the male genitalia completely everted and lying on the body of the animal (see plate 11). In fig. 1, the preputium is fully everted and the verge is extended to its fullest extent. In fig. 2, only the preputium is everted. In fig. 6, the organs are diagrammatically shown so that the relationship of the different parts may be seen under this condition. The flagellum, vergic sac, vas deferens, and retractor muscle remain in the body of the animal just behind the male opening. This is shown to better advantage in fig. 7.

Pilsbry (1934, p. 59, fig. 6, F) figured the penial complex of *lucidum* (from sketches by H. B. Baker). This figure differs from the specimens here examined in having a shorter flagellum and in having the penial retractor attached to the preputium instead of to the vergic sac. In all specimens of *Drepanotrema* examined, the retractor muscle was inserted at the end of the vergic sac near the flagellum and not at the summit of the preputium. As shown in fig. 8 on plate 10 (*hoffmani*), the vas deferens, flagellum, and retractor muscle may be so closely pressed together and bent downward at the summit of the preputium that relationship of the muscle is difficult to see clearly unless the parts are separated, as shown in fig. 4, plate 11 (*lucidum*). All specimens were torn apart to insure accuracy in this statement.

Pilsbry also figured the penial complex of *Drepanotrema cultratum* (Orb.) (plate 76, fig. 10) which is similar to that of *lucidum*, the vergic sac being but a trifle shorter than the preputium. The flagellum is somewhat more than half as long as the vergic sac. Pilsbry's figures are the only ones previously published on the anatomy of *Drepanotrema*.

Respiratory and Renal Systems. The pseudobranch (P) is a somewhat triangular process in *lucidum* (plate 11, figs. 1, 2) and *anatinum* (plate 9, fig. 3) but in *hoffmani* appears to be narrower and more cylindrical (plate 10, fig. 3). The rectum is very large and the anus discharges just above the base of the pseudobranch. The pneumostome is very large (PS).

The kidney of *Drepanotrema hoffmani* (plate 46, fig. 14) is very long and ribbon-like (15 mm. long). The ureter is very short and curves upward at right angles to the long axis of the kidney. A cross section near the middle (fig. 15) shows the kidney to be much flattened, the lumen wider than high, and the veins flattened and elongated in section. The kidney of *lucidum* is shorter and a section near the middle shows it to be more flattened than *hoffmani*, the lumen regularly long-ovate and the veins smaller and more regular in form (fig. 16).

Digestive System. The stomach (plate 48, fig. 11) is pyriform, the pyloris tapering to the intestine, which forms a loop over the oesophagus and another loop around the liver as in other genera of the subfamily. The blind sac is two-thirds as long as the stomach. The buccal sac is similar to that organ in *Tropicorbis*.

The jaw is horseshoe-shaped and is composed of many small plates arranged somewhat as in *Planorbis*. About seventy plates were counted on a jaw of *lucidum* (plate 50, fig. 27) and about as many on a jaw of *hoffmani* (plate 50, fig. 26).

The radula formula of *anatinum* (plate 68, fig. 3) is 18-1-18 with 158 rows of teeth. Center tooth squarish with two long, spade-shaped cusps reaching two-thirds of the way to the lower margin of the base of attachment. There is a very small cusp on each side of the center cusps high up on the reflection. Lateral teeth (1-6) very wide, with three long cusps, entocone, mesocone, and ectocone. Above the entocone there is a small additional cusp, and above the ectocone there is another small cusp on the first four laterals and two cusps on the 5th and 6th laterals. The intermediate teeth (7-10) are very wide with the three main cusps well-developed and with a small cusp above the entocone and a small interstitial cusp between the mesocone and the ectocone. Above the ectocone there are four small cusps on the outer margin of the teeth. The marginal teeth (11-18) are narrower than the intermediate teeth; there is a long entocone and mesocone with a small cusp above the entocone, three cusps between the entocone and mesocone, and five small cusps on the outer margin of the tooth where the ectocone would normally be.

In *lucidum* (plate 68, fig. 2), the formula is 28-1-28 with 240 rows of teeth. The center tooth is like that of *anatinum* except that the large cusps are longer. The lateral and marginal teeth are similar to those of *anatinum* except that the cusps are longer.

In *hoffmani* (plate 68, fig. 4), the formula is 27-1-27 with 230 rows of teeth. The center tooth is as in *lucidum* and *anatinum*. The lateral and marginal teeth are similar to those of the other species figured.

Dr. H. B. Baker (1930, p. 50) has examined the radula of *ahenum* and says 'The radula and jaw of *D. ahenum* are also much as in *D. lucidum*. The radula formula is 30-1-30, with 194 transverse rows. The marginal teeth are slightly broader at the tip of the cusped reflection and may develop two interstitials between the entocone and mesocone.'

The radula teeth of *Drepanotrema* are peculiar in the possession of the small interstitial cusps between the larger cusps. They somewhat resemble the multicuspid teeth of *Segmentina*, *Hippeutis*, *Intha*, etc., to which the genus is also allied by the presence of a flagellum. The radula of *Drepanotrema* is very uniform in the shape of the teeth, varying principally in the number of interstitial and accessory small cusps. The formulae, as well as the number of lateral and marginal teeth, vary in the different species.

For the above anatomical data, three species have been examined:

Drepanotrema anatinum (Orb.) Pueblo Viejo, Puerto Rico, collected by Dr. W. A. Hoffman. Five specimens dissected.

Drepanotrema hoffmani F. C. Baker. Isabela, Puerto Rico, collected by Dr. W. A. Hoffman. Eight specimens dissected.

Drepanotrema lucidum (Pfeiffer). Havana, Cuba. Received from Dr. C. G. Aguayo. Five specimens dissected.

Geographical Distribution. This genus is found more or less abundantly from southern Texas southward through Mexico and Central America to Brazil, Bolivia, and the Argentine Republic. It it also found in many of the West Indies Islands. It is purely an American genus and a number of species are known, including some names now considered synonyms.

Pilsbry (1934, p. 59) divided the genus into three sections, *Drepanotrema* proper, *Fossulorbis* Pilsbry, and *Platytaphius* Pilsbry. In the writer's opinion, the last section should be regarded as a separate genus until the type has been dissected and its anatomy made known. The other groups divide the genus *Drepanotrema* into two comprehensive subgenera.

Subgenus DREPANOTREMA Fischer et Crosse, 1880

Spire on the right side, narrow and deeply sunken; periphery broadly rounded (type *Drepanotrema anatinum* (Orb.) = *Planorbis yzabalensis* C. and F. (Pilsbry)

Species Considered as Valid.

Drepanotrema anatinum (Orbigny) Plate 79, figs. 16-18

Drepanotrema lucidum (Pfeiffer) Plate 78, figs. 11-13

Drepanotrema hoffmani F. C. Baker Plate 78, figs. 14-16

Drepanotrema chittyi Aguayo

Drepanotrema parapseide (Orbigny)

Drepanotrema aheneum H. B. Baker

Drepanotrema castaneonitens (Pils. and Van.)

Drepanotrema melleum (Lutz)

Subgenus FOSSULORBIS Pilsbry, 1934

Having a wide spiral on the right side, very slightly concave; the periphery from rounded to carinate. Type *Drepanotrema cultratum* (Orb.) Pilsbry.

Species Considered as Valid.

Drepanotrema (Fossulorbis) cultratum (Orbigny) Plate 78, figs. 17-19

Drepanotrema (Fossulorbis) c. anitense (Cooper)

Drepanotrema (Fossulorbis) c. duenasianum (Tristram)

Drepanotrema (Fossulorbis) c. labrosum Pilsbry

Drepanotrema (Fossulorbis) c. panuco Pilsbry

Drepanotrema (Fossulorbis) cimex (Moricand)

Drepanotrema (Fossulorbis) c. pistiae H. B. Baker

Drepanotrema (Fossulorbis) depressissimum (Moricand)

Drepanotrema (Fossulorbis) kermatoide (Orbigny)

Drepanotrema (Fossulorbis) sumichrasti (Crosse and Fischer)

Remarks. *Drepanotrema* differs in its genitalia and radula from all other American groups of Planorbidae. By its prostate, the diverticula club-shaped and placed in a single row on the sperm duct, it is allied to the subfamily Segmentininae. The prostate differs from the members of both Planorbinae and Segmentininae in having the diverticula placed directly on the sperm duct instead of on a separate prostate duct. The presence of the flagellum on the vergic sac places *Drepanotrema* near the European and Asiatic groups *Segmentina, Polypylis, Hippeutis*, and *Intha*. The nature of the radula also indicates relationship with these groups. Although departing from these groups in having the diverticula of the prostate placed directly on the sperm duct, the other characteristics place the genus in the subfamily Segmentininae with little doubt.

The form of the shell of typical *Drepanotrema* bears close resemblance to the edentate Oriental groups of Segmentininae, such as *Helicorbis, Intha,* and *Hippeutis,* all having the peculiar embracing whorls so characteristic of *Segmentina*. This feature alone marks the assemblage of genera as of subgeneric solidarity.

Genus PARAPLANORBIS Hanna, 1922

Type by original designation *Planorbis condoni* Hanna

1922. *Paraplanorbis* Hanna, Univ. Oregon Pub., I, No. 12, p. 4. Type *Planorbis (Paraplanorbis) condoni* Hanna. As section of *Planorbis*.

1934. *Paraplanorbis* Pilsbry, Proc. Acad. Nat. Sci. Phil., 86, p. 59. Type *Planorbis condoni* Hanna. As section or subgenus of *Drepanotrema*.

1935. *Paraplanorbis* Henderson, Non-Marine Moll. N. Amer., p. 245. Fossil. Type *Planorbis condoni* Hanna.

Shell (plate 81, fig. 5). Whorls rounded on the periphery as in *Helisoma* Swainson but aperture not expanded, umbilicus very narrow, and size minute (Hanna, 1922, p. 4, description of subgenus).

Hanna's description of the species *Planorbis condoni* is as follows: 'Shell ultradextral, planorboid, composed of about four and one-half regularly increasing whorls; apical cavity a cone of about 120 degrees. Last whorl slightly angulated about the upper margin and descending slightly at the aperture. Lines of growth fine and even, giving the shell a silky luster. Umbilicus deeply rimate 0.51 mm. in diameter. Aperture roughly triangular but rounded on the outer lip; not expanded or thickened but a depression both above and below the periphery. Diameter 2.67 mm.; altitude 0.35 mm.'

Geographical and Geological Distribution. Vicinity of Warner Lake, eastern Oregon, Hanna's locality No. 212. Pliocene period.

Species Considered as Valid. *Paraplanorbis condoni* (Hanna), genotype, is the only species ascribed to this originally monotypic genus.

Remarks. This fossil genus is related to *Drepanotrema* and is considered a section or subgenus of the genus by Pilsbry (1934, p. 59). While the whorls are of a clasping or embracing nature, as is usually the case in *Drepanotrema* and its allies, the spire (left side) appears entirely different, the depression being narrow and the whorls deeply immersed. In view of the difficulty in this family of placing a group in its correct position in the classification by the shell alone, it would seem that the interest of nomenclature is best served by considering *Paraplanorbis* a separate genus of Segmentininae related to *Drepanotrema*. Its geographical location, also, so far removed from the present day distribution of *Drepanotrema*, is another reason for such procedure.

Genus PLATYTAPHIUS Pilsbry, 1924

Type by original designation *Planorbis heteropleurus* Pils. and Van.

1896. *Planorbis heteropleurus* Pilsbry and Vanatta, Proc. Acad. Nat. Sci. Phil., 1896, p. 562, plate 26, figs. 1-3.

1924. *Platytaphius* Pilsbry, Proc. Acad. Nat. Sci. Phil., 76, p. 51. Type *Planorbis heteropleurus* P. and V. As section of *Planorbis*.

1931. *Platytaphius* Thiele, Handbuch, Teil 2, p. 479. Type *Planorbis heteropleurus* Pils. and Van. As section of *Planorbis*.

1934. *Platytaphius* Pilsbry, Proc. Acad. Nat. Sci. Phil., 86, p. 59. Type *Planorbis heteropleurus* Pils. and Van. As section of *Drepanotrema*.

1934. *Platytaphius* Henderson and Rodeck, Jour. Pal., VIII, p. 268. Type *Planorbis heteropleurus* Pils. and Van. As genus.

1935. *Platytaphius* Henderson, Non-Marine Moll. N. Amer., p. 254. Fossil. Cites two fossil species from Oregon.

Shell (plate 79, figs. 10-12). Of medium size, ultradextral, moderately solid, corneous-white, rather opaque, the surface with fine, close growth lines; earlier whorls rather deeply and about equally sunken on the two sides; convex, and strongly angulate or keeled in the middle, on the right side; periphery conspicuously carinated on the left side, which is shallowly vortex-shaped, the whorls nearly flat. Last whorl slightly wider on the right than on the left side. Whorls three and one-half, all visible on both sides, the last wider than the spire. Aperture very oblique, rounded-pentagonal, the right margin produced forward (Pilsbry and Vanatta, 1896, p. 562). There are fine punctations on the embryonic whorls.

Animal. At present unknown anatomically.

Geographical Distribution. Lake Titicaca, Peru.

Geological Distribution. Pliocene to Recent fauna.

Species Considered as Valid. *Platytaphius heteropleurus* (Pilsbry and Vanatta) is the only recognized species.

Remarks. In describing this peculiar mollusk, Pilsbry says: 'This remarkable species is totally unlike *P. titicacensis* Clessin, *P. montanus* d'Orbigny, and *P. andecola* d'Orbigny, species already known from this Andean lake. It is most like *P. andecola*, but much flatter with differently placed keels, and in fact, so diverse in characters that no profitable comparison can be made' (1896, p. 562). In 1924 (p. 51), this species was made the type of a section of *Planorbis* and in 1934 (p. 59), it was made a section of the genus *Drepanotrema*. In a paper by Henderson and Rodeck (1934, p. 268), the authors state that 'it is so distinct that it might be better to consider it a genus.' With this statement the present author is in complete agreement for the general form of the shell is so distinct from that of any other species of *Drepanotrema* that it does stand quite alone. What its real affinities are can not be known until its anatomy has been investigated. It may belong near *Drepanotrema* or it may belong elsewhere.

Henderson and Rodeck (1934, p. 268) have associated two extinct molluscan species from the Pliocene of Oregon with *Platytaphius*. The localities are sixteen miles southwest of Vale, Oregon. This locality is so far removed from Lake Titicaca, in Peru (more than 5000 miles), that it would seem impossible for species of any group without intermediate habitats to become established so far apart. Yet the two species from Oregon correspond fairly well with the diagnosis of the genus *Platytaphius*. Additional species, recent or fossil, may be found somewhere between these extreme points. At present there seems no alternative but to include the Oregon fossils in *Platytaphius*, since no diagnosis could be made that would include the one and exclude the other. The two species of fossils from Oregon are *Platytaphius malheurensis* and *P. milleri* Henderson and Rodeck, figured on plate 37 of the publication cited, figs. 6, a, b, c and 9, a, b, c.

Genus ACRORBIS Odhner, 1937

Type by original designation *Acrorbis petricola* Odhner

1937. *Acrorbis* ODHNER, Archiv. für Zoologi, Band 29B, No. 14, p. 1. Nov. 9, 1937. Type *Acrorbis petricola* Odhner. As genus.

1938. *Acrorbis* PILSBRY, Nautilus, LI, p. 107 (review).

Shell (plate 72, figs. 1-3). Ultradextral, very small, thin, but firm, of circular form, with elevated spire, shell covered with a shining cuticle, openly umbilicate; whorls slowly increasing, arched, high, simple; aperture very oblique, broadly ovate; lips simple, very thin because of the lack of lime in the mouth-building; shell brown, dark and reddish above, underside more grayish; apex deep brown, globular, smooth, the following whorls with very weak spiral lines. Height of aperture same as height of whorl. Height 1.5 mm.; diameter 2 mm. (translated from Odhner).

Animal (plate 72, figs. 5, 6). Gray, the upper surface of the mantle flecked with black. The head is darker gray and neck blackish. The foot is broadly oval with thin borders and without any furrows on the sides. The tentacles are narrow, when fully extended, on the end obliquely truncated. The eyes are on the inner side of the base of the tentacles. The left tentacle differs from the right tentacle in being bifid at the end. The head is sharply pigmented between the eyes.

ANATOMICAL CHARACTERISTICS

PLATE 72

GENITALIA. Male Organs (fig. 10). No seminal vesicle is shown in the figure or mentioned in the description. The prostate is almost as long as the uterus and oviduct and has eight large diverticula in a single series. Neither description nor figure indicates the presence of a separate prostate duct. The vas deferens (v) is a long and narrow tube. The penial complex (fig. 9) is elongated, the preputium, about one-third of the entire length, merging into the vergic sac without marked constriction between these sacs. There is a wide retractor muscle (rp) which appears to be attached about midway of the length of the vergic sac. Above the vergic sac there is a wide flagellum less than half as long as the vergic sac. Internally there is a long, tube-like verge and a diaphragm of fleshy ridge separating the preputium from the vergic sac. The upper end of the flagellum is said to have two cavities, one on each side of a central tube (fig. 9, a).

Female Organs (fig. 10). The spermatheca (b) is large and globular and is attached to the short, narrow vagina by a very short duct about one-third the length of the diameter of the spermatheca. The uterus (u) is at first as narrow as the vagina, but swells to several times this diameter posteriorly where it joins the nidamental gland. The oviduct is not shown clearly but evidently narrows to the point of junction with the ovisperm duct. The albumen gland is not figured.

Hermaphrodite Organs. The ovotestis (go) is few-lobed, consisting of but five diverticula, which are smaller than the diverticula of the prostate. It is not stated whether the lobes of the ovotestis are in a single or a double row. The ovisperm duct (od) is almost as long as the uterus and oviduct combined and is a very narrow tube.

Respiratory System. The pseudobranch (figs. 5, 6, k) is shown as bifid at the extremity. It is a narrow projection about twice as long as wide, and probably bears the anal outlet as in other Planorbidae. The kidney (fig. 5, n) is long and narrow without a superposed ridge.

Digestive System (fig. 8). There is a long and narrow oesophagus, an ovate stomach with a short pyloris and a very short blind sac (caecum, c), and a long intestine which makes a loop around the stomach and another around the liver, extending forward in the rectum (r) to the outlet near the pseudobranch.

The buccal sac (fig. 7) is elongated, wide at the posterior end and much elongated at the anterior end. There is an unusually long radula sac (t) which forms a narrow tube as long as the whole radula sac. The salivary glands (s) are short, entering the radula sac by a fine tube. The jaw is said to be like that of *Parapholyx* (*Pompholycodea*).

The radula (fig. 4) formula is not given but sixteen teeth show in one row in the figure which would make the formula 16-1-16. The center tooth has two wide cusps which do not reach the lower margin of the base of attachment. The laterals are squarish with a long, spade-shaped mesocone reaching the lower margin of the base of attachment, and a short entocone and ectocone about half as long as the mesocone. The intermediate teeth have the cusps more nearly equal in size. The marginals appear wide and low, the entocone and ectocone splitting into two smaller cusps.

The information concerning this genus has been drawn entirely from the original paper and figures by Odhner. His figures are reproduced on plate 72.

Geographical Distribution. State of Santa Catharina, Brazil. It lives in damp moss on rocks over which water trickles.

Species Considered as Valid. *Acrorbis petricola* Odhner, type of the genus, is the only species recognized.

Remarks. *Acrorbis* is apparently a very distinct group of South American Mollusca. It is not related to *Carinifex* or *Parapholyx* (*Pompholycodea*) as indicated by Odhner, these two genera belonging to another subfamily, the Helisomatinae, in which there is a penial gland in the male complex. It scarcely appears to belong with *Choanomphalus*. It is also compared with *Neoplanorbis* Pilsbry, but that group is referable to the family Ancylidae, not Planorbidae.

Pilsbry has stated (1938, p. 107) that it is related to either *Tropicorbis* or *Drepanotrema*. The presence of a flagellum indicates a relationship with *Drepanotrema* and the few diverticula of the prostate in a single series indicates the same relationship, although the diverticula are more crowded than has been observed in species of *Drepanotrema* examined. *Acrorbis* differs from *Drepanotrema* in the wide form of the flagellum, the shape of the penial complex, wide for the whole length with no differentiation between preputium and vergic sac, the globular spermatheca on a very short duct, and the helicoid form of the shell, quite different from the overlapping whorls of *Drepanotrema*. The very long radula sac is also a characteristic feature of the anatomy.

The radula appears very different from that of *Drepanotrema* (see plate 68) because of the apparent absence of interstitial cusps between the larger cusps. These might have been present but overlooked because of the small size of the radula teeth. The general shape of the mesocone in Odhner's figure (4) is suggestive of the same cusp in *Drepanotrema*, but the ectocone and entocone are much shorter. The radula is markedly different from that of *Tropicorbis*.

Acrorbis, therefore, appears to be another one of the peculiar groups of South American Planorbidae, related to *Drepanotrema*, but distinct by both shell and anatomy.

Subfamily HELISOMATINAE F. C. Baker, 1928

Prostate diverticula compound or multiple, consisting of a basal stem with branches grouping around a short prostate duct which is in intimate contact with the sperm duct. In cross section, the prostate exhibits a fan-like design. A penial gland is nearly always present with an external duct of greater or lesser length. The kidney is usually heavily ridged. The jaws are simple, of three pieces, a superior and two lateral jaws.

Type genus *Helisoma* Swainson.

The groups referred to this subfamily are noted below.

With one penial retractor muscle: *Helisoma* and subgenera *Seminolina*, *Pierosoma* and *Planorbella*.

With two penial retractor muscles: *Carinifex* and *Parapholyx*.

Without penial gland duct: *Planorbarius*.

The fossil groups *Vorticifex*, *Perrinilla*, and *Pompholopsis* are included in this subfamily because of likeness of shell to *Carinifex* or *Parapholyx*.

With the exception of *Planorbarius*, which appears to have characteristics admitting it to this group, the subfamily is wholly American and is perhaps the most important planorbid element in the North American molluscan fauna. It is widespread throughout the northern part of North America and the species are numerous.

Genus HELISOMA Swainson, 1840

Type by original designation *Planorbis bicarinatus* Sowerby (= *Planorbis bicarinatus* Say = *Planorbis anceps* Menke)

1840. *Helisoma* SWAINSON, Treat. Malac., p. 337. Type *Planorbis bicarinatus* Sowb. As subgenus.

1846. *Helisoma* HERRMANNSEN, Ind. Gen. Mal. Prim., I, p. 516. Type *Planorbis bicarinatus* Say. As subgenus.

1865. *Helisoma* BINNEY, L. and FW. Sh. N. A., II, p. 112. No type cited. As subgenus.

1870. *Helisoma* DALL, Ann. N. Y. Lyc. N. H., IX, p. 351. Type *Planorbis bicarinatus* Sowb. As subgenus of *Planorbis*.

1872. *Helisoma* TRYON, Mon. FW. Univ. Moll. U. S., pp. 188, 198. No type cited. As subgenus.

1880. *Helisoma* FISCHER and CROSSE, Moll. Terr. Fluv. Mexico et Guat., II, p. 60. As subgenus.

1884. *Helisoma* TRYON, S. and S. Conch., III, p. 106. Type *Planorbis bicarinatus* Say. As subgenus.

1886. *Helisoma* CLESSIN, Syst. Conch., XVII, p. 33. Type *Planorbis bicarinatus* Say. As subgenus.

1899. *Helisoma* MARTENS, Biol. Cent. Amer., Moll., p. 381. No type cited but includes *Pierosoma*. As subgenus.

1902. *Helisoma* F. C. BAKER, Moll. Chi. Area, II, p. 287. No type cited. As subgenus.

1905. *Helisoma* DALL, Alaska Moll., pp. 81, 84. Type *Planorbis bicarinatus* Sowb. As subgenus.

1912. *Helisoma* HANNIBAL, Proc. Mal. Soc. London, X, p. 157. Type *Planorbis antrosus* Conrad. As genus.

1918. *Helisoma* WALKER, Miscel. Pub., Mus. Zool., Univ. Mich., No. 6, p. 11. Type *Planorbis bicarinatus* Say. As subgenus.

1921. *Helisoma* GERMAIN, Rec. Ind. Mus., XXI, pp. 6, 64. Type *Planorbis carinatus* Say. As subgenus.

1923. *Helisoma* WENZ, Fossil. Cat., Pars 22, p. 1522. Genotype *Helisoma bicarinata* (Sowb.). As genus.

1926. *Helisoma* F. C. BAKER, Trans. Wis. Acad. Arts and Sci., XXII, p. 201. Type *Planorbis bicarinatus* Sowb. As genus.

1928. *Helisoma* F. C. BAKER, Fresh-water Moll. Wis., I, p. 311. Type *Planorbis bicarinatus* Sowb. As genus.

1929. *Helisoma* CHAMBERLIN and JONES, Bull. Univ. Utah, Biol. Ser., No. 1, p. 145. Genotype *Planorbis bicarinatus* Sowb. As genus.

1930. *Helisoma* H. B. BAKER, Occ. Papers, Mus. Zool., Univ. Mich., No. 210, p. 43. *Planorbis bicarinatus* Say. As genus.

1931. *Helisoma* F. C. BAKER, Proc. Zool. Soc. London, p. 584. Type *Planorbis bicarinatus* Sowb. As genus.

1931. *Helisoma* THIELE, Handbuch, Teil 2, p. 479. Type *Planorbis bicarinatus* Say. As section of *Planorbis*.

1934. *Helisoma* PILSBRY, Proc. Acad. Nat. Sci. Phil., 86, p. 47. Type *Planorbis bicarinatus* Say. As genus.

Subgenus HELISOMA SS.

Type *Planorbis anceps* Menke

Shell (plate 80, figs. 1-6). Large, sinistral, of comparatively few whorls which rapidly increase in size, carinated; spire and umbilicus funicular; aperture expanded, outer lip thickened.

Animal. Yellowish or brownish, flecked with whitish; there are spots of color near the eyes and between the tentacles, and the mantle is spotted with dark mottling, especially over the kidney. The tentacles are long and filiform and the velar area is notably developed. The shell is carried almost perpendicularly.

ANATOMICAL CHARACTERISTICS

PLATE 23. *Helisoma anceps* (Menke)

GENITALIA. Male Organs (fig. 11). Seminal vesicle (SV) short (about 1 mm. long) and widely rounded, composed of many small follicles. Anterior to the seminal vesicle, for the space of 2.5 mm., the ovisperm duct is bordered by many small follicles which may represent a portion of the seminal vesicle (SO). The sperm duct (SPD) is about 6 mm. long and is of wide diameter, somewhat sausage-shaped, the tube about 0.3 mm. in diameter. The prostate (PRS) is ovate in shape, about 2.5 mm. long, 1 mm. wide and less than 1 mm. in height. It is composed of numerous diverticula forming a pavement-like pattern when viewed externally. In section (fig. 9) the prostate is fan-shaped, composed of six to eight diverticula each of which is branched two to four times toward the distal end. The prostate is placed on a short prostate duct which unites with the sperm duct to form the vas deferens (plate 22, fig. 12). The vas deferens (VD) is about 14 mm. long, somewhat smaller in diameter than the sperm duct. It is still further diminished in diameter as it emerges from the muscular tissue to enter the penial complex (plate 23, fig. 3, VD). Near the summit of the vergic sac the vas deferens enlarges to form an epiphallus (EPI).

The penial complex (plate 23, fig. 3) is a short, somewhat pyriform organ about 4 mm. long. The preputium (PR) is very wide (1.7 mm.) and about 2.5 mm. long. The vergic sac (VS) is somewhat bullet-shaped, 1.5 mm. long and 1 mm. wide. There is no marked constriction between the preputium and the vergic sac. There is a wide retractor muscle (RM) attached to the preputium just above the male opening. On the right side of the preputium there is a group of supporting muscles (SM). This group may form a wide, solid band or it may be broken up into ten or twelve smaller muscular bands. The supporting muscles are attached to the roof of the mantle cavity. There is a short (2 mm. long), narrow, external tube or duct (DC) on the outside of the preputium and adherent thereto. This penial duct tapers to half its diameter as it enters the junction of the preputium with the vergic sac.

Internally (fig. 2) the penial complex shows two cavities, an upper vergic space and a lower preputial space, separated by a muscular ring or diaphragm (D) which is capable of great contraction and expansion (see fig. 5). In the preputial space there is one large, vertical fold or pilaster (PL) and several smaller vertical ridges. Attached to the wall of the preputium at the upper end of the large pilaster is a rounded, cup-shaped penial gland (GL). In section (fig. 1) this gland is seen to have the cup-shaped, bulbous termination divided into two parts, an upper portion with smooth or only slightly developed vertical folds (OC) and a lower portion (LC) lined with heavy vertical folds (GF). The floor of this cup is covered with pavement-like folds, from which a narrow duct (DC) extends through the neck of the gland and emerges through the body wall of the preputium and becomes the external penial duct. A section through the region at the junction of the two spaces (fig. 6) shows the relationship of the muscular ring or diaphragm (D) to the gland duct, the latter penetrating the thick wall of the lower portion of the vergic sac and opening into this cavity just above the diaphragm. In fig. 11, plate 22, the outer cup of the gland is turned back to expose more fully the folds of the inner cup (*Helisoma anceps percarinatum*).

The verge (plate 23, fig. 2, V) is normally short and wide and tapers abruptly to a narrow point. In fig. 1 on plate 22 (*Helisoma anceps latchfordi*) it is shown well-extended, exhibiting an elongated, cylindrical form, the supporting muscles (MS) plainly indicated at the upper end near the top of the vergic sac. The enlarged epiphallus is also indicated. At the terminal end of the verge the seminal opening is placed in the center of the organ with a small, sharp appendage or papilla extending slightly below the end of the verge. In fig. 10 on plate 22, the end of the verge is shown with this feature enlarged to show the pointed papilla and the centrally located seminal opening.

The penial complex may assume a number of shapes, depending upon the sexual condition of the animal. Often it is seen as shown in fig. 8, plate 23, the penial gland pushed upward causing the complex to assume a bilobed aspect. The penial gland and the verge may sometimes be seen protruding from the male opening and lying on the neck of the animal.

The verge is often extended into the preputial cavity as shown in figs. 2, 3, and 4 on plate 22.

Female Organs (plate 23, fig. 11). The spermatheca (S) and its duct are 5 mm. long, the spermatheca elongated, sausage-shaped and slightly less in length than the duct, which is rather wide and enlarged as it enters the long (1.5 mm.) and narrow vagina. The uterus (U) is about 5 mm. long, widening upward to the nidamental gland (NG), which is about 2 mm. long and 1 mm. wide. The oviduct (OD) is about 4 mm. long and 0.3 mm. in diameter. There is a large carrefour (CF) into which the small, narrow duct of the albumen gland enters (DA). The albumen gland (fig. 7) is squarish in form, about 2.5 mm. in diameter and is composed of small follicles. Near the albumen duct the lobules are much larger than in the body of the gland. A depression crosses the gland on the under side marking the space occupied by the intestine.

Hermaphrodite Organs (fig. 11). The ovotestis (OT) consists of many rows of club-shaped diverticula having a pavement-like appearance from the surface of the gland. In section (fig. 10), the ovotestis is seen to be composed of about a dozen diverticula extending fan-wise from the ovisperm duct. The free portion of the ovisperm duct (SO) is somewhat shorter, between the seminal vesicle and the ovotestis, than between the seminal vesicle and the oviduct, but about 1 mm. in both regions. The larger portion of the ovisperm duct is occupied by the seminal vesicle.

The genitalia of the races of *Helisoma anceps,* as far as they have been examined, are remarkably uniform. In specimens of *Helisoma anceps percarinatum* from Douglas Lake, Michigan, there was some variation in the form of the retractor muscle, this being often divided into several branches toward the columella muscle (plate 22, figs. 2, 3, 4). In one specimen (fig. 4) there were two muscles, an abnormal condition.

Respiratory and Renal Systems. The pseudobranch (plate 23, fig. 4, P) is squarish in shape, rounded below, pad-like, with a distinct ridge passing down the center from the rectal region. The pseudobranch is 2 mm. wide and about 1 mm. high. The rectum is very wide and there is an irregular crest or ridge extending down the center (R). This ridge extends backward on the rectum about a quarter of a whorl. It narrows notably as it nears the anal end of the rectum. The pneumostome (PS) is not notably large.

The kidney (plate 44, fig. 1) is 7 mm. long and 2 mm. wide at the upper (pericardial) part, tapering to about 1 mm. wide at the lower part. The ureter is less than 1 mm. long and is sharply reflexed parallel to the long axis of the kidney. The pericardium is nearly 2 mm. long and 1 mm. wide. There is a large and conspicuous superposed ridge extending from just below the pericardium to the urethral portion of the kidney and going beyond the kidney almost to the mantle margin.

In cross section (fig. 7), this ridge, at the point in fig. 1 marked by the arrow, is seen to form a long fold which extends over the kidney causing it to appear rounded in a ventral view of the kidney, as shown in fig. 1. The lumen is regularly rounded and the two blood vessels appear on each side at the lower part of the section. A small ridge to the left of the lumen is shown in the figure. This ridge in the mantle is present in all species of the family.

A cross section of the kidney of *Helisoma anceps latchfordi* (fig. 8), taken at about the middle of the kidney, shows a less extensive ridge (RK) but is otherwise similar to typical *anceps*. The form of the section may vary when taken from different parts of the kidney, as is shown in several species of *Helisoma*.

Digestive System. The stomach is bulbous and tapers into the pyloris. The intestine loops around the stomach, passes over the oesophagus, turns backward in a long loop around the liver and then runs forward to the pseudobranch in the form of the rectum. The general form is like that of *Helisoma trivolvis* shown in fig. 1 on plate 48.

The buccal sac is short-ovate. The salivary glands are narrow and about twice as long as the buccal sac. They are joined behind.

The jaw (plate 49, fig. 1). There is one wide, low, arched superior jaw (about 1 mm. wide) and two narrow, ribbon-like lateral jaws somewhat longer than the superior jaw. The superior jaw is finely striated on its anterior face.

The radula has the variable formula 22-1-22 to 30-1-30, with 150 to 193 rows of teeth. A radula from specimens from Maple River, Michigan, is figured on plate 53, fig. 1. The center tooth is squarish with two short, wide cusps. The lateral teeth (1-5) have a squarish reflection which extends well below the lower margin of the base of attachment. The cusps are spade-shaped, the mesocone the longest and the ectocone the shortest. The ectocone of the fourth tooth is split into four small cusps. The intermediate teeth (6-7) are narrower than the lateral teeth, the base of attachment very short. The entocone is broken up into two or three small cusps and several small cusps appear on the outer edge of the tooth above the ectocone. The marginal teeth (8-14) are much narrower, this feature increasing toward the outer margin of the membrane where the teeth are very long and narrow (14). In the marginal teeth the entocone is broken up into fine serrations numbering from five to ten cusps, the number increasing in the outer teeth (compare 8 and 14). The mesocone becomes somewhat smaller but is not modified. The ectocone is distinct in the 8th tooth with three small cusps above it. From the 10th tooth this area changes to small serrations five to six in number. The outer marginal teeth appear like a saw, with one large tooth (the mesocone) in the center (see 14). The extreme outer marginals are vestigial.

The radulae of *anceps* and its races vary considerably, principally in the numerical formulae, but also in the number and position of the cusps. The table below indicates the extent of this variation. The columns are all as follows, reading from left to right: Locality, formula, lateral teeth, intermediate teeth, plate, and figure.

Helisoma anceps (Menke).

Maple River, Michigan	23-1-23 to 24-1-24	1-5	6-7	Plate 53, fig. 1
Unionville, Connecticut	23-1-23 to 25-1-25	1-5	6-7	Plate 53, fig. 3
Chautauqua Lake, New York	22-1-22 to 25-1-25	1-7	8-9	Plate 53, fig. 2
Moose Ear Creek, Wisconsin	26-1-26 to 27-1-27	1-6	7-9	
Cleveland, Oneida L., New York	25-1-25 to 27-1-27	1-6	7-8	

There are 150 to 160 rows of teeth.

Helisoma anceps sayi F. C. Baker.

Bayfield, Wisconsin	27-1-27 to 27-1-27	1-5	6-7	Plate 53, fig. 4

Helisoma anceps percarinatum (Walker).

Douglas Lake, Michigan	27-1-27 to 30-1-30	1-8	9-10	Plate 54, fig. 1

There are 193 rows of teeth.

Helisoma anceps royalense (Walker).				
Bamiji Lake, Ontario	25-1-25 to 27-1-27	1-8	9	Plate 54, fig. 2
	There are 170 rows of teeth.			
Helisoma anceps cahni F. C. Baker.				
Big Muskallonge Lake, Ontario	27-1-27 to 27-1-27	1-6	7-9	Plate 54, fig. 3
	There are 160 rows of teeth.			
Helisoma anceps latchfordi (Pilsbry).				
Meach Lake, Quebec	27-1-27 to 30-1-30	1-6	7-9	Plate 54, fig. 4
	There are 190 rows of teeth.			

For the above data more than forty specimens have been examined. In general form of teeth, there is complete agreement in all radulae examined, both from the same locality and from different places. The formulae vary and along with this variation, the numbers of lateral and intermediate teeth likewise vary.

Abnormal teeth are common in radulae of *Helisoma anceps*. In a specimen from Maple River, Michigan, the fourth lateral of the fifteenth row had the ectocone broken up into four small cusps (plate 53, fig. 1). In a specimen from Chautauqua Lake, New York, the center tooth of the 118th row was broken up into three small cusps and one large cusp. In the first lateral of the same row, the entocone was split into two small cusps (plate 53, fig. 2). In a specimen from Unionville, Connecticut, the fifth lateral of the ninetieth row had a split ectocone. The 8th and 9th teeth of this row had the intermediate in unusual form. This row shows the shape of the teeth on the left side of the membrane (plate 53, fig. 3, lower row).

In the races of *anceps*, the same tendency to form abnormal teeth is observed. A specimen of *sayi* from Bayfield, Wisconsin, had the center tooth of the seventy-fifth row with three small cusps on the left side and one small cusp on the right side of a central cusp. All of the laterals in this row had the entocone broken up into two small cusps (plate 53, fig. 4, lower right row). In a radula of *percarinatum* from Douglas Lake, Michigan, the first and second laterals of the 100th row had the entocone split into two smaller cusps (plate 54, fig. 1, lower row). A specimen of *latchfordi*, in the sixtieth row, had the central tooth with an extra cusp on each side of two smaller central cusps (plate 54, fig. 4, 60). All of the teeth of this race examined had two very small denticulations on the edge of the reflection above the ectocones (plate 54, fig. 4).

Geographical Distribution. The species of typical *Helisoma* inhabit North America from British America (Hudsons Bay) southward to Louisiana and Alabama and westward to the Rocky Mountains.

Species Considered as Valid. This, the typical subgenus of the genus *Helisoma*, contains one species with many races and a second species with two recognizable races.

Helisoma anceps anceps (Menke) 1830 (=*Planorbis bicarinatus* Say 1819 (preoccupied), *P. antrosus* Conrad, 1834)
Helisoma anceps sayi F. C. Baker
Helisoma anceps shellense F. C. Baker
Helisoma anceps percarinatum (Walker)
Helisoma anceps royalense (Walker)
Helisoma anceps rushi F. C. Baker
Helisoma anceps jordanense (Winslow)
Helisoma anceps unicarinatum (Haldeman)
Helisoma anceps striatum (F. C. Baker)
Helisoma anceps cahni F. C. Baker
Helisoma anceps latchfordi (Pilsbry)
Helisoma anceps portagensis (F. C. Baker)
Helisoma anceps aroostookense (Pilsbry)
Helisoma eucosmium (Bartsch)
Helisoma eucosmium vaughani (Bartsch)

Geological Distribution. Miocene?, Pliocene to Recent fauna.

Remarks. Typical *Helisoma* is characterized by a short and wide, somewhat bulbous penial complex without a notable constriction between the preputium and the vergic sac. There is a cup-shaped penial gland with a short, narrow, almost straight penial gland duct. The prostate and ovotestis are made up of many small diverticula radiating from a duct in fan-like pattern when seen in cross section. *Helisoma* differs from *Pierosoma* in its shorter penial gland duct, wider and shorter vergic sac, and generally different penial complex. From *Seminolina,* which resembles *Helisoma* in its short penial gland duct, it differs by its shorter duct. The radular teeth also differ from *Seminolina* in having the cusps sharply aculeate instead of rounded. The shell of *Helisoma* is also quite different from *Pierosoma* and *Seminolina* in its general bicarinate form with the spire and umbilicus both deeply concave.

As a subgeneric name, *Helisoma* has been known in molluscan literature for many years. Binney (1865, p. 112), Tryon (1870, p. 188), and Dall (1905, p. 81) cite the name, using, however, only characteristics of the shell for its distinction. In 1926 (p. 201) and in 1928 (I, p. 311), Baker elevated the group to generic rank, basing the distinction on the peculiar genital complex of the male organ. In 1931 (p. 584), the genus was diagnosed by Baker and the distinctions of the genitalia described and figured.

Authors generally have misquoted the type of the genus. The *Planorbis bicarinatus* of Sowerby, while with little doubt the same as *Planorbis bicarinatus* Say, has nothing to do with Say's species and Sowerby was probably not aware that there was another *bicarinatus*. Dall (1905, p. 84) cited the type as *Planorbis bicarinatus* (Say) Sowerby, which is incorrect, although the type is correctly cited on page 81. The citation of *Planorbis bicarinatus* Say, as has been made by some authors, is also incorrect. Say's species dates from 1817, Sowerby's from 1824.

A careful study of Sowerby's description and his two figures on plate clxxvii (fig. 4) leaves little doubt about the unity of his species with that of Say. Binney (1865, p. 124) thought it might be *Planorbis campanulatus* Say, but both figures and description point to *bicarinatus*. Binney based his opinion evidently on the lower fig. 4 of the plate, which is not clear, and might be mistaken for *campanulatus*. There is little question about the upper figure being intended for *bicarinatus*. Unfortunately this appropriate name can not be used, as it is preoccupied for a Paris Basin fossil. Conrad's *Planorbis antrosus* 1834 has been used in place of *bicarinatus,* but Menke's name precedes this by four years and must be accepted.

Regarding the name *Helisoma,* it is a Greek noun in the neuter gender and all specific names must, of course, also be neuter (H. B. Baker, 1930, p. 139).

Subgenus SEMINOLINA Pilsbry, 1934

Type by original designation *Helisoma scalare* (Jay)

1870. *Ameria* Dall, Ann. N. Y. Lyc. N. H., IX, p. 356. Example *Physa scalaris* Jay (non H. and A. Adams, 1855).

1886. *Thomsonia* Ancey, Le Naturaliste, VIII, p. 358; not of Signoret, 1879 (Hemiptera).

1931. *Thomsonia* Thiele, Handbuch, Teil 2, p. 479. Type *Planorbis scalaris* (Jay). As section of *Planorbis*.

1934. *Seminolina* Pilsbry, Proc. Acad. Nat. Sci. Phil., 86, p. 31. Type *Helisoma scalare* (Jay). Anatomy. As subgenus of *Helisoma*.

Shell (plate 80, figs. 7-12). Large, sinistral, physa-shaped or planorboid, with every gradation between these forms, usually widely or deeply umbilicated; surface smooth, usually glossy, without the thread-like striae of *Pierosoma*.

Animal (plate 70, fig. 3 (adult), fig. 2 (young)). With large velar area and long tentacles as in *Helisoma*. Color variable. In *scalare* olivaceous, in *duryi* and varieties dark olivaceous in old specimens, purplish on top of head, flecked with white. Bottom of foot dark horn or purplish, flecked with fine light dots. Tentacles lead color. Mantle yellowish or grayish over lung and kidney, with few black or brown spots. Immature specimens are more yellowish with few or no dots. The young animal is hyaline and transparent, the internal organs yellowish or pinkish.

ANATOMICAL CHARACTERISTICS

PLATE 28

GENITALIA. Male Organs (fig. 14). Seminal vesicle (SV) about 2.5 mm. long, varying in width, but 1 mm. wide at the center and about 0.5 mm. wide anteriorly and posteriorly of this area. The seminal vesicle is composed of many small glands. The ovisperm duct bears many small vesicles along its side for over 1 mm. below the seminal vesicle. Sperm duct nearly 3 mm. in length, of large diameter. Prostate (PRS) oblong, over 2 mm. in length composed of many diverticula arranged in fan-like rows. A section of the prostate near the middle shows sixteen rows of club-shaped diverticula (fig. 12). The prostate diverticula discharge into a separate duct, the prostate duct, with which the sperm duct connects posteriorly and the vas deferens anteriorly (see fig. 14). The vas deferens (VD) is about 10 mm. long, and is about half the diameter of the sperm duct. It is slightly enlarged (epiphallus) as it enters the vergic sac.

The penial complex (fig. 10) is about 3.5 mm. long. The lower sac or preputium (PR) is pyriform, 1.3 mm. wide at the upper part and less than 0.5 mm. wide at the male opening. There is one large retractor muscle (RM) which is split into four branches at the preputium and in some specimens (fig. 9) there may be one wide muscle of three branches with a narrow, separate muscle below. The muscles are attached to the upper part of the preputium. The supporting muscles (SM) usually form a wide band, split into three branches at the upper part of the preputium. In one specimen there were five narrow, separate supporting muscles, each with two branches, all placed near the lower end of the preputium (fig. 9).

The duct of the penial gland (DC) is rather short (3.5 mm. long) and tapers in diameter toward the end entering the vergic sac (fig. 6). The vergic sac is of about the same length as the preputium, ovate-pyriform in shape, about 1 mm. wide near the upper part of the sac. In some specimens examined (fig. 9), the preputium was pushed upward and the vergic sac appeared as though attached to the lower part of the preputium. In this condition, the penial gland duct extends from the top of the preputium and enters the vergic sac below the level of the duct's exit. This condition is observed in specimens in breeding stage.

Internally (fig. 11), the preputial sac contains several (four or more) narrow, slight, vertical ridges or pilasters (PL). The cavity of the preputium is partly filled by an elongate-ovate (irregularly paralleliform) penial gland attached by a short neck of less diameter to the body wall of the preputium through which the penial duct extents (GL, DG). In section (fig. 7), this gland is seen to be composed of two cup-like cavities, one, the inner cup, has several large glandular folds (GF) and the other, the outer cup, has several smaller folds attached to the wall of the cup (OC). The larger folds extend transversely across the cavity as shown in fig. 11, GL. The small cup is at the extreme end or tip of the gland. The gland duct enters the smaller cavity, as shown in fig. 7, DC. There is a narrow ridge or diaphragm which separates the vergic sac space from the preputial cavity. The gland duct enters the vergic space above this diaphragm as shown in fig. 11. The verge (V) is pyriform or reversed conic 0.9 mm. wide at the upper part and tapering to a point. The sperm canal has a central outlet.

Female Organs (plate 28, fig. 14). The spermatheca (S) is bulbous, wide and about 1 mm. long. Its duct (SPD) is 2 mm. long, rather wide and increases notably in diameter at the lower end where it enters the short (1 mm. long) vagina. The vagina narrows to about half its diameter at the female opening (VG). The uterus (U) is about 3 mm. long and is as wide as the diameter of the spermatheca. The nidamental gland (NG) is short (about 1 mm. long) and sac-like. The oviduct (OD) is about as long as the uterus, very wide, and bears the nidamental gland about midway of its length. The albumen gland (AL) is somewhat longer than wide and is composed of many small, gland-like vesicles (fig. 14, AL).

Hermaphrodite Organs. The ovotestis occupies the first and a part of the second whorls and is composed of ten or more rows of club-shaped diverticula of unequal length (fig. 13, plate 28). The free portion of the ovisperm duct is very short (about 0.7 mm.) both anterior and posterior of the seminal vesicle.

The genitalia of *Helisoma scalare* examined agree perfectly with the figures published by Pilsbry (1934, fig. 1, b, c, d). The peculiarities are the wide and pyriform penial complex, the short gland duct, the elongated, two-cupped penial gland and the large, sacculated seminal vesicle.

The several varieties under the name of *Helisoma duryi* (Wetherby) show some differences from *scalare* in their anatomy (plate 33). In *Helisoma duryi normale* Pilsbry, the genitalia are much elongated, due to the more widely-coiled shell (fig. 15). The seminal vesicle (SV) is much shorter in comparison (2 mm. long) and the gland sacs are larger. The sperm duct (SPD) is a long and narrow tube (7.5 mm. long). The prostate (PRS) is more elongated (5.5 mm. long) and contains a greater number of diverticula. The prostate duct is longer and the space between the entrance of the sperm duct and of the vas deferens is several times wider. The vas deferens (VD) is a long and narrow tube (over 20 mm. long). The spermatheca (S) is much longer and larger (3.5 mm. long) and is more elongate-ovate in shape. Its duct is longer (5.5 mm.) and much narrower. The uterus and nidamental gland are longer and narrower and the oviduct (OD) is narrow and much elongated. The free portion of the ovisperm duct is also longer. The albumen gland (AL) is more irregular in shape.

The penial complex is usually short and wide but varies somewhat in this respect (see figs. 8, 9, 12, 17, 18). Normally (figs. 17, 18), the preputial sac is as long as, or only a trifle longer than, the vergic sac, and is always wide. The penial gland duct is short, as in *scalare*. There is usually more of a constriction between the preputium and the vergic sac than in *scalare*. Figure 8 shows an abnormal form of penial complex and fig. 12 shows another in which the part of the preputial sac containing the penial gland has been pushed upward. In fig. 9, this feature is still further emphasized.

In *Helisoma duryi* (Wetherby), the preputial sac has been pushed upward as in *normale*. In *Helisoma duryi eudiscus* Pilsbry, there is considerable variation. In fig. 1, the gland duct is swollen in a bilobed form, while in fig. 2 it is very narrow. In fig. 7, the penial complex is very wide. Figure 5 shows the penial gland pushed upward in the preputial sac. Figure 6 shows the wider penial complex in an immature specimen with a shell 6.5 mm. in diameter. In two specimens examined, the penial gland was extended from the male opening and lay outside on the neck of the animal (fig. 13, *duryi*; fig. 16, *H. d. normale*). In fig. 16, it is shown just below the female opening.

The penial gland in the *duryi* complex is of about the same shape as that organ in *scalare*. In *H. d. eudiscus*, the external form is shown in fig. 4 and a section in fig. 3. There is the same division into an inner and an outer cup as in *scalare*. In *H. d. normale* (fig. 10), a longitudinal section shows the same features. In *Helisoma duryi*, the penial gland is short and wide. The gland of a half-grown specimen is shown in fig. 19.

The figures of the *duryi* complex agree with those by Pilsbry (1934, p. 34, fig. 1, f, g, h, i, j, k). As Pilsbry remarks on page 36, the anatomical differences are sufficient to separate *scalare* from *duryi* and its races.

Respiratory and Renal Systems. The pseudobranch (plate 28, fig. 8) is short and wide (P). There is a large crenulated ridge on the rectum (R) which runs out on the pseudobranch in a curve, to the right of the anal opening (A). The pseudobranch is 1.5 mm. long and about 1 mm. high. It is contractile and its size varies greatly in preserved specimens. There is a large pneumostome.

The kidney (plate 44, fig. 4) of *scalare* is rather short (4 mm. long), wider at the upper part near the pericardium (1 mm. wide). The ureter is directed diagonally backward. The pericardium is about 1 mm. long. A cross section of the kidney near the middle (fig. 25) shows a rather long, narrow crest or ridge, a small ovate lumen and two small veins placed just below the middle of the lumen. The small ridge in the mantle is shown to the left in both figures.

In *H. d. normale* (fig. 5), the kidney is longer (17 mm. long) and comparatively narrower (3 mm.) than in *scalare*. The ureter is about 2 mm. long and is bent backward against the lower part of the kidney. A cross section of the kidney near the middle (fig. 26) shows it to be more compressed than that of *scalare*, the crest or ridge bent more to the left but of about the same form. The lumen is more elongated and about two and one-half times as wide as high. The two veins are placed near the lower border of the lumen. The kidney of *Seminolina* is more depressed than in *Helisoma* and the lumen is comparatively larger.

Digestive System. The stomach and intestine are as in *Helisoma*, as are also the buccal sac and salivary glands.

Jaw (plate 49, fig. 4, *scalare*; fig. 14, *H. duryi normale*) as in *Helisoma*, the superior jaw with vertical striations on the inner face.

Radula (plate 64). In *scalare*, the center tooth (figs. 1, 89) is almost twice as wide at the base as at the summit of the reflection, the two broadly aculeate cusps of which reach the lower margin of the base of attachment. The lateral teeth (1-8) are about as broad as high and the reflection, which is tricuspid, extends below the base of attachment. The mesocone is roundly blunt, the entocone and ectocone broadly aculeate. The intermediate teeth (9-11) have the mesocone as in the lateral teeth, but narrower, the entocone as in the laterals. On the eleventh tooth, the entocone is split into two short, aculeate cusps. The ectocone in all intermediate teeth is split into two sharp cusps. The marginal teeth (12-21) are very long and narrow and claw-like. The mesocone is aculeate in all teeth but is always distinct. The entocone becomes very wide and is split into from four to seven small cusps. The ectoconic region on the outer margin of the tooth bears three very small cusps.

In another specimen from the same locality, the teeth are somewhat smaller (fig. 2). In *H. duryi normale*, from the Tamiami Trail (fig. 3), the teeth are all narrower than those of *scalare*, although the shell is much larger. The two cusps of the center tooth do not reach the lower margin of the base of attachment. The laterals (1-11) and the intermediate tooth (12) are narrow but the cuspidation is the same as in *scalare*. The marginal teeth (13-29) are similar to those of *scalare* differing only in being somewhat narrower. In a specimen from Paines Prairie (fig. 4), the teeth are more like those of *scalare*. Two rows are figured, the 55th and the 140th. The number of intermediate teeth is smaller in *normale* than in *scalare*. The figures on plate 64 agree with those published by Pilsbry (1934, p. 34, fig. 1a).

The formula for *scalare* is 27-1-27 to 29-1-29 and there are 160 to 190 rows of teeth. Pilsbry gives 33-1-33 as the formula (1934, p. 35). A number of membranes were examined but none gave the larger formula. The outer teeth are small and vestigial.

The formula of *normale* from the Tamiami Trail is 28-1-28 to 31-1-31 with 175 rows of teeth. In specimens from High Springs several radulae gave 27-1-27 as the formula. These specimens vary toward the race *intercalare*. From Paines Prairie, several membranes gave 28-1-28 and 29-1-29 with 165 rows of teeth. *H. d. eudiscus* from Silver Springs gave a formula of 27-1-27 to 28-1-28 with 154 rows of teeth. The variation in formulae is from 27-1-27 to 31-1-31 for the complex of *duryi* and to 33-1-33 for *scalare* as examined by Pilsbry.

For the anatomical data herein presented thirty-five specimens have been examined from the following localities, all in Florida:

Helisoma scalare
- Lake Butler. Collected by Dr. E. A. Andrews of the Johns Hopkins University

Helisoma duryi normale
- Tamiami Trail, 40 miles west of Miami. Collected by Paul P. McGinty, Boynton, Florida
- Canal west of Boynton, Palm Beach County. Collected by Paul P. McGinty, Boynton, Florida
- Bridge No. 32, on canal west of Miami. Collected by W. F. Shay, St. Louis, Missouri
- Paines Prairie, near Gainsville. Collected by T. van Hyning, Florida State Museum
- Santa Fe River, High Springs. Collected by T. van Hyning

H. duryi intercalare
Canal west of Boynton. Collected by W. F. Shay
Santa Fe River, High Springs. Collected by T. van Hyning

H. duryi eudiscus
Silver Springs, Marion County. Collected by T. van Hyning

Geographical Distribution. As far as known, this group is found only in the peninsula of Florida north to Bradford County. It is particularly abundant in the Everglade region of southern Florida.

Species Considered as Valid. Three species are recognized, one with several races.

Helisoma (Seminolina) scalare (Jay)
Helisoma (Seminolina) duryi (Wetherby)
Helisoma (Seminolina) duryi seminole Pilsbry
Helisoma (Seminolina) duryi normale Pilsbry
Helisoma (Seminolina) duryi intercalare (Pilsbry)
Helisoma (Seminolina) duryi eudiscus Pilsbry
Helisoma (Seminolina) preglabratum (Marshall)

For an extended account of the species of this subgenus see Pilsbry 1934, pp. 31-43.

Geological Distribution. Pliocene to Recent fauna.

Remarks. *Seminolina* is a characteristic group of *Helisoma*, differing from typical *Helisoma* in the presence of a physoid shell, not only in one distinct species, but in the variations of the races of another species. In its anatomy, it differs from typical *Helisoma* in the rounded mesocone of the lateral teeth which are distinctly aculeate in *Helisoma*. The duct of the penial gland is about twice as long as in *Helisoma* and the penial gland is more elongated, narrower, and less cup-shaped than in *Helisoma*.

Seminolina is a notable group of the subfamily Helisomatinae and one of the most variable genera as regards species. The physoid aspect of its type species, *Paludina scalaris* Jay, led the older conchologists to include it in *Physa* and in the genus *Ameria* of the family Bulinidae. The largest species, *Helisoma duryi* (Wetherby), is perhaps more variable than any other species found in America, its extremes being from typical Physa-shaped to flatly discoidal shell. The elongation of the spire always produces a physoid aspect. The races of *duryi* blend into each other and often three forms will occur in the same lot, as *normale*, *intercalare*, and *duryi*.

The *Helisoma duryi* complex includes several races more or less heavily infested with parasitic worms. These include *normale*, *intercalare*, *eudiscus*, and *duryi*. Many specimens were so badly infested that most of the organs, especially the genitalia and liver, were completely obliterated. *Helisoma scalare* was the least affected.

Subgenus PIEROSOMA Dall, 1905

Type by original designation *Planorbis trivolvis* Say

1865. *Helisoma* Binney (non Swainson), Land and FW. Sh. N. A., II, p. 112. No type cited. Includes mostly species belonging to *Pierosoma*

1872. *Helisoma* Tryon (non Swainson), Mon. Univ. FW. Moll. U. S., pp. 188, 198. Includes mostly species of *Pierosoma*. As subgenus

1883. *Helisoma* Fischer (non Swainson), Man. de Conch., p. 509. Type *Planorbis trivolvis* Say. As section of *Planorbis*

1899. *Helisoma* Martens (non Swainson), Biol. Cent. Amer. Moll., p. 381. Includes species now referred to *Pierosoma*

1905. *Pierosoma* DALL, Alaska Moll., pp. 81, 85. Type *Planorbis trivolvis* Say. As section under subgenus *Helisoma*

1918. *Pierosoma* WALKER, Miscel. Pub. Mus. Zool., Univ. Mich., No. 6, p. 11. Type *Planorbis trivolvis* Say. As section of subgenus *Helisoma*

1921. *Pierosoma* GERMAIN, Rec. Ind. Mus., XXI, pp. 6, 49. Type *Planorbis trivolvis* Say. As subgenus

1923. *Pierosoma* WENZ, Fossil. Cat., Pars 22, p. 1522. Genotype *H. (Pierosoma) trivolvis* (Say.) As subgenus.

1926. *Pierosoma* F. C. BAKER, Trans. Wis. Acad. Arts and Science, XXII, p. 202. Type *Planorbis trivolvis* Say. As subgenus

1928. *Pierosoma* F. C. BAKER, Fresh-water Moll. Wis., I, p. 329. Type *Planorbis trivolvis* Say. Genitalia and radula. As subgenus

1931. *Pierosoma* F. C. BAKER, Proc. Zool. Soc. London, p. 586. Type *Planorbis trivolvis* Say. Genitalia and radula. As subgenus

1931. *Pierosoma* THIELE, Handbuch, Teil 2, p. 479. Type *Planorbis trivolvis* Say. As section of *Planorbis*

1934. *Pierosoma* PILSBRY, Proc. Acad. Nat Sci. Phil., 86, p. 30. As subgenus

Shell (plate 80, figs. 13-15). Large, sinistral, of few whorls, the last whorl large and capacious, the early whorls usually flattened and carinate above, widely umbilicate below; spire of the adult shell usually flattened and sunk below the level of the body whorl; aperture notably expanding, even flaring in some specimens, the outer lip thickened within; sculpture of coarse growth lines and conspicuous spiral lines; surface usually dull, never glossy as in *Seminolina*.

Animal (plate 70, fig. 7, *H. trivolvis macrostomum;* fig. 8, *H. trivolvis fallax*). Body long and somewhat narrow, rounded before, the foot narrowly pointed behind; velar area well-developed; tentacles long and filiform; eyes at base of tentacles as in other Planorbidae. Color usually dark horn, in some species reddish or yellowish, the body flecked with streaks or spots; mantle spotted, as in *trivolvis,* or without spots, as in *pilsbryi;* the head and foot are usually lead color. In the young, the tentacles are very long and slender, the body dark horn color flecked with white spots; the eyes black; viscera reddish through the shell; foot also somewhat reddish, especially on the front portion (plate 70, fig. 6).

ANATOMICAL CHARACTERISTICS

PLATE 24 (*Planorbis trivolvis* Say)

GENITALIA. Male Organs (fig. 15). Seminal vesicle (SV) elongated (3.5 mm. long, 0.5 mm. wide) composed of many small vesicles. It occupies almost half of the length of the ovisperm duct. Sperm duct (SPD) long and narrow (about 4 mm. long). Prostate (PRS) about 4.5 mm. long and 1 mm. wide, composed of fourteen rows of diverticula emptying into a short prostate duct which connects with the sperm duct and from which the long (15 mm.) vas deferens (VD) extends and passes to the vergic sac. There is only a very slight enlargement (epiphallus) of the vas deferens as it enters the vergic sac. A cross section of the prostate (fig. 13) shows the fourteen rows of diverticula to be of unequal length and the whole section to be fan-shaped.

The penial complex (fig. 11) is usually about 5 mm. long. The preputium (PR) is very wide (1.5 mm.) and cylindrical in shape. The vergic sac (VS) is of the same length as the preputium but is very narrow, the preputium rapidly narrowing as it receives the vergic sac. The vergic sac increases to double its diameter near the end where the vas deferens enters. There is a single, wide retractor muscle (RM) which may be split into several branches (figs. 1, 5). The duct of the penial gland (DC) is very long and narrow (8 mm. to 9 mm. long) and extends from the upper part of the preputium to a point just above the diaphragm (see fig. 8). Normally the duct lies coiled on the preputium just over the penial gland and adherent to the preputium, bound down by many small muscles covering the preputial sac. There is usually one wide band of supporting muscle (SM). The duct is shown in fig. 5 partly uncoiled.

Internally (fig. 8), the preputial cavity (PR) contains a number of small vertical folds or pilasters. There is a large, cup-shaped penial gland (GL) about 1 mm. in diameter, which is contracted near its attachment to the body wall of the preputium to form a narrow, rounded neck. The duct (DG) passes through the wall of the preputium and extends to the vergic sac where it enters just above the diaphragm (DV). A vertical section of the gland (fig. 4) shows the circular cup to be of considerable depth (about 1 mm.), the inner walls lined with many vertical folds (GF). The bottom of the cup contains many small folds placed longitudinally. The gland duct (DC) enters the bottom folds of the cup. The walls of the cup (BW) are very thick. Another form of gland is shown in fig. 14.

The vergic sac contains the elongated verge (V) which is enlarged at the upper end and tapers downward to a point. The seminal canal has a central exit beyond which a small, triangular papilla extends, as shown in fig. 10. There is a large muscular ring or diaphragm (D) which is capable of considerable extension and contraction, causing the diaphragm to be a narrow muscular ring or a comparatively thin membrane which nearly closes the opening between the preputium and vergic sac. Figure 10, somewhat diagrammatic, shows the relationship between the diaphragm, the verge, and the entrance of the penial gland duct, which is a trifle too high in the figure.

The penial complex often assumes a bilobate form, the preputium extending upward until it is higher than the vergic sac (fig. 1). A vertical section of such a condition (fig. 2) shows the penial gland to be placed at the summit of the preputial extension. The relationship of the verge and the penial gland duct is also shown in this section. In young specimens of three and one-half whorls, the preputium and vergic sac form a single wide, elongate-pyriform penial complex with a short penial gland duct (fig. 3). This condition is suggestive of typical *Helisoma*, which has a wide penial complex and a short duct, and indicates, it would seem, a development of the *Pierosoma* group from the *Helisoma* group.

Female Organs (fig. 15). The spermatheca (S) is elongate-pyriform and about 2 mm. long. The spermathecal duct (SD) is 3 mm. long, narrow, and somewhat enlarged at the lower end where it enters the short and wide vagina (VG). The uterus (U) is about 7 mm. long, narrow at the vagina and widening to double this diameter near the prostate where it unites with the nidamental gland (NG), which is wide and bulbous. The oviduct (OD) is short and wide (about 3.5 mm. long and 0.5 mm. wide) and somewhat coiled. The albumen gland (fig. 7) is squarish and is composed of many small follicles. In side view, it is seen to be cleft to accommodate the passage of the intestine on its lower surface (fig. 6, IN). There is a large carrefour (fig. 15, CF) into which the duct of the albumen gland enters (DA).

Hermaphrodite Organs (fig. 15). The ovotestis (OT) occupies about one whorl of the shell. It is composed of about thirteen rows of diverticula which radiate from the ovisperm duct. In a cross section near the anterior end (fig. 9), there are six diverticula entering the ovisperm duct, four of which branch twice, one is simple, unbranched, and one is branched four times. The branching is not uniform throughout the ovotestis. The free portion of the ovisperm duct (SO) is short, that portion near the ovotestis being very short (about 1 mm.). The end near the oviduct is longer (1.5 mm.). A portion of the duct beyond the seminal vesicle (for about 1.5 mm.) is provided with small vesicles along the side which are probably to be considered as parts of the seminal vesicle.

No figures other than those by the writer (1923, 1931) have been published. The chief characteristic is the large, wide, and somewhat pyriform preputium and the very long penial gland duct. This duct is similar in mature specimens of the different races and species, but there is some variation in the details of the sexual organs, as would be expected.

The genitalia of the races of *Helisoma trivolvis* vary in minor details which are figured on plate 29. In *H. t. pseudotrivolvis* (=*lentum*, figs. 1-6), there is considerable variation. Figure 1 shows the penial complex a trifle wider than in typical *trivolvis*. In fig. 2, the penial complex is vertically sectioned showing a wider verge and a somewhat differently shaped penial gland. Figure 3 shows the manner in which the penial gland duct is coiled on the outside of the preputium (DC). In fig. 4, the penial gland is shown in vertical section, the cup being somewhat diagonal. As this gland is capable of some muscular contraction and expansion this variation in shape is of no taxonomic importance. In fig. 5, the preputial sac has been pushed upward placing the vergic sac on the side of the preputium. The form of the penial gland, the verge, and the great length of the penial gland duct is indicated. In fig. 6, the penial gland has been protruded from the male opening and is lying on the neck of the animal, near the female opening.

The genitalia of a race of *trivolvis* (*lentum*) from the type locality, New Orleans, Louisiana, are shown in figs. 7-13. Figure 8 shows the general form of the penial complex. In fig. 11, the penial gland has been extended from the male opening, and is shown in its typical cup-shaped condition. Figure 12 shows the gland exserted with the verge beside it, also exserted. In fig. 13, the shape of the entire verge of this specimen is shown. It is peculiarly shaped at the distal end. In fig. 7, the penial complex is shown in its typical position when the gland is exserted from the male opening. The cup-shaped gland (GL) is normal. Characteristics of the verge are shown in figs. 9 and 10. Figure 9 shows the entire verge which has been sectioned in two places to show the location of the sperm canal near the center of the verge. The waist-like constriction just above the middle of the verge shows where this organ was compressed when it was protruded through the muscular ring or diaphragm. The shape and central position of the sperm canal outlet is shown in fig. 10, from the front and from the side. The small papilla at the end of the verge is well shown. This feature is characteristic of all members of the group *Pierosoma*.

The large race of *trivolvis* (*macrostomum*) differs little from the typical form. Figures 14 and 16 on plate 29 show the normal condition of the penial complex and fig. 15 a condition in which the preputium has been greatly pushed upward.

In *H. trivolvis fallax*, a small race of *trivolvis*, a specimen was examined in which the penial complex had a very large, pyriform preputium and a small, cylindrical vergic sac (fig. 17). The penial gland of this specimen was quite normal (fig. 18).

The great variation in the form of the retractor muscle is well shown on plate 29, especially in figs. 1, 2, 3, 5, 7, 8, 14, 15, 16, and 17. It varies from a narrow band of muscle to a wide band with several branches.

THE GENITALIA OF SPECIES ALLIED TO TRIVOLVIS

Species East of the Rocky Mountains

A closely related species, *Helisoma chautauquense* F. C. Baker (plate 29, figs. 19-22), differs from the *trivolvis* complex in the wider, more pyriform preputium, shorter and wider vergic sac, and especially the much shorter penial gland duct (DC) which recalls the *Seminolina* group (fig. 22). The penial gland, however, does not differ from that of *trivolvis*. In the immature stage of this species, the whole penial complex is wider, especially the vergic sac, and the gland duct is very short, the whole male organ resembling that of typical *Helisoma* (fig. 19).

In a rather distinct species, *Helisoma truncatum* (Miles), the genitalia are similar in general form but show some minor peculiarities (plate 26, fig. 13). The seminal vesicle (SV) is of greater diameter and less length, and the ovisperm duct is of slightly greater length (4 mm.). The prostate (PRS) is much shorter (1.7 mm.) and wider, and consists of fifteen diverticula, which are on a short prostate duct placed at the right edge of the group of diverticula (fig. 10). There are about eleven main diverticula, several of which are branched at the end. The cross section of the prostate of *truncatum* differs slightly from that of *trivolvis*. The duct of the spermatheca is somewhat longer than in *trivolvis*. The penial complex is wider than in *trivolvis* and is similar to some of the races, *lentum* for example (figs. 6, 7, 12). The penial gland (fig. 9) does not differ from that of *trivolvis*.

A larger species, *Helisoma pilsbryi* (F. C. Baker), living in Wisconsin, Michigan, and the northern part of the United States and southern Canada, is figured on plate 25. The genitalia (fig. 4) are similar in general form to those of *trivolvis*, but there are some differences. The spermatheca (S) is narrower and shorter (1.3 mm.) but the duct is long. The prostate is shorter. The seminal vesicle is shorter and wider. The ovotestis diverticula are very long. In the penial complex (fig. 5), the preputium is twice as long as the vergic sac and both are wider than in *trivolvis*. Variations in shape and position of the vergic sac are shown in figures 1, 6, and 7. In the penial gland, the cup is much shallower than in *trivolvis* (fig. 2). The genitalia are somewhat shorter than in *Helisoma corpulentum*.

A larger form than *pilsbryi* is known as *H. pilsbryi infracarinatum* F. C. Baker which is common in southern Canada. While regarded as a race of *pilsbryi* there are some features of the genitalia which indicate that is a very distinct race (plate 25, fig. 13). The seminal vesicle (SV) and ovisperm duct (SO) are similar to these organs in *pilsbryi*, but the prostate (PRS) is twice as long (5.7 mm.) and much larger, comparatively. There is also a greater number of diverticula. The spermatheca is twice as long (3 mm.) and the duct is longer (3.5 mm.). A cross section of the prostate near the lower end shows seventeen rows of long, club-shaped diverticula (fig. 12). In the penial complex (fig. 8), the preputium is normally very wide, pyriform, with the vergic sac small and narrow and about half as long as the preputium. In fig. 9, a penial complex is shown with the preputium pushed upward. The immature penial complex (fig. 10) is very wide with a short duct, as in other immature forms of *Pierosoma*.

Helisoma corpulentum (Say) and its races inhabit the northern part of the United States and southern Canada. The genitalia greatly resemble those of *H. pilsbryi infracarinatum*. The principal features of the genitalia are figured on plate 31.

In *corpulentum* (fig. 3), the seminal vesicle (SV) is long and wide (4 mm. long, 0.7 mm. wide). The prostate is 5 mm. long, 1.5 mm. wide, and 1.5 mm. high (fig. 2). In cross section, this is seen to be composed of twenty long diverticula arranged fan-wise. The ovotestis (OT) occupies a trifle over one whorl and consists of about eighteen rows of long diverticula (fig. 1). The spermatheca (S) is 2 mm. long and is placed at the end of a very long duct (5 mm.). In form, the spermatheca is more nearly like that of *infracarinatum*. The normal form of the penial complex is shown in fig. 5, the preputium and vergic sac being about equal in length. Figure 4 shows a specimen in which the vergic sac is shortened and the upper part of the preputium has been pushed upward, a common characteristic in *Pierosoma*. The form of the penial complex in immature individuals is shown in figs. 6 and 7, fig. 6 being from a younger specimen.

A race of *corpulentum*, *multicostatum* F. C. Baker, has the genitalia much as in the typical form. Figures 9 and 10 show the form of the penial complex in immature individuals. Figure 11 is from an immature individual in which the vergic sac has been lowered to the side of the preputium. Figure 12 also shows an immature condition. In fig. 13, the penial complex of a fully mature individual is shown, the preputium pushed upward and the long penial gland duct uncoiled (it is 14 mm. long). The penial gland is shown in section in fig. 8.

Another race found only in Lake Vermilion, Minnesota, *H. c. vermilionense* F. C. Baker, shows no essential differences in its genitalia. The penial gland is rather shallow (fig. 15) but this could be from contraction. Figure 14 shows one form of the penial complex when the preputium is pushed upward. The gland duct is partly uncoiled. Figures 16, 17, and 18 show the penial complex of immature individuals, progressively from 16 to 18. The penial duct is short in figs. 16 and 17 but much longer in fig. 18, the latter nearer maturity. Two forms assumed by the verge are shown in figs. 17 and 18.

Helisoma whiteavesi F. C. Baker, a related species, apparently rare in Canada, is similar in its genitalia to *Helisoma corpulentum*. The penial complex of an adult individual is shown in fig. 19. The vergic sac differs from that of the *corpulentum* group in being very long (5.5 mm.) and slender. It is about as long as the preputium. The gland duct is very long (24 mm.). Compare fig. 19 with fig. 13, the shells being of the same size and age.

A large *Pierosoma*, *Helisoma magnificum* (Pilsbry), living in Greenfield pond, near Wilmington, North Carolina, resembles the northern *pilsbryi* and *corpulentum*. The prostate is 7 mm. long and more than 1 mm. wide and high. There are thirteen rows of diverticula. The spermathecal duct is very long (12 mm.) and narrow, and the spermatheca is 3 mm. long. The organs of the female system are long and narrow. The penial complex (fig. 20) has a pyriform preputium and a cylindrical vergic sac. The penial gland duct is very long. Internally, the complex shows a large gland and a cylindrical verge, both nearly filling their respective cavities (fig. 21). A cross section of the penial gland is shown in fig. 22. It is much like that of *trivolvis*.

SPECIES OF THE ROCKY MOUNTAINS AND WESTWARD

Several species and races of *Pierosoma* occur in the western part of the United States and Canada. One of the most abundant and widely distributed species is *Helisoma subcrenatum* (Carpenter), the genitalia of which are figured on plate 30 (specimen not quite mature). Figure 15 pictures the whole genitalia, the organs spread out. The seminal vesicle is 2 mm. long and is notable for the number of rather long vesicles, principally bordering the gland, which is much wider than the ovisperm duct. The sperm duct (SPD) is short (2 mm. long) and the vas deferens is narrow and about 7 mm. long. The prostate is about 2 mm. long and is composed of twenty-four rows of diverticula, arranged fan-wise when seen in section (fig. 12). There is a short prostate duct at each end of the prostate which joins the sperm duct beneath the prostate. The spermatheca (S) is about 1 mm. long and the duct is long and narrow and about 2 mm. long. The uterus (U) is narrow anteriorly and widens posteriorly into the nidamental gland (NG), which is a large organ 1 mm. wide. The oviduct (OD) is a narrow tube about 2 mm. long.

The penial complex is about 3.5 mm. long in fully adult specimens (figs. 17, 19). The vergic sac is slightly shorter than the preputium. The preputium is widely pyriform while the vergic sac is narrow and cylindrical. The penial gland duct is not very long (3 to 4 mm.) and is normally coiled on the preputium. In vertical section (fig. 13), the penial complex shows a large penial gland (GL), a rather thick diaphragm (D), and a thick, somewhat sausage-shaped verge (V). In section, the penial gland (fig. 11) is similar to that organ in *trivolvis*. In immature individuals, the penial complex is very wide and the duct is very short (fig. 10). In fig. 15, the penial duct and complex is of a young specimen. In adult or old specimens, there is more difference between the preputium and vergic sac and the duct is always longer. These differences are shown in figs. 17 and 18 (compare with figs. 10 and 15).

The genitalia of *subcrenatum* differ from those of the *trivolvis* group in the greater number of prostate diverticula, shorter penial gland duct, when adult, and the presence of the aculeate vesicles in the seminal vesicle.

A relative of *subcrenatum*, *H. plexatum* (Ingersoll), is figured on plate 30, fig. 4 (genitalia). The general characteristics of *plexatum* are like *subcrenatum*. The seminal vesicle (SV), however, is different in the absence of the digitate vesicles and is more like the seminal vesicle in *pilsbryi*. The prostate is 5 mm. long and more than 1 mm. wide. The spermatheca (S) is very narrow, over 2 mm. long, and the duct is 5 mm. long or nearly three times the length of the spermatheca. It resembles the spermatheca of *trivolvis*. The vergic sac is small and less than half the length of the preputium (fig. 1). In vertical section, the penial complex shows the penial gland to be compressed as in *subcrenatum* (fig. 3) and not globular as in *trivolvis*. The penial gland duct is longer than in *subcrenatum* (figs. 1, 2, 3), resembling *trivolvis* in this respect (compare figs. 1 and 17). The penial gland is shown in section in fig. 5. The verge (V) is large and long ovate in form when at rest (fig. 6). The shapes assumed during extension into the vergic sac cavity are shown in figs. 7, 8, and 9. The retractor muscles are as in *subcrenatum*.

The penial complex of a form of *subcrenatum* from Pass Lake, Fidalgo Island, Puget Sound, Washington, is figured on plate 32 (fig. 8). It is similar in form to the penial complex of *subcrenatum* figured on plate 30 (fig. 17), the preputium, however, being more cylindrical and less pear-shaped and the vergic sac is relatively longer. The presence of the two small and narrow retractor muscles is noteworthy.

Another form related to *subcrenatum*, but believed to be of specific rank, is *Helisoma horni* (Tryon) from Paul Lake, British Columbia. The genitalia are different from both *subcrenatum* and *plexatum* (plate 26, fig. 3). The seminal vesicle is similar to that of *plexatum*. The prostate is about 3 mm. long, and 1 mm. wide and has thirteen rows of large, club-shaped diverticula (fig. 5). These are much wider and less in number than in *subcrenatum*. The spermatheca (S) is bulbous, about 1 mm. in length and the duct is 3 mm. long, widening as it enters the narrow vagina. The penial complex (fig. 1) has a long vergic sac enlarged at the outer end. The preputium is pushed upward. The gland duct is about as long as in *plexatum*. The penial gland (fig. 2) is like that organ in *trivolvis*. A section through the sperm duct, oviduct and nidamental gland (fig. 4) indicates the relationship between these organs.

Many years ago Tryon described a small *Planorbis* from Pueblo Valley, Oregon, calling it *Planorbis oregonensis* (now *Helisoma oregonense*). This species has been one of the rarities of western Planorbidae. Specimens collected in Tooele County, Utah, by Mr. J. Henderson belong to this species and the anatomy of this small planorbid is now available. On plate 28, fig. 2, the principal organs of the genitalia are shown.

The seminal vesicle is about 1 mm. long and the ovisperm duct about 3 mm. long. The latter bears short lateral vesicles for a large part of its length, as in *plexatum*. The prostate is short (about 2 mm. long) and bears sixteen rows of long and narrow diverticula (fig. 3). The spermatheca is bulbous, about 0.7 mm. in length and connects with the long and narrow vagina by a duct slightly more than 1 mm. in length. The shape of the spermatheca is like that of *horni* but the duct is shorter. The penial complex (fig. 1) has a large, pyriform preputium with the lower part lengthened. The vergic sac is short, swollen at the end, and almost half the length of the preputium. The penial gland duct is very long (5 mm.). There is one retractor muscle (sometimes split into two smaller muscles), attached to the lower part of the preputium, and one band of supporting muscle. The penial gland (fig. 4) is round, rather short, and attached to the wall of the preputium by a short, wide neck. In vertical section (fig. 5), the cup is circular, with relatively few large vertical folds and a number of pavement-like folds in the bottom of the cup, to which the gland duct is connected (DC).

A *Helisoma* abundantly distributed in California, and believed to be a race of the Mexican *Helisoma tenue* (Phil.), has been named *H. tenue californiense* by F. C. Baker. The genitalia are shown on plate 32, fig. 1. The seminal vesicle (SV) is wide and long (5 mm.). It swells in the center and tapers at each end. It is made up of many small vesicles. The ovisperm duct is 5.5 mm. long, narrow, and for two-thirds of its length is bordered, on one side only, by many small, rounded vesicles. These are probably part of the seminal vesicle system. The sperm duct (SPD) is 3 mm. long and is very narrow. The prostate is short (1.3 mm. long) and wide (1 mm.) and has twelve rows of long, club-shaped diverticula (fig. 6, the prostate in section). The vas deferens (VD) is a long, narrow tube 11 mm. long. The spermatheca (S) is pyriform, 1.5 mm. long, with a long, narrow duct about 2.5 mm. long, enlarged as it enters the long and narrow vagina (VG). The ovotestis is made up of very large, club-shaped diverticula in eleven rows.

The penial complex (fig. 3) has a large, pyriform preputium 2.2 mm. long and a cylindrical vergic sac 1.5 mm. long. The penial gland (fig. 5) is short and cup-shaped with many vertical folds. Its duct is relatively short (5 mm.). Figure 2 shows the penial complex with the preputium pushed upward, the vergic sac placed at the side. There is a wide, very muscular diaphragm. The verge (fig. 2, V) is wide above but tapers to a narrow point below. Figure 7 shows the penial complex of a specimen from Prospect Park, near Redlands, California. The preputium is pyriform and very wide at the summit. It is 3 mm. long. The verge is 3 mm. in length and is not as pyriform in shape as in the other Californian specimens examined. The gland duct is over twice as long (14 mm.) as in the Shandon specimens. The Prospect Park specimens are very large, which probably accounts for the great length of the duct. There is one large retractor muscle and one or two supporting muscles.

The genitalia of *californiense* are peculiar in the great length and size of the seminal vesicle, in the very short prostate, and in the sessile penial gland.

One of the largest of west American planorbids is *Helisoma traskii* (Lea). The genitalia of this species are shown in fig. 17 on plate 32. The seminal vesicle is shaped like that organ in *californiense* (see fig. 1) and is coiled in much the same manner. It is about 9 mm. long (when extended) and 1 mm. wide and is composed of many small vesicles. The ovisperm duct (SO) is very long (16 mm.) two-thirds of which bears small, widely-spaced vesicles on the lateral margin. The sperm duct is 6 mm. long and 0.5 mm. wide for two-thirds of its length and tapers to about half this diameter near the point of contact with the prostate duct. The prostate (PRS) is very long (6.5 mm.) and about one-fourth as wide as long (1.5 mm. wide). There is a short prostate duct branch at each end of the sperm duct beneath the prostate. In section (fig. 12), the prostate shows fourteen rows of diverticula of varying length, unbranched. In the section, the nidamental gland (NG) is composed of several large diverticula. The vas deferens is a long, narrow tube (25 mm. long). The spermatheca (S) is of unusual length (3.5 mm.), is club-shaped and is placed at the end of a very long duct (10 mm.) which enlarges at its point of entrance into the short, narrow vagina (VG). The ovotestis (OT) consists of large, club-shaped diverticula of varying length, thirteen rows being counted in a section at the proximal end of the ovotestis (see fig. 17, OT). The albumen gland (AL) is squarish and is made up of small follicles.

The penial complex (fig. 14) has a pyriform preputium 4 mm. long and a sausage-shaped vergic sac 3 mm. long (PR, VS). The penial gland duct (DC) is of medium length (9 mm. long) and is a narrow tube. The retractor muscle (RM) is wide and is divided into two main branches, united at their attachment near the upper part of the preputium. The supporting muscle (SM) is rather narrow and is branched several times in its attachment to the upper part of the preputium on the opposite side from the retractor muscle.

Internally (fig. 11), the preputium has a large penial gland (GL) which is attached to the wall of the preputium by a thick neck or base. Sectioned vertically (fig. 13) the penial gland is seen to have a large cup bordered by large vertical folds (GF). The base of the cup has many folds to which the penial gland duct is attached (DC). One specimen of *traskii* had a bifid tentacle (fig. 16).

The genitalia of *Helisoma traskii* are peculiar in the large prostate, the elongated spermatheca on an unusually long duct, and in the generally long and narrow uterus and vas deferens. It is different from *californiense* in the size of the prostate and in the size and length of the spermathecal duct. The shorter penial gland duct allies *traskii* with *californiense* and separates it from *plexatum*.

Another large species found in California is *Helisoma occidentale* (Cooper), living characteristically in Klamath Lake, Oregon. Unfortunately, the material had been preserved in formalin and the anatomy could not be worked out in a satisfactory manner. The penial complex is like that of *californiense* figured on plate 32, fig. 3. The vergic sac, however, is more elongated at the distal end. The greater number of specimens examined had the penial complex as shown in fig. 10, the preputium pushed upward and the vergic sac attached to the side about halfway between the extremities of the penial complex. The penial gland was about as in *traskii* (fig. 13). The verge, coiled in the vergic sac, is shown in fig. 9. Other details are not available from these specimens.

Respiratory and Renal Systems. The pseudobranch of *Helisoma trivolvis* (plate 24, fig. 12) is very wide, somewhat bilobed, with a narrow crest or ridge extending down the rectum (R) and over the pseudobranch at about the center. The anal opening is to the left of the ridge. There is a large pneumostome (PS).

The shape of the pseudobranch does not vary to any degree in the different species and races of *Pierosoma*, excepting in the general shape which in many cases is broadly rounded below and not bilobed (see plate 25, fig. 11). Several of these are figured on the following plates: *pilsbryi*, plate 25, fig. 3; *infracarinatum*, plate 25, fig. 11; *truncatum*, plate 26, fig. 11; *subcrenatum*, plate 30, fig. 16; *californiense*, plate 32, fig. 4; *traskii*, plate 32, fig. 15.

The kidney of *Helisoma trivolvis* (plate 44, fig. 2) is elongated, 12.5 mm. long and 2 mm. wide at the upper part near the pericardium. The ureter is 1 mm. long and is directed backward, parallel to the length of the kidney. There is a conspicuous crest or ridge extending down the center of the kidney from just below the pericardium to within 1 mm. of the lower end of the organ. A cross section of the kidney made at about the middle portion (plate 44, fig. 9) shows the ridge to be rather short and narrow and placed at about the middle of the kidney. The lumen is rounded and the veins at each end are large and placed at the center of the margin of the lumen. In the race *lentum* (plate 44, fig. 11), a section near the lower end shows a large, ovate lumen with the veins at the lower corners. The ridge is approximately like that feature in *trivolvis*. In *macrostomum*, the largest race of *trivolvis*, a section made near the lower end shows a small, much-elongated lumen with the veins at the lower lateral corners (fig. 10). The whole kidney is much larger and much thicker with a relatively small ridge.

The species and races of *Pierosoma* show considerable variation in the form of the lumen, and especially in the form and position of the ridge, which is found in all species of *Helisoma* and its subgenera. Several of these are figured on plate 44 and need no special comment. Those figured are: *pilsbryi*, section near middle, fig. 12; *infracarinatum*, near middle, fig. 17; *magnificum*, near middle, fig. 14; *corpulentum*, near middle, fig. 15; *multicostatum*, section near lower end, fig. 16; *truncatum*, near middle, fig. 13; *subcrenatum*, near middle, fig. 21; *plexatum*, section near lower end, fig. 22; (compare figs. 21 and 22 and note difference in ridges); *horni*, near middle, fig. 23; *occidentale*, near middle, fig. 18; *depressum*, near middle, fig. 19 (note difference in two races); *traskii*, near middle, fig. 20; *californiense*, near middle, fig. 24; *oregonense*, near lower end, fig. 6.

The kidney of *corpulentum* (fig. 3) is somewhat shortened and bent toward the pericardium. The ridge is broad at the upper part and then narrowed for the greater part of its length. A cross section is shown in fig. 15. Compare this with the kidney of *trivolvis*, figs. 2 and 9.

The kidney of *californiense* is figured on plate 45 (fig. 4). It is relatively short and variable in width. A cross section made through the upper part (fig. 5, at B in fig. 4) shows the roundly-ovate lumen occupying the greater part of the kidney, with the veins at the middle on each side. A section made near the lower end of the kidney (fig. 6, at A in fig. 4) shows a very wide and flattened lumen with the veins at each end, and a high, pointed ridge. Compare with fig. 21 on plate 44.

Digestive System. The digestive system of *Helisoma trivolvis* (plate 48, figs. 1, 2) is characteristic of that of all species of *Pierosoma*. The size of the organs differs in the various species. The oesophagus (OE) is a narrow tube as it leaves the buccal sac, increasing several times in diameter as it passes to the crop portion of the stomach. It is about 10 mm. long. The stomach is composed of a short crop (CR), a bilobed gizzard (GZ), and an elongated pyloris (PY). The intestine (IN) makes a complete turn over the oesophagus, extends backward around the liver, performs another loop, and runs forward to the columella muscle. The intestine is 33 mm. long from the end of the pyloris to the rectum. The rectum is 10 mm. long, is larger in diameter than the intestine, and is particularly characterized by the presence of a frilled crest or ridge (RD) which extends the whole length of the rectum and ends over the pseudobranch. In fig. 2, the stomach is seen from below showing the position and form of the blind sac or caecum (BS) which is attached to the pyloris just below the opening of the liver (OLV). This blind sac is present in all species of *Pierosoma*.

The buccal sac (BP) is a pear-shaped organ, 2 mm. long and 1.5 mm. high. The oesophagus leaves the oral cavity near the upper posterior portion of the pouch. There are two strong buccal retractor muscles (BR). The salivary glands (SG) are two in number, 3 mm. long, which enter the buccal cavity near the oesophagus by a long, narrow duct (1 mm. long) on each side. The salivary glands form a loop, their posterior ends connected.

There is not much variation in the form of the buccal sac in *Pierosoma*. In some species, as *pilsbryi, corpulentum, tenue californiense*, and *subcrenatum* (plate 70, fig. 12), the whole sac is a trifle more elongated, especially in the fore part. There is reason to believe, however, that the more elongated aspect may be due to distortion in the animal when killed. At the back end of all sacs there is a rounded or elongated radula sac (plate 70, fig. 13, RL) which has to do with the formation of the radula membrane. This varies in form in some of the species.

The jaw in *Pierosoma* is always of three parts. The superior jaw is oblong, wide and low, sometimes somewhat arcuated. The face of the superior jaw is marked by fine striations which form a more or less denticulate border to the jaw when seen with high magnification. There are two long and narrow lateral jaws one on each side bordering the lips of the animal, and usually seen in the form of a question mark. The jaw of *Helisoma trivolvis* is shown on plate 49, fig. 2, and this is characteristic of all members of the subgenus. The jaws of some other species are figured as follows:
truncatum, plate 49, fig. 3; *pilsbryi*, fig. 5; *infracarinatum*, fig. 8; *corpulentum*, fig. 15; *magnificum*, fig. 16; *oregonense*, fig. 6; *subcrenatum*, fig. 7; *horni*, fig. 9; *plexatum*, fig. 10; *traskii*, fig. 12; *occidentale*, fig. 13; *californiense*, plate 50, fig. 1.

Radula. The radula of *Pierosoma* is similar to that of *Seminolina* in the bluntly rounded mesocone of the lateral teeth. The radula of the type species, *Helisoma trivolvis*, is shown on plate 55, fig. 1.

The center tooth has two spade-shaped cusps which do not reach the lower margin of the base of attachment. The lateral teeth (1-10) have a quadrate reflection which is tricuspid, the entocone and ectocone sharp and spade-shaped, the mesocone rounded. The intermediate teeth (11-13) have the reflection somewhat narrower and more elongated than the lateral teeth, the entocone breaking up into three small, sharp cusps and the ectocone region developing two or three cusps above the ectocone on the outer margin of the tooth. Marginal teeth (14-18) still narrower, claw-like, with the entocone broken up into four to five small cusps and the ectocone into four or more small cusps on the upper, outer margin of the tooth. The extreme outer marginal teeth are small, very narrow, and with slight denticulations. There is some variation from the type described above, some of the lateral teeth developing two cusps in place of the one ectocone, as shown in fig. 4.

The radulae of the races of *trivolvis* differ little from the type species. On plate 55, several of these are shown, *lentum* (figs. 6, 7) and *pseudotrivolvis* (=*lentum*) figs. 2, 3. The radula of the large race, *macrostomum*, is shown on plate 56, fig. 2. In *chautauquense* (plate 55, fig. 5), the lateral teeth (1-11) are narrower than in *trivolvis*. In *winslowi* (plate 56, fig. 1), the lateral teeth are also narrower. In *pilsbryi* (plate 56, fig. 3) and *infracarinatum* (plate 56, figs. 4, 5) the laterals are more quadrate, similar to those of *trivolvis*, but the marginals show some variation. In *truncatum* (plate 57, figs. 1, 2) the laterals are narrower (as in *chautauquense* and *winslowi*). In several laterals of *truncatum*, there was observed to be considerable splitting of the entocone and ectocone cusps (see fig. 2, plate 57, teeth 1, 5-10). In the large *magnificum*, the intermediate teeth are very long and narrow, the ectocone is placed high up on the margin, and the extra cusps of the entocone appear later in the series (plate 57, fig. 4, 21-26). The marginal teeth are also narrow and the cuspidation is different from that in *trivolvis* and other species of *Pierosoma* (fig. 4, 27-41). In *corpulentum*, the teeth are arranged in a similar manner to those of *trivolvis* (plate 57, fig. 3). The races *vermilionense* and *multicostatum* (plate 58, figs. 2, 3) are similar in form. In *whitcavesi* (plate 58, fig. 1), the teeth are similar in form to those of the *corpulentum* group.

In the western group of *Pierosoma*, *Helisoma plexatum* has narrower lateral teeth than *trivolvis* (plate 59, fig. 1). In specimens from another locality, however, the early laterals are quadrate (fig. 2). In specimens of *plexatum* from Rexburg, Idaho, many of the laterals, and some of the marginals, in one specimen had the mesocone broken and wavy and otherwise modified (plate 58, fig. 4). Other individuals were normal (fig. 5). A lateral and two intermediate teeth of a specimen from Smartweed Lake, Colorado, are shown in fig. 6 on plate 58. A form of *subcrenatum* from Pass Lake, Puget Sound, Washington, has quadrate teeth, similar to those of *trivolvis* (plate 59, fig. 5). Another form from Lost Lake, Puget Sound, had very wide, low lateral teeth (plate 60, fig. 1). In one specimen from this locality, the center tooth of the eighty-eighth row had seven small cusps and the fifth lateral had two sharp entoconic cusps (plate 60, fig. 2). Specimens from Skagit County, Washington, were normal, with quadrate laterals (plate 60, fig. 2).

Typical *subcrenatum* from Cottonwood Pass, near Gypsum, Colorado, is shown on plate 61, fig. 2. There are eight subquadrate lateral teeth and four intermediate teeth. The marginal teeth are normal as to cuspidation. An allied species, *horni*, has a large, somewhat obliquely formed mesocone on the lateral teeth, which are not as quadrate as in *subcrenatum* (1-9), the intermediate teeth are narrow and the entocone and ectocone are not broken into smaller cusps (10-14). The marginal teeth (15-32) are less cuspidate than similar teeth in *subcrenatum*. The outer marginals (32) are small and more or less vestigial (see plate 60, fig. 7).

The large *traskii* from Kern Lake, California, is peculiar in several respects (plate 60, figs. 4-6). A nearly complete row (the ninetieth) is shown in fig. 5. In the center tooth, the two large cusps extend a considerable distance below the lower margin of the base of attachment. The lateral teeth (1-8) are longer than wide and are unmodified tricuspid. The intermediate teeth (9-10) have the entocone and ectocone split into small cusps. The marginal teeth (11-22) are wide and the denticulation is very irregular, small interstitial cusps appearing among the larger cusps in some teeth (as 11, 13, 14, 17). In another row (eightieth), the last intermediate tooth and the first marginal tooth were peculiar in this respect (fig. 6). In the eighty-second row of another specimen, this feature was well marked (fig. 4).

In another large species of *Pierosoma* from Klamath Lake, Oregon (*occidentale*, plate 61, fig. 1), the teeth are more uniform with but little splitting of the cusps. The radula differences between the two species *occidentale* and *traskii* are very marked, as shown on plates 60 and 61.

In specimens of *tenue californiense* from Shandon, California (plate 63, fig. 2), the center tooth has two wide, spade-shaped cusps extending below the base of attachment. The laterals (1-11) are at first wider than high, the cusps rather short, but toward the marginal teeth they become narrower. The entocone and the ectocone tend to split in some teeth (as 1, 3, 6, 7). There is one narrow intermediate tooth (12). The marginal teeth (13-19) are narrow, the entocones 4-6 cuspidate. In the 100th row of the same membrane, the entocone and ectocone of the lateral teeth were largely modified by splitting (see fig. 2).

In a radula from a specimen living in the San Bernardino Mountains, there were eleven laterals, one intermediate tooth and nine or more marginals. No splitting was observed in this radula but in another membrane all of the laterals were abnormal (plate 59, fig. 4) in the sixtieth row, small cusps appearing irregularly on the entoconic region. The entocone of the first lateral was broken up into four small cusps. The intermediate and marginal teeth were narrow and many of them abnormal in the splitting of the entocone (as 14, 16, 17). The mesocone in all teeth was more or less irregular. In fig. 6, a very abnormal eleventh tooth from another specimen is figured. The relatively small species *oregonense* (plate 61, fig. 3) has narrow laterals (1-8) and intermediate teeth (9-10). The marginals are normal for the group.

The radula formulae of the different species vary more or less and the individual radulae may differ in number of teeth in a row. For comparison all of the species of *Pierosoma* which have been examined, together with all of the localities represented, are shown in the following table. This also indicates the material studied and the source from which the material was obtained. More specimens were dissected for the genitalia than for the radulae. From one to seven specimens of each were examined.

Species	*Formulae*	*Locality*	*Rows*	*Collector*
trivolvis	23-1-23 to 26-1-26	Canandaigua L., New York	143-167	F. C. Baker
trivolvis	23-1-23 to 24-1-24	Green Lake, Wisconsin	148	F. C. Baker
trivolvis	23-1-23 to 24-1-24	Devils Lake, Wisconsin	126	F. C. Baker
trivolvis	23-1-23 to 25-1-25	Murphy Creek, Wisconsin	150-152	F. C. Baker
trivolvis	23-1-23 to 24-1-24	Sturgeon Bay, Wisconsin	110-134	F. C. Baker
pseudotrivolvis (=*lentum*)	23-1-23 to 24-1-24	St. Joseph, Illinois	141-167	F. C. Baker
pseudotrivolvis	24-1-24 to 25-1-25	Peoria, Illinois	149	F. C. Baker
pseudotrivolvis	22-1-22 to 24-1-24	Reelfoot L., Tennessee	180	Mr. Firkins
pseudotrivolvis	23-1-23 to 24-1-24	Mammoth Spgs., Arkansas	131-155	C. A. Lloyde
pseudotrivolvis	24-1-24..........	Ada Lake, Oklahoma	150-160	A. D. Buck
pseudotrivolvis	23-1-23 to 25-1-25	Trinity R., Texas	150-181	E. P. Cheatum
lentum	26-1-26 to 28-1-28	New Orleans, Louisiana	147-186	E. C. Faust
fallax	26-1-26 to 28-1-28	Near Boston, Massachusetts	144-170	W. J. Clench
macrostomum	27-1-27 to 30-1-30	Bayfield, Wisconsin	180	F. C. Baker
macrostomum	27-1-27..........	Moose Ear Creek, Wisconsin	185	F. C. Baker
macrostomum	31-1-31 to 32-1-32	Saskatoon, Canada	173	D. S. Rawson
macrostomum	37-1-37 to 39-1-39	L. Grauveau, Canada	154-210	A. LaRocque
chautauquense	24-1-24 to 26-1-26	Chautauqua L., New York	127	F. C. Baker
truncatum	20-1-20 to 21-1-21	Winnebago L., Wisconsin	126-129	F. C. Baker
winslowi	27-1-27 to 29-1-29	Arbor Vitae L., Wisconsin	125	A. R. Cahn

magnificum	42-1-42 to 43-1-43	Wilmington, North Carolina	180	P. Bartsch
pilsbryi	27-1-27 to 29-1-29	Chetek L., Wisconsin	180-185	F. C. Baker
pilsbryi	27-1-27 to 29-1-29	Prairie L., Wisconsin	205	F. C. Baker
pilsbryi	28-1-28 to 29-1-29	Chetek L., Wisconsin	185	F. C. Baker
pilsbryi	28-1-28.	Moose Ear Creek, Wisconsin	185	F. C. Baker
infracarinatum	32-1-32 to 37-1-37	Basswood R., Ontario	140-163	A. R. Cahn
infracarinatum	31-1-31 to 38-1-38	Bimaji L., Ontario	140-151	A. R. Cahn
infracarinatum	25-1-25 to 27-1-27	As above (immature)	140-153	A. R. Cahn
infracarinatum	30-1-30 to 37-1-37	Mille Lacs, Ontario	140-155	A. R. Cahn
infracarinatum	32-1-32 to 35-1-35	Rideau R., Ontario	171-177	A. LaRocque
corpulentum	36-1-36 to 41-1-41	Lake La Croix, Ontario	165-190	A. R. Cahn
corpulentum	25-1-25 to 28-1-28	As above (immature)	109-117	A. R. Cahn
corpulentum	32-1-32 to 35-1-35	Knife Lake, Minnesota	140-150	A. R. Cahn
multicostatum	40-1-40 to 45-1-45	Kahnipiminanikok L., Minnesota	163-170	A. R. Cahn
multicostatum	38-1-38 to 41-1-41	Mille Lacs swamp, Ontario	145-150	A. R. Cahn
multicostatum	30-1-30 to 37-1-37	As above (immature)	152	A. R. Cahn
vermilionense	30-1-30 to 31-1-31	Vermilion L., Minnesota	120-123	F. C. Baker
vermilionense	25-1-25 to 27-1-27	As above (immature)	119	F. C. Baker
whiteavesi	36-1-36 to 42-1-42	Mille Lacs, Ontario	139-154	A. R. Cahn
subcrenatum	25-1-25 to 27-1-27	Gypsum, Colorado	123-130	J. Henderson
subcrenatum var.	29-1-29 to 32-1-32	Pass Lake, Washington	150-160	J. Henderson
subcrenatum var.	28-1-28 to 29-1-29	Lost Lake, Washington	134-146	J. Henderson
subcrenatum var.	28-1-28 to 31-1-31	Pondilla L., Washington	175-180	J. Henderson
subcrenatum	30-1-30 to 32-1-32	McMurray, Washington	150-170	J. Henderson
plexatum	26-1-26 to 30-1-30	Columbine L., Colorado	140-173	J. Henderson
plexatum	25-1-25 to 30-1-30	Smartweed L., Colorado	155-170	J. Henderson
plexatum	26-1-26 to 30-1-30	Grand Mesa, Colorado	155	J. Henderson
plexatum	27-1-27 to 28-1-28	Gooseberry Creek, Utah	150-165	J. Henderson
plexatum	27-1-27 to 31-1-31	Rexburg, Idaho	145-155	J. Henderson
horni	32-1-32.	Paul Lake, British Columbia	110-114	D. S. Rawson
oregonense	20-1-20 to 21-1-21	Tooele Co., Utah	111-117	J. Henderson
occidentale	31-1-31 to 32-1-32	Klamath L., Oregon	150-160	J. Henderson
traskii	28-1-28 to 30-1-30	Kern Lake, California	161-182	S. Siegfus
californiense	24-1-24 to 25-1-25	Shandon, California	155-160	Hanna & Church
californiense	26-1-26 to 27-1-27	San Juan R., California	150	J. D. Hanna
californiense	24-1-24 to 27-1-27	Near Redlands, California	140-157	S. S. Berry

TABLE SHOWING RANGE OF FORMULAE IN DIFFERENT SPECIES

23 to 27	*25 to 28*	*20 to 21*	*28 to 32*	*32 to 47*
trivolvis	*fallax*	*truncatum*	*subcrenatum* var.	*infracarinatum*
pseudotrivolvis	*lentum*	*oregonense*	*occidentale*	*corpulentum*
chautauquense	*subcrenatum*		*traskii*	*multicostatum*
californiense	*plexatum*			*whiteavesi*
				horni

This table shows that, while there is wide variation in the formulae of the radulae in *Pierosoma*, the range within the species is fairly constant. The difference in many membranes is due to the presence of several extra marginal teeth on some radulae which do not appear on others. It is to be observed, also, that the immature animal usually has a smaller formula than the same species when adult. This is noted in the table under several species (*infracarinatum*, *corpulentum*, *vermilionense*, and *multicostatum*). *Magnificum* has the largest formula, 42-1-42 to 43-1-43.

Geographical Distribution. The subgenus *Pierosoma* is distributed from Ungava, Labrador, Mackenzie, and Alaska southward to Georgia, Louisiana, Texas, and California, the whole of Mexico, and southward, on the west coast of South America, to Peru. In the West Indies, it is known from Cuba, Jamaica, Haiti, and other islands. The metropolis of the group is in North America, principally in southern Canada and northern United States, where the largest number of species and races is found. Southward the number of species rapidly decreases, only two species being known from South America and four from the West Indies. These appear to be species which have migrated southward in past geological time, possibly by the aid of migrating birds.

In the recent fauna, no member of the *Helisoma* group is found outside of North and South America. In Pleistocene deposits, however, a form of *Helisoma* allied to *trivolvis* has been reported by Lindholm (1933) from the Kolyma River in northeast Siberia beyond the Arctic Circle. It would appear that this planorbid is not referable to *trivolvis* but to some form like *horni* or *subcrenatum*. The latter species is common in northwestern British America and also occurs in Alaska. The Siberian form should probably be allied with *subcrenatum*. Lindholm called it *Helisoma trivolvis kolymense* but it might be better to designate it simply as *Helisoma kolymense* Lindholm until more is known about its affinities. As suggested by Pilsbry (1933, p. 137), it might represent a migration by the way of the old land bridge between Alaska and Siberia, used by both man and other mammals during Pliocene and Pleistocene times.

Species Considered as Valid. The large number of species attributable to the genus *Helisoma*, subgenus *Pierosoma*, are listed below. The names *Helisoma (Pierosoma)* are understood to be prefixed before each specific name in the list.

ammon (Gould)
binneyi (Tryon)
calodermum (Pilsbry)
caribaeum caribaeum (d'Orbigny)
caribaeum guatemalense (Clessin)
chautauquense F. C. Baker
contrerasi (Pilsbry)
corpulentum corpulentum (Say)
corpulentum vermilionense F. C. Baker
costaricense (Preston)
equatorium (Cousin)
eyerdami Clench and Aguayo
foveale (Menke) (= *affine* C. B. Adams)
horni (Tryon)
kolymense Lindholm
magnificum (Pilsbry)
multicostatum multicostatum F. C. Baker
multicostatum whiteavesi F. C. Baker
occidentale occidentale (Cooper)
occidentale depressum F. C. Baker
oregonense (Tryon)
peruvianum (Brod.)
pilsbryi pilsbryi (F. C. Baker)
pilsbryi infracarinatum F. C. Baker
plexatum (Ingersoll)
salvini (Clessin)
subcrenatum subcrenatum (Carpenter)
subcrenatum disjectum (Cooper)
tenue tenue (Philippi)
tenue boucardi (Fischer and Crosse)
tenue californiense F. C. Baker
tenue chapalense (Pilsbry)
tenue exaggeratum (Martens)
tenue pertenue F. C. Baker
(= *applanatus* Martens preoccupied)
tenue sinuosum (Bonnet)
tenue strebelianum (Fisch. and Crosse)
traskii (Lea)
trivolvis trivolvis (Say)
trivolvis fallax (Haldeman)
trivolvis lentum (Say)
trivolvis macrostomum (Whiteaves)
trivolvis turgidum (Jeffreys)
(= *intertextum* (Sowb.))
truncatum (Miles)
tumens (Carpenter)
winslowi (F. C. Baker)
wyldii (Tristram)

Remarks. *Pierosoma* is a very distinct group of *Helisoma*, distinguished from the subgenera *Helisoma* and *Seminolina* by peculiarities of genitalia and radula. The duct of the penial gland is always longer in adult animals than in the other groups mentioned. Some of the special anatomical features have been described and figured in the preceding pages. The shell is large and distinctly sinistral, especially in immature specimens. *Pierosoma* is the dominant planorbid group in North America north of Mexico.

Subgenus PLANORBELLA Haldeman, 1842

Type by original designation *Planorbis campanulatus* Say

1842. *Planorbella* Haldeman, Mon. FW. Univ. Moll., Physidae, p. 14. Type *Planorbis campanulatus* Say (plate 1, figs. 7-11, 1844)
1861. *Adula* H. Adams, Proc. Zool. Soc., p. 145. Type *Planorbis multivolvis* Case. Non *Adula* H. and A. Adams, 1857
1865. *Planorbella* Binney, L. FW. Sh. N. A., II, p. 109. Type *Planorbis campanulatus* Say. As subgenus
1865. *Adula* Binney, op. cit., p. 111. Type *Planorbis multivolvis* Case. As subgenus
1869. *Ancaeus* H. Adams, Proc. Zool. Soc., p. 275. Non *Ancaeus* Fauvel, 1863. In place of *Adula*, preoccupied
1870. *Planorbella* Dall, Ann. Lyc. Nat. Hist. N. Y., IX, p. 351. Type *Planorbis campanulatus* Say. As subgenus
1870. *Adula* Dall, op. cit., p. 351. Type *Planorbis multivolvis* Case. As subgenus
1870. *Planorbella* Tryon, Contr. Hald. Mon., pp. 188, 196. Type *Planorbis campanulatus* Say. As subgenus
1870. *Adula* Tryon, op. cit., pp. 188, 197. Type *Planorbis multivolvis* Case. As subgenus
1883. *Planorbella* Fischer, Man. de Conch., p. 509. Type *Planorbis campanulatus* Say. As section of *Planorbis*
1883. *Adula* Fischer, Man. de Conch., p. 509. Type *Planorbis multivolvis* Case. As section of *Planorbis*
1884. *Planorbella* Tryon, S. and S. Conch., III, p. 106. Type *Planorbis campanulatus* Say. As subgenus
1884. *Adula* Tryon, op cit., p. 106. Type *Planorbis multivolvis* Case. As subgenus.
1886. *Adula* Clessin, Conch. Cab., XVII, p. 33. Type *Planorbis multivolvis* Case. As subgenus
1886. *Planorbella* Clessin, op. cit., p. 33. Type *Planorbis campanulatus* Say. As subgenus
1902. *Planorbella* F. C. Baker, Moll. Chi. Area, II, p. 294. Type *Planorbis campanulatus* Say. As subgenus
1905. *Planorbella* Dall, Alaska Moll., pp. 81, 85. Type *Planorbis campanulatus* Say. As section of subgenus *Helisoma*
1912. *Planorbella* Hannibal, Proc. Mal. Soc. London, X, p. 159. Type *Planorbis campanulatus* Say. As subgenus
1918. *Planorbella* Walker, Miscel. Pub. Mus. Zool., Univ. Mich., No. 6, pp. 12, 94. Type *Planorbis campanulatus* Say. As subgenus
1921. *Planorbella* Germain, Rec. Ind. Mus., XXI, pp. 7, 66. Type *Planorbis campanulatus* Say. As subgenus
1926. *Planorbella* F. C. Baker, Trans. Wis. Acad. Sci. Arts, XXII, p. 202. Type *Planorbis campanulatus* Say. As subgenus
1927. *Hypsogyra* Lindholm, Trav. Com. l'Etude Lac Baikal, II, p. 181. New name for *Adula* H. Adams, 1861, preoccupied
1928. *Planorbella* F. C. Baker, Fresh-water Moll. Wis., I, p. 345. Type *Planorbis campanulatus* Say. Radula and genitalia. As subgenus
1931. *Planorbella* F. C. Baker, Proc. Zool. Soc., p. 586. Type *Planorbis campanulatus* Say. Genitalia and radula. As subgenus
1931. *Adula* F. C. Baker, op. cit., p. 566. Type *Planorbis multivolvis* Case. As synonym of *Planorbella*
1931. *Hypsogyra* Thiele, Handbuch, Teil 2, p. 479. Type *Planorbis multivolvis* Case. As section of *Planorbis*
1931. *Planorbella* Thiele, Handbuch, Teil 2, p. 479. Type *Planorbis campanulatus* Say. As section of *Planorbis*

Shell. Sinistral, of medium size, resembling *Pierosoma* in general form but the last whorl notably restricted behind the aperture which is campanulate (plate 80, figs. 16-18, *campanulatum* (Say); figs. 19-21, *multivolvis* (Case)).

Animal (plate 70, fig. 1, *campanulatum*). With short, wide foot, oval in shape, otherwise like *Picrosoma*. Color dark reddish brown or blackish, bottom of foot very dark reddish with flecks of white, tentacles dark colored with indistinct white rings. There is some variation in the shades of color. The animal is usually very slow in movement.

ANATOMICAL CHARACTERISTICS

PLATE 27 (*Helisoma campanulatum* (Say))

GENITALIA. Male Organs (fig. 15). The seminal vesicle (SV) is short and wide (about 2 mm. long and 0.5 mm. wide) and the vesicles are very large and comparatively few in number. They are mostly attached laterally. A few short vesicles extend down the ovisperm duct for about 1 mm. The sperm duct (SPD) is about 4 mm. long and 0.3 mm. wide. The prostate (PRS) is long (4.5 mm.) with a short prostate duct at each end which connects with the sperm duct and the vas deferens. There are fourteen rows of diverticula of varying length, the median ones the largest, the outer ones the smallest. Some of the diverticula are branched toward the end, the section figured (fig. 12) showing four such branches. The section also shows the fan-like pattern of the diverticula. The vas deferens (VD) is a long and narrow duct (16 mm. long).

The penial complex (fig. 11) is much like that of *Helisoma trivolvis*. The preputium is distinctly pear-shaped, 1.5 mm. long, the vergic sac (VS) smaller, shorter (1.5 mm. long) and club-shaped, and very narrow at its junction with the preputium. The penial gland duct (DC) is very long (5.5 mm.) and narrows considerably at each end where it enters the preputium and the vergic sac. Normally, the long penial gland duct is coiled on the preputium between this organ and the vergic sac, as shown in fig. 9, DC. Usually, there is one more or less branched retractor muscle (RM) but in some specimens two retractors were observed (fig. 9). There are several (1-3) narrow supporting muscles (figs. 5-8, 10, 11) or there may be one wide band with several smaller muscles. In fig. 9, two small muscles are shown below the retractor muscles. These are attached to the wall of the mantle cavity and not to the columella muscle.

Internally (fig. 10), the preputium has several vertical folds or pilasters and a muscular, cup-shaped penial gland (GL) which is attached by a small neck to the wall of the upper third of the preputium. In section (fig. 1), the gland is cup-shaped, one side of the cup being thicker than the other as shown in the figure (BW). There are many vertical, thick-walled folds (GF) and a number of small, flat, pavement-like folds in the bottom of the cup from which the gland duct (DC) proceeds to the exterior of the preputium. The space between the preputium and the vergic sac is almost closed by a thick muscular ring or diaphragm (fig. 3, D) which is dependent between the walls of the preputium. The penial gland duct enters the vergic sac immediately above this diaphragm (DV). The verge (fig. 10, V) is club-shaped, tapering rapidly toward the end.

In figs. 5 to 7, the penial complex of *H. campanulatum smithi* is shown indicating how the preputium becomes pushed upward and the vergic sac appears to descend to the middle of the preputium. In fig. 8, the penial complex of *H. campanulatum canadense* is shown with the preputium notably pushed upward.

Female Organs (fig. 15). The spermatheca (S) is very long (2.5 mm.), sac-like and tapers to the long (5.5 mm.), narrow spermathecal duct (SD). The vagina (VG) is 1 mm. long and is very narrow. The uterus (U) is long (7.5 mm.) and narrow. The nidamental gland (NG) is about 4 mm. long, very wide, and sac-like. The free oviduct (OD) is about 2 mm. long and is about twice as wide as the sperm duct. There is a large, elongated carrefour (CF). The albumen gland (fig. 2) is ovately rounded and is composed of many small follicles. The space for the passage of the intestine is conspicuous (fig. 2, IX).

Hermaphrodite Organs (fig. 15). The ovotestis (OT) consists of eight or more rows of club-shaped diverticula, some of which may branch two or three times, as shown in the section fig. 4 (FOV), this branching rendering the counting of rows difficult. The figure shows fourteen rows on the surface and but eight entering the ovisperm duct. The free portion of the ovisperm duct (SO) is 3 mm. long near the oviduct but only 1 mm. long near the ovotestis.

The only previous description and figures of the genitalia of *Helisoma campanulatum* are by F. C. Baker (1931, p. 585, plate iv) where the penial complex is shown (plate 27, figs. 10-11 of this work).

Respiratory and Renal Systems. The pseudobranch (plate 27, fig. 13) is leaf-shaped, broadly ovate, with a ridge down the center which is a continuation of the ridge on the rectum (R). The pneumostome is large.

The kidney (plate 45) is similar to that of *Pierosoma* as represented by *Helisoma trivolvis*. Sections through the kidney of *H. campanulatum wisconsinense* are shown in figs. 15, 16, and 17. In fig. 15, the section through the upper part shows a large rounded lumen with a large vein on each side near the middle. The ridge does not begin until lower down on the kidney. Figure 16 shows a section through the middle of the kidney. The lumen is larger than in fig. 15, the veins are at the lower part on each side, and the ridge is just beginning to show. In fig. 17, taken through the lower part of the kidney, the lumen is smaller, the veins relatively larger, and the ridge forms a high crest. All varieties of *campanulatum* show essentially this form of kidney.

Digestive System. The general digestive system does not differ from that of *Helisoma trivolvis*. The buccal sac is much elongated, differing in this respect from many of the species of *Pierosoma*.

The jaw (plate 49). The superior jaw (of *smithi*, fig. 11) is elongated and low, somewhat arched, its face covered with vertical striations as shown in fig. 20. The lateral jaws are about as in *Pierosoma*.

The radula (plate 62). Typical *campanulatum* (fig. 1) has a wide, bicuspid center tooth, the cusps not reaching the lower margin of the base of attachment. The lateral teeth (1-7) are squarish, tricuspid, with the mesocone bluntly rounded, the entocone and ectocone aculeate. The intermediate teeth (8-9) have smaller, sharper mesocones and the entocone and ectocone are modified by the addition of smaller cusps. The marginal teeth (10-13) are long and narrow, somewhat claw-like, with the entocone wide and armed with from four to eight small cusps. The mesocone is small and spade-shaped. The ectocone is modified to form three small cusps. The outer marginal teeth (20) are simply serrated and much smaller than the earlier marginal teeth.

The races *wisconsinense* and *canadense* (figs. 2, 3) differ little in their radulae from typical *campanulatum*. *H. campanulatum smithi* is also similar (fig. 4), the lateral teeth showing a gradual change in the form of the mesocone. The teeth 6-9 might all be called intermediate, since the mesocone is alike in all. *Smithi* has a larger tooth formula than any of the other races of *campanulatum*. The radulae of the subgenus *Planorbella* are in all respects like those of *Pierosoma*.

The formulae of the different races are shown in the table below:

Race	*Formula*	*Locality*	*Rows*	*Collector*
campanulatum	20-1-20 to 22-1-22	Oneida Lake, New York	120	F. C. Baker
c. wisconsinense	21-1-21 to 22-1-22	Muskellunge L., Wisconsin	125	A. R. Cahn
c. wisconsinense	21-1-21	North Star Lake, Wisconsin	132	F. C. Baker
c. canadense	21-1-21 to 23-1-23	Sturgeon L., Ontario	123-129	A. R. Cahn
c. canadense	21-1-21 to 23-1-23	Basswood R., Ontario	139	A. R. Cahn
c. smithi	26-1-26.	Douglas L., Michigan	130-135	F. Smith

Helisoma campanulatum wisconsinense was also studied anatomically from Lake Nipissing, Ontario.

Geographical Distribution. *Planorbella* has been collected from Great Slave Lake, Labrador, Quebec, and Ontario south to New York, Ohio, and Illinois. Westward it extends to North Dakota and Nebraska. It is essentially a group of the northern part of the United States and Canada. In this area it varies considerably and several races have been recognized. These appear to be mostly local races, not geographical, possibly environmental variations.

Species Considered as Valid. The following species and races are recognized:

Helisoma (Planorbella) campanulatum campanulatum (Say)
Helisoma (Planorbella) campanulatum wisconsinense (Winslow)
Helisoma (Planorbella) campanulatum davisi (Winslow)
Helisoma (Planorbella) campanulatum canadense F. C. Baker
Helisoma (Planorbella) campanulatum collinsi F. C. Baker
Helisoma (Planorbella) campanulatum michiganense F. C. Baker
Helisoma (Planorbella) campanulatum rudentis (Dall)
Helisoma (Planorbella) campanulatum smithi (F. C. Baker)
Helisoma (Planorbella) multivolvis (Case)

Geological Distribution. Pleistocene to Recent fauna.

Remarks. Except for the campanulate aperture of the shell there is nothing in the anatomy to separate *Planorbella* from *Pierosoma*. The genitalia, with the long penial gland duct and the cup-shaped penial gland, the pseudobranch, and the kidney are all like these organs in *Pierosoma*. The radula is also the same. The shape of the shell, with its closely-coiled whorls and particularly the bell-shaped form of the aperture, may be features characteristic enough to retain *Planorbella* as a subgenus of *Helisoma*.

H. Adams has erected the group *Adula* (preoccupied) to admit the very peculiar *Planorbis multivolvis* Case, a species living in Howe Lake, Michigan. As the race *collinsi* of *Helisoma campanulatum* approaches this species in the form of the shell, it would appear that the group name is without value in nomenclature. Lindholm (1927) coined a new name, *Hypsogyra*, in place of the preoccupied names *Adula* and *Ancaeus*. Should this species prove, after anatomical investigation, to have characteristics different from *Planorbella*, it should bear Lindholm's name. It is very rare and the animal is wholly unknown. It seems, from the features of the shell, perfectly safe to merge the group with *Planorbella* (see plate 80, figs. 19-21).

Genus CARINIFEX W. G. Binney, 1863

Type by original designation *Planorbis newberryi* Lea

1863. *Carinifex* Binney, Smith. Check-List of Shells. Type *Planorbis newberryi* Lea. As genus

1864. *Megasystropha* Lea, Proc. Acad. Nat. Sci. Phil., p. 5 (footnote). Type *Planorbis newberryi* Lea. As genus

1865. *Carinifex* Binney, L. and FW. Sh. N. A., II, p. 74. Type *Carnifex newberryi* (Lea). As genus

1865. *Carinifex*, Amer. Jour. Conch., I, p. 50, plate vii, figs. 6-7

1870. *Megasystropha* Tryon, Con. Hald. Mon., p. 84

1870. *Carinifex* Tryon, Con. Hald. Mon., pp. 187, 214 Type *Carinifex newberryi* (Lea). As genus

1870. *Carinifex* Dall, Ann. N. Y. Lyc. Nat. Hist., IX, pp. 344, 353. Type *Planorbis newberryi* Lea. As genus

1883. *Carinifex* Fischer, Man. de Conch., p. 508. Type *Carinifex newberryi* (Lea). As subgenus of *Choanomphalus*

1884. *Carinifex* Tryon, S. and S. Conch., III, p. 105. Type *Carinifex newberryi* (Lea). As genus

1912. *Carinifex* Hannibal, Proc. Mal. Soc. London, X, p. 162. Type *Carinifex newberryi* (Lea). As subgenus of *Pompholyx*

1918. *Carinifex* Walker, Miscel. Pub. Mus. Zool. Univ. Mich., No. 6, pp. 15, 106. Type *Planorbis newberryi* Lea. As genus

1923. *Carinifex* Germain, Rec. Ind. Mus., XXI, p. 188. Type *Carinifex newberryi* (Lea). As genus

1923. *Carinifex* Wenz, Fossil. Cat., Pars 22, p. 1671. Genotype *Carinifex newberryi* (Lea). As genus

1924. *Carinifex* Dall, Prof. Papers U. S. Geol. Surv., No. 132 (G) p. 112. As synonym of *Megasystropha* Lea

1924. *Megasystropha* Dall, op. cit., p. 112. Type *Planorbis newberryi* Lea. As genus

1925. *Megasystropha* Lea, Smith. Miscel. Coll., LXXIII, No. 3, Dec. 16. Opinion 87, Int. Com. on Zool. Nomenclature

1926. *Carinifex* Pilsbry, Science, LXIV, p. 248, Sept. 10. Defending use of this name instead of *Megasystropha* Lea

1929. *Carinifex* J. Henderson, Univ. Col. Studies, XVII, No. 2, p. 143. Type *Carinifex newberryi* (Lea). As genus

1929. *Carinifex* Chamberlin and Jones, Bull. Univ. Utah, XIX, No. 4, p. 155. Biol. Series I, No. 1. Genotype *Planorbis newberryi* Lea. As genus.

1931. *Carinifex* Thiele, Handbuch, Teil 2, p. 480. Type *Carinifex newberryi* (Lea). As genus

1934. *Carinifex* Pilsbry, Proc. Acad. Nat. Sci. Phil., 86, p. 48. Type *Planorbis newberryi* Lea. As genus. Figures genitalia of *Carinifex ponsonbyi* and *C. newberryi subrotunda*

1935. *Carinifex* J. Henderson, Non-Marine Moll. N. A., p. 255. Discussion of genus and listing of fossil species *C. malheurensis* Henderson and Rodeck

Shell (plate 78, figs. 23-25). Medium to large, ultradextral, body whorl angulated; spire depressed or elevated, the whorls terraced and angular; base funicular; last whorl broad at the periphery, rapidly attenuated below; aperture triangular, outer lip thin; inner lip with slight callus.

When the spire of *Carinifex* becomes elongated the shell is dextral although anatomically the animal is sinistral like that of *Helisoma*.

Animal. Resembling *Helisoma* in general form, but the tentacles are shorter (see plate 34, fig. 1).

ANATOMICAL CHARACTERISTICS

PLATE 34 (*Carinifex ponsonbyi* E. A. Smith)

GENITALIA. Male Organs (fig. 4). Seminal vesicle (SV) represented by many short vesicles bordering the ovisperm duct for a length of 4.5 mm. Sperm duct (SPD) long and narrow (2.5 mm. long), diminishing to less than half its diameter as it joins the vas deferens, which is a tube of fine diameter, 14-15 mm. long. The prostate (PRS) is elongated (3.5 mm. long). A section, through the prostate and uterus (fig. 7) shows that the prostate is peculiar in having the diverticula (14 in this section) occurring laterally from a main pouch into which they empty and which, in turn, empties into the sperm duct. There appears to be no special prostate duct at each end, as in *Helisoma*. A section through the upper end of the prostate (fig. 8) shows only 11 diverticula but the arrangement is the same.

Penial complex (fig. 2). The preputium (PR) is elongated and sac-like, 4.5 mm. long and about 1 mm. wide at its greatest diameter. The vergic sac (VS) is short (1.5 mm. in length) and there is no marked constriction between the two sacs, as in *Pierosoma*. The musculature is different from that feature in *Helisoma*. There are two sets of retractor muscles (RM), one set, composed of two main branches with several small branches, is attached to the vergic sac and the upper part of the preputium; the other set, composed of two or more branching divisions, is attached to the upper part of the vergic sac, with one branch connecting with a branch of the first set. The vas deferens passes under this branch. There are three sets of supporting muscles (SM) attached to the preputium. These are divided several times in their attachment to the preputium and to the roof of the mantle cavity. Several small muscles appear on the base of the preputium below the first set of retractor muscles.

Another specimen of *ponsonbyi* (plate 35, fig. 1) had a variation of this musculature, there being but one main retractor in the first set, and several narrow muscles, much branched, in the second set. The supporting muscles (SM) were also somewhat different. All specimens have a very short (about 0.5 mm. long) penial gland duct on the outside of the penial complex between the vergic sac and the preputium (DC). This duct does not vary in any of the specimens examined.

Internally (plate 34, fig. 3), there are two fleshy pilasters in the preputium (PL). These are shown in section in fig. 12. The penial gland (GL) is an elongated, somewhat pyriform sac, narrowed at its junction with the body wall of the preputium and enlarged at the cup-shaped cavity. A section of the gland (fig. 10) shows many vertical glandular folds on the wall of the cup and a number of pavement-like folds in the bottom of the cup (IC). The gland duct (DC) extends into the cup and connects with the vertical and pavement-like folds. The verge (V) is short and thick. There is a muscular ridge or diaphragm (D) separating the cavity of the vergic sac from the preputial cavity.

Female Organs. The spermatheca (S) is about 1 mm. long, long-ovate in shape and has a narrow duct (SD) almost 2 mm. in length, which enters the short vagina (VG) without marked swelling. Another form of spermatheca and duct, from another specimen, is shown in fig. 11. The uterus (U) is tough and leathery, long and wide (6 mm. long and 1 mm. wide), and is covered with wart-like prominences. The nidamental gland (NG) is wide and somewhat globular, covered with small follicles. The oviduct (OD) is much narrower than the uterus and is about 3 mm. long and 0.3 mm. wide. There is a large, swollen carrefour (CF). The relationship of the organs near the junction with the ovisperm duct is shown in fig. 6. The albumen gland (fig. 5) is about twice as long as wide and lies crosswise of the body. The space for the passage of the intestine is shown near the center of the figure.

Hermaphrodite Organs (fig. 4). The ovotestis (OT) is composed of large club-shaped diverticula. A section of this organ near the front end is shown in fig. 9. Six rows of diverticula of varying length are to be seen. The sections vary in different parts of the ovotestis. There may be only six unbranched diverticula of large size, or there may be six or seven main branches, each branch subdivided two or three times to form a surface aspect of fourteen, fifteen, or eighteen diverticula. The free ovisperm duct (SO) is very short and appears only between the oviduct and the seminal vesicle.

In another species, *Carinifex jacksonensis* (plate 35, fig. 5), there is some deviation from the structures as seen in *ponsonbyi*. The seminal vesicle (SV) forms a grape-like bunching just beyond the ovotestis (about 1 mm. long and 0.7 mm. wide) with lateral vesicles on the ovisperm duct as in *ponsonbyi*, and for the succeeding 2 mm. with very small vesicles which appear as fine crenulations on one side only. The prostate (PRS) is shorter (only 3 mm. long) and is connected with the sperm duct in the same manner as in *ponsonbyi*. The diverticula are of the same form and condition as in *ponsonbyi*. The spermatheca and its duct are also of about the same form (see fig. 9). In figs. 6 and 7, the features near the junction of the ovisperm duct are shown. There is a large carrefour (CF). The albumen gland (fig. 8) is relatively shorter than in *ponsonbyi*.

The penial gland is of the same form as in *ponsonbyi* (fig. 3) and has the same short gland duct. The retractor muscles (RM), however, are much more complicated in form and position. They are much smaller, narrower, and more numerous. The supporting muscles (SM) are small and numerous and are attached to both vergic sac and preputium. Small muscles on the retractor muscle side of the preputium and on its lower half, are attached to the wall of the mantle cavity. These are believed to be supporting muscles. The attachment of the retractor muscles to the vergic sac is shown in fig. 2, which is the reverse of fig. 3.

Pilsbry (1934, p. 50) figured the genitalia of *Carinifex ponsonbyi* differing in some respects from the drawings on plate 34. The musculature is nearly the same but is not shown in as great detail as in the figures on plate 34. The spermatheca is more nearly spherical in Pilsbry's figure. The seminal vesicle is shown as a mass of small vesicles, much as seen in *Carinifex jacksonensis* on plate 35 (fig. 5). The penial complex and penial gland in *C. newberryi subrotunda* are figured. It is probable that the sex organs vary somewhat in form, especially those that are evertible. Also, the condition of the preserved material will make a great difference, especially in those organs like the nidamental gland, the uterus and the oviduct, which may become swollen and thus alter the true form of these organs.

Three species of *Carinifex* have been dissected by Pilsbry and the writer, *ponsonbyi*, *jacksonensis*, and *newberryi subrotunda*, and all show the homogeneity of the group and its distinctness from *Helisoma*.

Respiratory and Renal Systems. The pseudobranch (plate 34, fig. 1) of *ponsonbyi* is a rounded extension from the rectal region, in form like that in *Helisoma*, including the rectal ridge which extends over the pseudobranch. In *jacksonensis* (plate 35, fig. 4), the pseudobranch is narrower. In the specimen figured, the pseudobranch was folded in such a manner as to make the ridge appear on the left margin of the organ.

The kidney (plate 45, fig. 2) is long and narrow (15 mm. long, 1 to 1.2 mm. wide) and the ureter is reflexed at right angles to the kidney. A section of the kidney near the middle (fig. 12) shows it to be much flattened, with a bottle-shaped lumen and roundly elongated and flattened veins. There is no superposed ridge like that in *Helisoma*. The ridge on the mantle to the left of the kidney is seen in the section to be flattened and wide.

Digestive System. The digestive system is similar to that of *Pierosoma*. The stomach region is shown on plate 48, fig. 3. The intestine is looped about the stomach and liver. The buccal sac is similar to that organ in *Helisoma*.

The jaw is peculiar. There is but one jaw which is horseshoe-shaped, narrow, composed of many small, vertical plates which produce a saw-like edge. In *ponsonbyi* (plate 49, fig. 19), there are spiral striae on the jaw plates. In *jacksonensis* this striation is not visible (plate 49, fig. 18). The jaw is attached to a very large cartilage which has the relative shape and size shown in fig. 17. In fig. 19, the jaw is somewhat distorted. The jaw of *Carinifex* bears some resemblance to the fragmented jaw of the Planorbinae, but the general form is different.

Radula. The radula of *Carinifex ponsonbyi* (plate 67, fig. 8) has a square, bicuspid center tooth, the spade-shaped cusps extending below the lower border of the base of attachment. The lateral teeth (1-6) are tricuspid, all cusps sharply spade-shaped, including the mesocone. In some rows, single cusps may become bifid, as the ectocone in the fifth lateral tooth in fig. 8. The intermediate teeth (7-8) differ only in the splitting of the ectocone into two sharp cusps. The marginal teeth (9-27) are long and narrow, the entocone remaining unchanged at first (9-10) but the ectocone undergoing additional splitting. On the eleventh tooth the entocone begins to split, developing three small, sharp cusps. In the outer part of the membrane, the marginal teeth become narrower and the entocone splits into seven very small, sharp cusps and the ectoconic area becomes simply serrated along the outer margin. The mesocone remains unchanged throughout the entire row.

In *Carinifex jacksonensis* (plate 65, fig. 4), the teeth have practically the same shape, but are smaller. There are ten lateral teeth and two intermediate teeth. In the splitting of the marginal teeth, the inner cusp of the entocone is larger than the four cusps on the inner side of the mesocone. This feature persists throughout the radula. The radula formulae of the two species are as follows:

ponsonbyi	32-1-32	Klamath Lake, Oregon	210-217	J. Henderson
jacksonensis	25-1-25	Jackson Lake, Wyoming	215-221	J. Henderson

The data for the specimens examined are as follows: *ponsonbyi*, from lower end of Upper Klamath Lake, Klamath Falls, Oregon, collected by Mr. and Mrs. J. Henderson, August 7, 1931; ten specimens dissected. *Jacksonensis*, from Jackson Lake, at Moran, Wyoming, in shallow water just above dam at very low water stage, collected by Mr. and Mrs. Henderson, August 20, 1931; eight specimens dissected.

Geographical Distribution. *Carinifex* is a purely American group found only in western America from California eastward to Wyoming. Pilsbry believes that all of the described species and races of *Carinifex* are subspecies of a single stock comparable to the subspecies of *Helisoma anceps* (Menke). There are, indeed, comparable characteristics between these two groups, although the *anceps* group is much more widely distributed, both in latitude and area, and is subject to more diverse environmental influences than is *Carinifex*.

Species Considered as Valid. A careful study of all species, many specimens from the type lots, leads the writer to the following conclusion concerning the specific range of the genus. There are doubtless anatomical characteristics which separate some of the species as has been noted in *ponsonbyi* and *jacksonensis*.

Carinifex newberryi newberryi (Lea)
Carinifex newberryi minor Cooper
Carinifex newberryi malleata Pilsbry
Carinifex newberryi subrotunda Pilsbry
Carinifex occidentalis Hanna
Carinifex ponsonbyi E. A. Smith
Carinifex jacksonensis J. Henderson

Geological Distribution. Pliocene to Recent fauna. The genus may extend as far back as the Miocene period.

Remarks. *Carinifex* has been thought to be closely allied to *Helisoma* and Pilsbry states (1934, p. 48) that there is very little structural difference between the two groups. There are, however, characteristics of both shell and anatomy which, in the judgment of the writer, are sufficient to mark *Carinifex* as of generic rank. The ultradextral shell bears some resemblance to certain forms of typical *Helisoma* but the anatomy, especially the genitalia, exhibits features of importance. The external penial gland duct is shorter than in any form of *Helisoma* and is of different form. The prostate, when seen in section, shows the diverticula to be formed in a totally different manner from those of *Helisoma*. The musculature of the penial complex is far more complex with two distinct retractor muscles. The jaw is also of entirely different shape and nature. The radula teeth have the mesocone as it is in typical *Helisoma*. The kidney is without a superposed ridge.

By a ruling of the International Commission on Zoological Nomenclature (Opinion 87), the name *Carinifex* of W. G. Binney has been ruled out of systematic nomenclature because of its publication in what is termed a 'proof sheet' and therefore not usable as a nomenclatorial reference. Proof sheets are obviously not to be quoted as systematic references to publication, but the example chosen to sustain this ruling was most unfortunate, since the publication in which the name *Carinifex* appeared (Smithsonian Miscellaneous Collections), is an octavo pamphlet of twelve leaves, printed on one side (the left) for corrections. This pamphlet was widely distributed among conchologists and is even now available among secondhand book dealers. The contention that this pamphlet is merely a 'proof sheet' seems unwarranted and the writer fully agrees with Pilsbry (1926, p. 248) that *Carinifex* was sufficiently 'published' by Binney and that this name should be used in place of *Megasystropha* Lea, which is ruled by the Commission to be used instead of *Carinifex*.

Dall (1870) says (in footnote under *Carinifex*) '*Megasystropha* Lea. Neither genus was characterized by the author, and the former is in general use and has priority.' In 1924, however, Dall reversed this opinion (Prof. Papers, p. 112) and used *Megasystropha* as the name for this group, contending that the earlier 'proof sheets' of 1863 were simply proofs and should not be quoted. However, in a general review of the literature of this genus, it is evident that the name *Carinifex* has been almost universally used, as noted in the bibliography of the genus on a previous page of this volume. Henderson (1929, p. 143) well states the situation in the following words. 'It must not be forgotten that the purpose of rules of nomenclature is to insure, so far as possible, stability of names and certainty in their use in the designation of species, etc., which purpose would be defeated rather than accomplished by this proposed substitution.' The name *Carinifex* is, therefore, adopted in this work.

Genus VORTICIFEX Meek, 1870

Type by original designation *Carinifex tryoni* Meek

1870. *Vortifex* Meek, Proc. Acad. Nat. Sci. Phil., p. 59. Type *Carinifex (Vortifex) tryoni* Meek, new species. Proposed as subgenus of *Carinifex* Binney

1870. *Vorticifex* Dall, Ann. N. Y. Lyc. Nat. Hist., IX, p. 353. Correction of *Vortifex,* originally misspelled. Type *Carinifex tryoni* Meek.

1871. *Vorticifex* Meek, Tryon, Amer. Jour. Conch., VI, p. 285, April, 1871. Review of Meek's paper. *Vortifex* corrected to *Vorticifex* and *Carinifex tryoni* stated to be the type

1877. *Vorticifex* Meek, U. S. Geol. Surv. 40th Parallel, IV, p. 187. Subgenus described and *Carinifex binneyi* and *tryoni* both placed therein

1883. *Vorticifex* Fischer, Man. de Conch., p. 508. Type *Carinifex tryoni* Meek. As subgenus of *Carinifex*

1884. *Vorticifex* Tryon, S. and S. Conch., III, p. 105. Type wrongly stated to be *Carinifex binneyi* Meek. As subgenus of *Carinifex*

1888. *Vorticifex* Call, Amer. Geol., I, p. 148. Genus formally described and *Carinifex binneyi* Meek wrongly designated as type

1922. *Vorticifex* Hanna, Univ. Oregon Pub., I, No. 12, p. 7. Type *Carinifex tryoni* Meek. As genus

1924. *Paradines* Dall, U. S. G. S., Prof. Papers, No. 132, p. 112. Type by original designation *Carinifex binneyi* Meek. As section of genus *Megasystropha*

1935. *Vorticifex* Henderson, Fossil Non-Marine Moll. N. A., p. 255. Type *Carinifex tryoni* Meek. As genus

Shell (plate 76, fig. 12 *tryoni;* fig. 13, *binneyi*). Large, ultradextral, of few rapidly enlarging, rounded whorls, the body whorl very large, rounded, and sculptured with distinct, rib-like striae parallel with the lines of growth; right side flatly convex; left side with deep 'umbilical' depression almost completely obscuring the inner whorls; aperture large, rounded.

'The chief distinguishing features of the genus are (1), lack of carinae, either at periphery, suture or around umbilicus; (2), much rounder body whorl than *Carinifex;* and (3), much less triangular aperture than *Carinifex*' (Hanna, 1922, p. 7).

Geological Horizon and Distribution. *Eocene*, Truckee Lake beds, Nevada; Payette Lake beds, Idaho; Fossil Hill, Kawsoh Mts., Nevada; *Pliocene*, Cache Valley, Mendon, Collinston, Utah; Tulare formation, Kettleman Hills, California; Warner Lake beds, eastern Oregon. A single species, *Vorticifex stearnsii* (White) has been reported from the Morrison formation in Wyoming, belonging in the upper Jurassic or Lower Cretaceous period.

Species Considered as Valid. The following species and races have been referred to this genus.

Vorticifex tryoni (Meek)
Vorticifex tryoni concava (Meek)
Vorticifex tryoni ventricosa (Meek)
Vorticifex binneyi (Meek)
Vorticifex stearnsii (White)

Remarks. *Vorticifex* appears to be a rather distinct genus related to both *Carinifex* and *Parapholyx*. The wide body-whorl with its distinct costae is quite characteristic. The name *Paradines* Dall (1924, p. 112) founded upon the larger species *Carinifex binneyi* Meek does not appear more than specifically distinct from the smaller *Carinifex tryoni* Meek. Both species seem, from the published figures, to be generically closely related and to be distinct from the genus *Carinifex*.

Several species referred to *Vorticifex* appear to belong elsewhere. *Vorticifex sanctaeclarae* Hannibal and *V. sanctaeclarae marshalli* Arnold seem rather to belong in *Carinifex* as originally described rather than in *Vorticifex* as listed by Henderson (1935, p. 257). They were placed in *Carinifex* by Pilsbry (1934, p. 567). The *Vorticifex laxus* of Chamberlin and Berry (Nautilus, XLVII, p. 26, 1933) does not appear to fit into the genus *Vorticifex*, but might be included in the genus *Carinifex*. It appears to be an internal cast and the external characteristics would not show clearly in such a condition.

Genus PERRINILLA Hannibal, 1912

Type by original designation *Helisoma cordillerana* Hannibal

1912. *Perrinilla* HANNIBAL, Proc. Mal. Soc. London, X, p. 159. Type *Helisoma cordillerana* Hannibal. As subgenus of *Helisoma*

1923. *Perrinilla* WENZ, Fossil. Cat., Pars 22, p. 1518. Genotype *Planorbina (Perrinilla) cordillerana* (Hannibal). As subgenus of *Planorbina* Haldeman

1934. *Perrinilla* PILSBRY, Proc. Acad. Nat. Sci. Phil., 86, p. 48. Type *Helisoma cordillerana* Hannibal. Presumably considered as genus

1935. *Perrinilla* J. HENDERSON, Fossil Non-Marine Moll. of N. A., p. 246. Type *Helisoma cordillerana* Hannibal

Shell (plate 79, figs. 31-32). 'Similar to *Planorbella*, except that it is totally ultra-sinistral; spire-pit deep and narrow, umbilicus but slightly excavated, superior and inferior peripheries subangular' (Hannibal for subgenus).

'Shell of considerable size, whorls large, somewhat compressed, and strongly ultrasinistral, the umbilicus barely concave, superior and inferior peripheries subangular in young stages, becoming rounded in adult, growth striae strong, spiral striae occasionally preserved, aperture expanded somewhat in adult; habitat apparently lacustrine. Diameter 22, alt. 9, diameter of aperture 12 mm.' (Hannibal, p. 161, description of *Helisoma cordillerana*).

Geological Horizon and Distribution. *Eocene* period. Truckee Lake beds, Nevada, several localities. *Miocene.* Contra Costa Lake beds, California, *Planorbis pabloanus* J. G. Cooper, 1894, is believed by Hannibal to be congeneric.

Species Considered as Valid. *Perrinilla cordillerana* (Hannibal), the genotype, is the only recognized species of the genus.

Remarks. *Perrinilla* appears to be more closely related to *Carinifex* than to *Helisoma*, as suggested by Pilsbry (1934, p. 49), who says

> *Perrinilla* Hannibal, 1912 . . . . seems to stand near the form of the *Carinifex* phylum to be expected in the Eocene, and it may possibly belong in the ancestral line of *Carinifex*.

The best disposition of the group in planorbid classification appears to be as a distinct genus near *Carinifex*.

Genus PARAPHOLYX Hanna, 1922

Type by original designation *Pompholyx effusa* Lea

1856. *Pompholyx* LEA, Proc. Acad. Nat. Sci. Phil., VIII, p. 80. Type *Pompholyx effusa* Lea. Not *Pompholyx* Goose, 1851, Rotifera. As genus

1857. *Pompholyx* LEA, Journ. de Conch., VI, p. 208. As genus

1865. *Pompholyx* W. G. BINNEY, L. and FW. Sh. N. A., II, p. 73. Type *Pompholyx effusa* Lea. As genus

1866. *Pompholyx* DALL, Proc. Cal. Acad. Sci., III, pp. 265, 268. Description of subfamily Pompholiginae

1868. *Pompholyx* J. E. GRAY, Ann. Mag. Nat. Hist., (4) II, p. 387. As genus

1870. *Pompholyx* DALL, Ann. N. Y. Lyc. Nat. Hist., IX, pp. 334, 344, 353. Type *Pompholyx effusa* Lea. As genus. Anatomy imperfectly described

1870. *Pompholyx* TRYON, Con. Hald. Mon., pp. 83, 174. Type *Pompholyx effusa* Lea. As genus

1883. *Pompholyx* FISCHER, Man. de. Conch., 507. Type *Pompholyx effusa* Lea. As genus

1884. *Pompholyx* TRYON, S. and S. Conch., III, p. 105. Type *Pompholyx effusa* Lea. As genus

1886. *Pompholyx* CLESSIN, Conch. Cab., XVII, p. 226. Type *Pompholyx effusa* Lea. As genus

1912. *Pompholyx* HANNIBAL, Proc. Mal. Soc. London, X, p. 162. Type *Pompholyx effusa* Lea. As genus

1918. *Pompholyx* WALKER, Miscel. Pub. Mus. Zool., Univ. Mich., No. 6, pp. 14, 105. Type *Pompholyx effusa* Lea. As genus

1922. *Pompholyx* GERMAIN, Rec. Ind. Mus., XXI, p. 185. Type *Pompholyx effusa* Lea. As genus

1922. *Parapholyx* HANNA, Univ. Oregon Pub., I, No. 12, p. 5. New name for *Pompholyx* Lea, 1856, non Goose, 1851

1927. *Pompholycodea* LINDHOLM, Proc. Commission for study of Lake Baikal, II, p. 180. New name for *Pompholyx* Lea, not Goose

1929. *Parapholyx* J. HENDERSON, Univ. Col. Studies, XVII, No. 2, p. 145. Type *Pompholyx effusa* Lea. As genus

1931. *Pompholycodea* THIELE, Handbuch, Teil 2, p. 480. Type *Pompholyx effusa* Lea. As genus

1934. *Parapholyx* PILSBRY, Proc. Acad. Nat. Sci. Phil., 86, pp. 46, 51. Type *Pompholyx effusa* Lea. As genus

1935. *Parapholyx* J. HENDERSON, Fossil Non-Marine Moll. N. A., p. 254. As genus

1936. *Parapholyx* F. C. BAKER, Nautilus, L, pp. 30-31. Notes on anatomy

Shell (plate 78, figs. 20-22). Of medium size, ultradextral, globose, the spire short and but little raised above the body whorl which is ventricose and embraces most of the shell; aperture wide, greatly expanded; outer lip thin, acute, somewhat reflexed in adult or old specimens; inner lip more or less thickened; base convex or conical, imperforate or with but a small chink.

Animal (plate 36, fig. 1). Foot short, about half as broad as long. Velum as in *Helisoma*. Tentacles short, cylindrical, blunt at the end, not tapering. Eyes sessile at the inner base of the tentacles. The eyes are not conspicuous in some preserved specimens. The body is darkly pigmented, the pigmented areas extending to the head and sometimes forming streaks on the tentacles. The posterior portion of the body is light gray. The ovotestis area is yellowish.

ANATOMICAL CHARACTERISTICS

PLATE 36 (*Parapholyx effusa klamathensis* F. C. Baker)

GENITALIA. Male Organs (fig. 3). Seminal vesicle (SV) about 4 mm. long, swollen, with many small vesicles projecting from the otherwise smooth surface. The sperm duct (SPD) is about 3 mm. long and of large diameter (0.4 mm.). The prostate (PRS) is long (3.5 mm.) and wide and is composed of many small diverticula. In section (fig. 4), these diverticula are seen to be composed of about a dozen irregular follicles linked together like sausages. From the outside of the prostate, these diverticula appear to be covered with small tubercles irregularly placed. These follicles enter the sperm duct at a common center, shown at X in the figure. The vas deferens is about half the diameter of the sperm duct and is 11 mm. long.

The penial complex (fig. 7) is sac-like and is nearly 4 mm. in length. The preputium is 1 mm. wide and occupies most of the length of the penial complex. The vergic sac (VS) is 1 mm. long and 0.7 mm. wide. There is only a slight constriction between the preputium and the vergic sac. The penial gland duct is relatively short (about 1.5 mm. long) and rather thick. It extends from the preputium near its upper third and enters the vergic sac at the constricted area. The portion of the duct entering the vergic sac and the preputium is very small and narrow, the duct swelling greatly in diameter on the surface of the preputium. There are two sets of retractor muscles, each set consisting of two main branches which subdivide several times at the penial sac insertions and at the connections in the columella muscle. All insertions are on the preputium, none on the vergic sac. There are several narrow supporting muscles (SM) attached to the preputium.

Internally (fig. 9), the preputium has two large, fleshy folds or pilasters (PL). There is a much elongated, cylindrical penial gland (1.7 mm. long) which resembles a pipe-stem, with a cup-shaped or bowl-shaped gland (about 0.5 mm. in diameter) placed at the lower end (GL). The duct (DC and X) enters the cylindrical portion of the gland and extends through this stem-like portion, then enters the bowl-like cup of the gland where it is enlarged into a bulb-like body (fig. 11, X). The cup-shaped gland resembles the bowl of a pipe. In section (fig. 11), the cup shows a shallow area at the top and the sides are lined with wide, thick folds (GF). The bottom of the bowl-like cup is covered with small follicles which are placed at the upper end of the rounded enlargement of the penial gland duct. The right pilaster is attached to the gland at its upper end, curving toward the gland beneath the gland duct.

There is a thick ring or diaphragm (D) which separates the cavity of the preputium from the vergic cavity. This diaphragm has a circular canal into which the upper end of the penial gland duct, which is greatly diminished in diameter, enters. This feature is shown in fig. 10. The verge (V) is narrowly pyriform, tapering to a point at its lower end. The sperm canal extends through the center of the verge and has a central outlet (fig. 12). A large nerve and blood vessel supply the penial complex (fig. 8).

Female Organs (fig. 3). The spermatheca (S) is large and egg-shaped, almost globular. It is connected with the short, narrow vagina (VG) by a narrow duct shorter than the length of the spermatheca (SD). The uterus (U) is narrow as it passes upward from the vagina but increases abruptly in diameter to three times the width of that region, combining with the nidamental gland. This region is concealed by the prostate in fig. 3. The oviduct (OD) contracts in diameter to form a sac-like organ of small diameter. There is a large carrefour (CF). The albumen gland (AL) is 4 mm. long and is longer than wide. The duct of this gland is long (0.5 mm.).

Hermaphrodite Organs. The ovotestis (OT) is long and sac-like and is composed of several club-shaped diverticula. A section near the middle of the ovotestis (fig. 5) shows eight rather long diverticula, the longest follicles being in the center. A section near the posterior end (fig. 6) shows six diverticula in less fan-like pattern. Sections from the middle to the anterior end show eight diverticula all in fan-shaped pattern, but sections made toward the posterior end show but six diverticula which are more or less irregularly arranged. The ovisperm duct is very short in the portion between the ovotestis and the seminal vesicle. The free portion near the oviduct is somewhat longer. The seminal vesicle (SV) occupies about two-thirds of the length of the ovisperm duct.

The genitalia of *Parapholyx effusa diagonalis* Henderson, also dissected, do not differ from the figures and descriptions herein presented.

In 1870, Dall dissected *Pompholyx solida* and published descriptions and several figures of the genitalia. These are not in sufficient detail and embrace some errors, such as the presence of a distinct testicle on the male system. This might have been the albumen gland. As far as can be seen, the anatomy of *solida* is similar to that of the species personally examined and herein figured.

Respiratory and Renal Systems. The pseudobranch (fig. 2) is a triangular appendage extending from the rectal region. There is a distinct ridge extending over the rectum in a broad curve, ending above the anus.

The kidney (plate 46, fig. 1) is short and wide (about 3 mm. long and 1 mm. wide); the ureter is large and sharply reflexed, directed upward into the mantle cavity. The pericardium is also large (about 1 mm. long). A cross section of the kidney near the middle (fig. 2) shows a much flattened form with a wide lumen, the veins ovate and flattened, and placed at the lower lateral sides of the lumen. There is no ridge and the section resembles that of *Carinifex*.

Digestive System. The stomach is like that of *Carinifex* and essentially as described by Dall for *Pompholyx solida*. The oesophagus is short and is enlarged just behind the buccal sac. The salivary glands form a loop. The buccal sac is short, high and pyriform, as in *Carinifex*.

The jaws are three in number, differing markedly from the single horse-shoe-shaped jaw of *Carinifex*. The superior jaw is low and about three times as wide as high. The side jaws are as in *Helisoma*. The face of the superior jaw is striated vertically. There is little difference between the jaws of *klamathensis* and *diagonalis*. Dall says there are no accessory plates (side jaws) but they occurred in all specimens personally examined. The jaw figured by Dall (his plate 2, fig. 11a) is different from the jaws found in the two races examined.

The radula of *P. effusa klamathensis* (plate 65, fig. 3) has a squarish center tooth, the bicuspid reflection not reaching the lower margin of the base of attachment. The lateral teeth (1-8) are squarish and tricuspid, all cusps being sharp and spade-shaped. The intermediate teeth (9-11) are narrow, the ectocone splitting into two sharp cusps as long as, or nearly as long as, the mesocone. There are two small cusps on the outer border of the tooth, above the ectocone. The marginal teeth (13-15) are narrow, the entocone with four to five small cusps, the ectoconic region with three cusps. The outer marginal teeth (16-19) are very narrow and are simply serrated on the ectoconic side, there being no division into entocone, mesocone, and ectocone. Dall's figure of the radula of *solida* (his plate 2, fig. 9) shows the lateral teeth with a rounded mesocone and all cusps appear too blunt. The marginal teeth are too wide and the small cusps are not shown.

RADULA FORMULAE OF *Parapholyx*

Species	*Formula*	*Locality*	*Rows*	*Collector*
klamathensis	19-1-19	Klamath Lake, Oregon	125	J. Henderson
diagonalis	21-1-21	Crater Lake, Oregon	100-114	J. Henderson
solida	22-1-22	White Pine, Nevada	150	Dall's paper

The following material has been examined for the anatomical data contained in this work. *P. effusa klamathensis* from outlet of Upper Klamath Lake, Oregon, eight specimens examined. *P. effusa diagonalis* from Crater Lake, Oregon, eight specimens examined. Both lots collected by J. Henderson.

Geographical Distribution. *Parapholyx* is purely an American genus confined to the west coast of America from Washington southward to California and eastward to Nevada. *Pompholyx leana* H. and A. Adams was described from 'West Columbia,' but no specimen of this genus has been seen from British Columbia and it is very doubtful that the genus is found north of the United States. A number of species and races have been described and the same opinion expressed for the division of *Carinifex* may also apply to this genus.

Species Considered as Valid.

Parapholyx effusa effusa (Lea)
Parapholyx effusa costata (Hemphill)
Parapholyx effusa diagonalis J. Henderson
Parapholyx effusa klamathensis F. C. Baker
Parapholyx nevadensis J. Henderson
Parapholyx mailliardi Hanna
Parapholyx solida solida (Dall)
Parapholyx solida optima (Pilsbry)
Parapholyx leana (H. and A. Adams)
Species practically unknown

Geological Distribution. *Parapholyx* is certainly known from the Pliocene to the Recent fauna. It may occur in earlier deposits. One extinct species is known, *Parapholyx packardi* Hanna, from Warner Lake deposits in eastern Oregon.

Remarks. *Parapholyx* is a very distinct genus both in shell and anatomy. The shell is depressed and almost neritaeform. The anatomy is peculiar in several respects. The prostate is not composed of distinct club-shaped diverticula, but of small gland-like bodies arranged like a string of sausages. The penial gland is not a short, cup-shaped organ, as in *Carinifex*, but an elongated, pipe-shaped body with a cup-like termination, with a long duct passing through the center of the longitudinal, sac-like 'stem' of the gland. The termination of the duct is swollen and bulb-like, expanding in the bottom of the penial gland cup. The penial gland duct is external as in *Carinifex*, but it is somewhat longer and of greater diameter. The jaw is like that of *Helisoma* and is not fragmented like that of *Carinifex*. The genus stands out as one of the most distinct among American planorbids.

In 1866, Dall instituted a subfamily Pompholiginae for *Pompholyx effusa*, basing the separation on the supposition that there were two pairs of eyes, one at the inner base of the tentacles and one at the end of the tentacles. The fact of this peculiar condition was positively stated by Mr. William M. Gabb, who made drawings of the animal. Dr. J. E. Gray (1868, p. 387) questioned this statement. In 1870, Dall obtained specimens of a *Pompholyx* (*Parapholyx*) different specifically from the known species, which he called *solida*. An examination of the tentacles of this species at once cleared up the anomaly of the four eyes, the supposed eyes on the end of the tentacles being simply an aggregation of pigment. Only one pair of eyes is present, at the inner base of the tentacles, as is the case in other species of Planorbidae.

Dall still retained the subfamily Pompholiginae (1870, p. 352) although the chief reason for its adoption, the four eyes, had been found to be invalid. The subfamily has been used by most writers on fresh-water Mollusca, including Fischer (1883, p. 507), Tryon (1884, p. 105), Walker (1918, p. 14), Germain (1922, p. 185), Henderson (1929, p. 143), and Chamberlin and Jones (1929, p. 155). Hannibal (1912, p. 161) elevated it to family status as Pompholigidae. Dall has also used the name Pompholiginae for a section of the marine genus Divaricella (Proc. U. S. Nat. Mus., XXIII, p. 814, 1901).

The study of the animals of *Carinifex* and *Parapholyx* shows that they have no general anatomical characteristics not shared by *Helisoma* and the subfamily Pompholiginae must therefore be abandoned. This course was indicated by Pilsbry in 1934 (p. 46). In 1936 (Nautilus, L, p. 30), the writer indicated the general anatomical features of *Parapholyx*, showing its general relationship to *Helisoma* and *Carinifex* and stating that the old subfamily Pompholiginae was without anatomical distinction.

Genus POMPHOLOPSIS Call, 1888

Type by original designation *Pompholopsis whitei* Call

1888. *Pompholopsis* Call, Amer. Geol., I, No. 3, p. 147. Type *Pompholopsis whitei* Call. As genus

1935. *Pompholopsis* J. Henderson, Fossil Non-Marine Moll. N. A., p. 255. Type *Pompholopsis whitei* Call. As genus

Shell (plate 76, fig. 11). 'Dextral, globose, rather solid, deeply umbilicated; whorls three to three and one-half, convex, body-whorl very large; spire short, apex obtuse; aperture roundly ovate; peritreme continuous, forming a heavy callus on the parietal wall of the body-whorl. Growth lines inconspicuous, surface of the shell smooth; sutures rather irregularly impressed. Length 7.26 mm.; diameter 8.13 mm.' (Call, 1888, p. 147).

Geological Horizon and Distribution. Post-pliocene (Pleistocene). Tassajara Lake beds, California.

Species Considered as Valid. *Pompholopsis whitei* Call is the only species assigned to this genus.

Remarks. *Pompholopsis* differs from *Parapholyx* in being deeply umbilicated and in having a high spire and smaller, rounder aperture. It is related to *Parapholyx* but appears sufficiently distinct to justify a genus. A series of shells might add greatly to our knowledge of the relationship of this species.

Genus PLANORBARIUS Froriep, 1806

Type by original designation *Helix cornea* Linn.

1806. *Planorbarius* Froriep, in Duméril, Analyt. Zool., p. 165. Type *Helix cornea* Linn. As genus

1810. *Planorbis* Montfort, Conch. Syst., II, p. 270. Type *Planorbis corneus* (Linn.). Non Geoffroy or Müller. As genus

1840. *Planorbis* Swainson, Treat. Malac., p. 337. Type *Planorbis corneus* (Linn.). As genus

1847. *Coretus* (Adanson, 1757) Gray, Proc. Zool. Soc. London, p. 180. Type *Planorbis corneus* (Linn.). As genus

1850. *Spirodiscus* Stein, Schn. u. Muscheln Berlin, p. 73. Type (1st species): *Planorbis corneus* (Linn.)

1855. *Coretus* Moquin-Tandon, Hist. Moll. Terr. Fluv. France, II, pp. 424, 445. Type *Planorbis corneus* (Linn.)

1870. *Planorbis* Dall, Ann. N. Y. Lyc. N. H., IX, p. 351. Type *Planorbis corneus* (Linn.). As genus

1883. *Spirodiscus* Fischer, Man. de Conch., p. 509. Type *Helix corneus* Linn. As section of *Planorbis*

1884. *Planorbis* Tryon, S. and S. Conch., III, p. 106. Type *Planorbis corneus* (Linn.). As genus

1885. *Coretus* Westerlund, Fauna Pal. Reg., V, p. 64. No type cited. As subgenus of *Planorbis*

1886. *Coretus* Clessin, Conch. Cab., XVII, p. 32. Type *Planorbis corneus* (Linn.). As subgenus

1902. *Spirodiscus* Westerlund, Rad. Jugoslav. Akad., 151, p. 120. Type *Helix cornea* Linn. As subgenus

1905. *Planorbis* Dall, Alaska Moll., p. 81. Type *Planorbis corneus* (Linn.). As genus

1917. *Planorbis* Soos, Ann. Musei Nat. Hungarici, XV, pp. 37, 140. Type *Planorbis corneus* (Linn.)

1918. *Planorbis* Walker, Miscel. Pub. Mus. Zool., Univ. Mich., No. 6, p. 94. Type *Planorbis corneus* (Linn.). As subgenus of *Planorbis*

1921. *Planorbis* Germain, Rec. Ind. Mus., XXI, pp. 6, 9. Type *Planorbis corneus* (Linn.). As subgenus of *Planorbis*

1923. *Coretus* (Gray 1847) Wenz, Fossil. Cat., Pars 22, p. 1421. Genotype *Coretus corneus* (Linn.). As genus

1924. *Planorbarius* Kennard and Woodward, Proc. Mal. Soc. London, XVI, p. 10. Type *Helix cornea* Linn.

1926. *Planorbarius* KENNARD and WOODWARD, Syn. Brit. Non-Marine Moll., p. 67. Type *Helix cornea* Linn. As subgenus

1926. *Planorbis* LINDHOLM, Archiv. für Mollusk., Heft 6, year 58, p. 252. Ideogenotype *Helix cornea* Linn. As genus, type by Montfort

1927. *Planorbis* PILSBRY and BEQUAERT, Bull. Amer. Mus. N. H., LIII, pp. 115, 116. Type *Planorbis corneus* (Linn.). As genus

1929. *Coretus* (Gray 1847) HAAS, Trab. Museo Cien. Nat. Barcelona, XIII, p. 378. Type evidently *Helix cornea* Linn. As genus

1931. *Planorbis* F. C. BAKER, Proc. Zool. Soc., London, p. 583. Genotype *Helix cornea* Linn. As genus

1931. *Coretus* (Andanson, 1757) GERMAIN, Moll. Terr. Fluv. France, II, p. 517. No type cited but *Planorbis corneus* (Linn.) described. As subgenus of *Planorbis*

1931. *Planorbis* THIELE, Handbuch, Teil 2, p. 479. Type *Planorbis corneus* (Linn.). Subgenus of *Planorbis* Müller, 1774

Shell (plate 80, figs. 22-24). Large, sinistral, discoidal, rather solid, of few gradually enlarging whorls, equally visible above and below; aperture slightly enlarged, in the same plane as the whorls; lips sharp, not thickened.

Animal. With short, wide foot, rounded before, tapering behind, the vela area large; tentacles long, wide at the base, and tapering to a point, eyes sessile at their inner bases. Color of living animal lead, sometimes nearly black tinged with brown; tentacles bluish black. Sometimes the whole body is reddish.

The young snail of two whorls, recently hatched from the egg capsule, is very translucent, the organs plainly visible through the hyaline shell. The body shows pinkish through the shell, head and foot with border of white on edge. The radula sac may be seen working backward and forward, when feeding, as in the adult animal. The heart may be observed beating rapidly. The young snails are distinctly physoid in form and glide about like *Physa*. Specimens of the young with bifid tentacles are not uncommon.

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PLATE 20 (*Planorbarius corneus* (Linn.))

GENITALIA. Male Organs (fig. 13). The seminal vesicle (SV) is about 4 mm. long and 1 mm. wide, narrowing at the anterior end to the diameter of the ovisperm duct. This organ is a rounded mass of small vesicles. A number of small vesicles continue down one side of the ovisperm duct. The sperm duct (SPD) is about 10 mm. long. Where it leaves the ovisperm duct it is of small diameter, but it gradually enlarges to twice this diameter near the prostate where it abruptly expands to several times the first diameter, and then suddenly diminishes again to almost its original diameter. The prostate (PRS) is elongated and somewhat fan-shaped, 4.5 mm. long. The duct of the prostate is a continuation of the vas deferens and is about 1 mm. long. It lies over the sperm duct with which it is connected, the prostate diverticula radiating from this duct. The vas deferens (VD) is a narrow tube about 12 mm. long.

The prostate in section (fig. 4) is radiate or fan-shaped in form, the seven to nine main diverticula branching several times (usually four) toward the outer part of the section. Figure 4 also shows the relationship between the uterus, the nidamental gland, and the prostate, the figure being a cross section cutting through these organs. The prostate diverticula may be noted to enter the prostate duct directly.

The penial complex (fig. 12) consists of a very large, pyriform preputium (PR), 3.5 mm. long and 2 mm. wide at the upper part, tapering to 0.5 mm. wide at the male opening. The vergic sac (VS) is very small (about 1 mm. long) and is placed at the summit of the preputium, lying on that organ. There are two retractor muscles (RM), an upper one attached to the preputium near the vergic sac by two branches, one branch on each side of the vergic sac, and a lower muscle attached at about midway of the preputium. There are four or five supporting muscles (SM) on the opposite side from the lower retractor muscle. In some specimens, the two retractor muscles are placed one above the other attached to the preputium near the upper part, with smaller muscles joining the two larger muscles and a small muscle extending to the vas deferens (fig. 7, RM, VM). This form of musculature was more common than the one shown in fig. 12. The vergic sac and a part of the vas deferens are attached to the surface of the preputium, as shown in fig. 12.

Internally (fig. 11), the large preputial cavity has two heavy, vertical pilasters (PL). In the upper part of the preputium, there is a peculiarly shaped penial gland (GL). It is shown somewhat restricted in fig. 11 and drawn upward in the preputial sac. There is a conspicuous gland appendage (GA). The verge (V) is very small (0.7 mm. long) and very narrow and is attached to the vas deferens at about the apex of the preputial sac. When fully extended, the penial gland has the form shown in fig. 1. The gland becomes a rosette surrounding the opening into the vergic sac (X in figure), and the gland appendage (GA) extends forward (or downward) in the preputial cavity, ending in two lateral swellings which notably resemble the glans penis of the human genitalia. There is a narrow canal or channel which extends down the center of the appendage for its entire length (C). A cross section of the appendage indicating the position of this canal is shown in fig. 2 (C).

The verge (highly magnified) is shown in fig. 6. It is short and narrow, somewhat enlarged toward the lower end, with a centrally located sperm canal and exit. There is a narrow vergic sac cavity (VO). The channel which extends down the center of the penial gland appendage is seen to extend upward and into the vergic sac cavity (C). There is a small penial appendage beside the sperm canal outlet of the verge which is flattened and extends diagonally from the end of the verge, as shown in fig. 8 (PA).

Female Organs. The spermatheca (S) is large and pyriform in general shape (fig. 13), about 1.5 mm. long and 1 mm. wide. The duct (SO) is 2.5 mm. long and is a narrow tube. The vagina (VG) is narrow, a trifle more than 1 mm. long and less than 0.5 mm. wide. The uterus (U) begins with the same diameter as the vagina but rapidly enlarges to about 1 mm. wide. It is about 8 mm. long. The nidamental gland (NG) is a large sac-like organ 3.5 mm. long and about 2 mm. in diameter (see fig. 4, NG). The oviduct (OD) is over 4 mm. long and is a large flattened tube about 0.5 mm. in diameter. There is a large carrefour (CF). The albumen gland (fig. 9) is squarish in shape and is composed of many small follicles.

Hermaphrodite Organs (fig. 13). The ovotestis (OT) is very long and occupies a little more than one whorl. It is composed of many diverticula which form a pavement-like pattern on the surface of the ovotestis. In section (fig. 5), the organ shows seven main diverticula each of which is divided into four secondary branches. In fig. 3, a single ripe ovum is shown in the diverticulum. The free portion of the ovisperm duct (SO) is about 5 mm. long between the seminal vesicle and the oviduct and only 1 mm. long between the vesicle and the ovotestis.

The published figures of the genitalia of *Planorbarius corneus* vary considerably. That of Simroth (1912, tafel 26, fig. 3) is one of the best and agrees with our fig. 13 on plate 20 in general gross anatomy. Lacaze-Duthier's figures are also accurate as regards general anatomy and nerve organization (1872, plate 20). L. Soos's figure (1917, p. 37) lacks detail. Germain's figure of the genitalia of *Planorbis corneus* (1931, p. 518) lacks details of structure and is less clear than that of Simroth.

The published figures of the external and internal aspects of the penial complex have been inaccurate, either in figuring or in the interpretation of parts of the organs. Moquin-Tandon (1855) on his plate 32, fig. 3, shows the gland of *corneus* which is called the penis (verge), the lower part being designated as a dilation and the end of the groove is said to represent the stylet. Buchner (1891, tafel 5, fig. 1, copied by Simroth, 1912, p. 502) shows the penial complex incorrectly. Internally, the first type of the penis (penis complex) of *corneus* is an error of interpretation, the penis of Buchner not being the true verge but the gland appendage, which has a channel down the center, thought to be the sperm canal by Buchner. F. C. Baker (1928, I, p. 308) has copied these figures and has erroneously accepted the division into types of the male organ in *Planorbis*. Other authors, as Annandale (1922), have also used these penial subdivisions. Baudelot (1863, plate 4) correctly figures the cylindrical appendage and gland but the appendage is erroneously called the penis. Taylor (1900, p. 366) figures the terminal bulbous portion, calling it the vibratile stimulating appendage, which it probably is.

The true nature of the gland and its appendage and the very small true verge have not been recognized and figured until F. C. Baker's paper appeared in 1931 (p. 579, plate 1). The small verge appears to be an enlargement of the vas deferens and has been completely overlooked.

Respiratory and Renal Systems. The pseudobranch (plate 20, fig. 10) is an oval, elongated body extending from the anal region. It is usually somewhat leaf-like but, as in the figure, it may often be folded forming a rounded tube (P). The rectum (R) is large, rounded, and bears a simple, rounded crest or ridge, which does not extend over the pseudobranch as in *Helisoma*. The anal opening is above the pseudobranch (A). There is a large pneumostome (PS).

The kidney is in general like that of *Helisoma corpulentum* (plate 44, fig. 3) except that it is longer and wider (14 mm. long and 4 mm. wide at the upper part). The portion of the kidney bordering the pericardium is flattened or even a trifle concave, the lower part is rounded and lobate on both margins, the lobations being more numerous than in *Helisoma corpulentum*. There is a large ridge extending down the center of the kidney. A cross section of the kidney near the lower end (plate 45, fig. 18) shows a rounded lumen (TK) with a vein on each side at the lower angle of the lumen (RA, AP). There is a high, sharp crest or ridge (RK) causing the section to be higher than wide. The ridge on the mantle, to the left in the section, is wide, high, and curved (RD).

Digestive System. The digestive system is like that of the Helisomatinae in general. The stomach region is rather narrow and resembles that of *Promenetus exacuous* figured on plate 48 (figs. 4, 5). There is a large blind sac or caecum. The intestine makes a coil about the stomach and another around the liver. The buccal sac is pyriform, elongated, with a short, rounded radula sac. The salivary glands are short and are composed of large branched follicles, in this respect differing from the salivary glands of *Helisoma*.

The superior jaw (plate 50, fig. 14) is wide and low, convex, the ends attenuated and bent downward. The face of the jaw is heavily vertically striated. The side jaws are very narrow and as long as the width of the superior jaw.

Radula (plate 66, fig. 2). Center tooth higher than wide, the two spade-shaped cusps not reaching the lower margin of the base of attachment. Lateral teeth (1-9) squarish, tricuspid, the cusps sharply pointed, the mesocone larger than either the entocone or ectocone. Intermediate teeth (10-14) narrower than the lateral teeth, the entocone breaking up into two to four sharp, pointed cusps, the ectocone becoming bicuspid. Marginal teeth (15-38) narrow, the entocone breaking up into five to six subequal cusps, all in a straight row, the ectocone becoming tricuspid, the cusps very small. The mesocone remains large in all teeth with but little modification. The outer marginals (39-42) are very narrow, much smaller than the other marginals, the cusps becoming very small and forming a serrated outer margin of the teeth.

Germain (1931, p. 518) figures the radula of *corneus* as having interstitial cusps, but such were not observed in the material personally examined. Taylor (1900, p. 270) figures the laterals as bicuspid and in this he is followed by Simroth (1912, p. 316). All specimens studied have had tricuspid lateral teeth, as has been noted for every genus in the family as yet examined. Taylor also figures thirty-three teeth in a row while in specimens personally examined the number has been from forty-two to forty-five. In some specimens from Germany, there were odd teeth (72nd row, 12-15, marginal) in which the cusps of the endocone were uneven and the smaller ones might be assumed to be interstitial cusps. Some outer marginals (17, 20, 22) were of a like nature.

The following radulae have been examined:

Locality	*Formula*	*Rows*	*Source*
Poland, near Warsaw	42-1-42	200-217	Mr. A. Jankowski
Germany	45-1-45	170-210	Dr. F. Haas
Florida (aquarium specimen)	45-1-45	200-218	Mr. Roger P. Gray

Material from the following sources has been used for the above data: Branch of Wista River at Morysinek, 5 km. south of Warsaw, Poland, collected by Mr. A. Jankowski; Germany (locality unknown) from Dr. F. Haas; Ojus, Florida; Copenhagen red snails, bred for aquaria, Mr. Roger P. Gray, sent by Mr. T. Van Hyning.

Geographical Distribution. Great Britain and Europe east to northern and western Asia, south to Portugal and Italy. It has been introduced into New Jersey, Puerto Rico, and probably other places. Whether the larger species found in northern Africa are referable to *Planorbarius* can only be determined by an antomical examination.

Just how many species may be included in *Planorbarius* is somewhat of a question. Germain (1921, 1931) includes one species with several varieties. In the catalogue of Planorbidae in the Indian Museum, Germain includes in *Planorbis* (= *Planorbarius*) several species which belong in other genera, principally *Afroplanorbis*.

Species Considered as Valid. Since the members of this genus are extralimital, the species listed by Westerlund which appear to be referable to *Planorbarius* are cited here.

Planorbarius corneus (Linn.)
Planorbarius elophilus (Bgt.)
Planorbarius kabylianus (Let.)
Planorbarius metidjensis (Forbes)
Planorbarius stenostoma (Bgt.)

Geological Distribution. According to Wenz (1923, p. 1481), the genus *Corneus* (= *Planorbarius*) begins in the late Eocene period.

Remarks. The genus *Planorbarius* is at once distinguished from all other groups of Planorbidae by characteristics of the genitalia. The very large preputium and very small vergic sac are particularly noteworthy, and the form of the penial gland with its elongated appendage and the very small verge are unique features of the genus. The two retractors of the penial complex are also diagnostic features. The structure of the prostate and ovotestis is likewise distinctive. No specimens with everted gland or verge have been observed and one can only surmise that the gland is everted as an excitatory organ and probably the small vergic sac and verge are extended from the male opening, as has been observed in *Helisoma*.

Almost all writers on European fresh-water Mollusca have mistaken the penial gland appendage for the true penis (verge) and have completely missed the small, vestigial true penis. Other authors have ignored all details of the internal anatomy of the penial complex, simply figuring the large preputium and the vas deferens as directly entering this organ.

The systematic position of *Planorbarius* is without doubt in the subfamily Helisomatinae. The presence of the penial gland and the multiple character of the diverticula of both prostate and ovotestis indicate this relationship. The strongly ridged kidney is also another evidence of this kinship. It is the only group of the subfamily thus far known outside of America. The large shell resembles that of *Helisoma* especially the subgenus *Pierosoma*.

The proper genus for the reception of the *Helix cornea* of Linn. has been in some dispute. Many authors have considered it the type of the genus *Planorbis* of Müller. Dall (1905) considered it the type of *Planorbis*, dating it from Montfort, 1810, who definitely established *cornea* as the type of the genus. This procedure has been followed by Germain (1921), Pilsbry and Bequaert (1927), Lindholm (1926), Baker (1931), and Thiele (1931). Dall's conclusions were questioned by Kennard and Woodward (1924) who maintained that the type of the genus *Planorbis* is the *Helix planorbis* of Linn. by absolute tautonomy. H. B. Baker (1930) has also expressed the same opinion. Germain, in a later work (1931), cites the *Helix planorbis* of Linn. as the type of *Planorbis* Guettard 1756 and Geoffroy 1767.

The generic name *Coretus* is in current use by many European conchologists. Some of these use the *Coretus* of Adanson 1757 (as Clessin 1886 and Germain 1931) but that author was non-binomial and pre-

Linnean, furthermore, he applied the name to a minute species about an eighth of an inch in diameter. In 1847, Gray (P.Z.S., p. 508) used the name *Coretus*, as of Adanson, but definitely cited the *Helix cornea* of Linnaeus as the type. Later authors (Wenz, 1923, Haas, 1929) use *Coretus* Gray, 1847, with the type *Helix cornea*.

In 1806, Duméril (Zool. Analyt., p. 164) coined the name *Planorbarius* for a group of mollusks, without an operculum, inhabiting fresh water. Except for the name, which suggests *Planorbis*, the group might pass for anything among fresh-water pulmonates and the name is absolutely useless for purposes of nomenclature. In a German edition of Duméril's work, however, Froriep used this name and supplied a type, the *Helix cornea* of Linnaeus which, according to Opinion 46 of the International Code, becomes the monogenotype of the genus *Planorbarius* of Froriep. This antedates Montfort's use of *corneus* as a genotype by four years.

Froriep says of *Planorbarius* in his German translation (p. 165):

> Die Scheibenschnecken (*Planorbarius*) unterscheiden sich (die Schaele uberrücksichtiget) von den vorigen nur durch den mangelnden Schliessdeckel. Es sind dies Flussschnecken. Z.B., *Helix cornea*.

The case is much better than that of *Coretus* Gray and there appears to be no reason why *Planorbarius*, as published by Froriep. should not be used for the large European snail previously known as *Planorbis corneus*. The rarity of Froriep's translation in libraries has doubtless been the cause of its being omitted in most previous discussions of planorbid nomenclature.

Subfamily PLANORBULINAE Pilsbry, 1934

Prostate diverticula compound but not fan-like in section, there being a main division from which branch, on one side, several (four to six) smaller diverticula. The ovotestis diverticula are placed in pairs. There is a penial gland but no external duct, which is always placed inside of the preputium. The jaws are as in Helisomatinae.

Type genus *Planorbula* Haldeman.

The few groups belonging in this subfamily are noted below:

With short, tube-like duct: *Planorbula*, *Promenetus*.
Without distinct duct but with open channel: *Menetus*, *Micromenetus*.

The fossil group *Planobifex* Pilsbry doubtless belongs in this subfamily.

Genus PLANORBULA Haldeman, 1840

Type by original designation *Planorbis armigerus* Say

1840. *Discus* Haldeman, Mon. Limn. Part I, p. 4 of cover, July, 1840. Non Fitzinger, 1833, a land genus. Type *Planorbis armigerus* Say. As subgenus

1840. *Planorbula* Haldeman, op. cit., Suppl. to Part I, p. 2 (Oct. 1840). New name for *Discus* Haldeman, preoccupied

1842. *Planorbula* Haldeman, Mon. Limn., Part IV, Physidae, p. 14. Monotype *Planorbis armigerus* Say. As subgenus

1847. *Dentatus* Gray, Proc. Zool. Soc. London, p. 181, non Beck, 1837. Type *Planorbis armatus* Gray, supposed to be the same as *Planorbis armigerus* Say. As subgenus of *Coretus*

1855. *Planorbula* H. and A. Adams, Genera of Rec. Moll., II, p. 265. Type *Planorbis armigerus* Say. As subgenus

1865. *Planorbula* Binney, L. and FW. Sh. N. A., II, p. 136. No type cited, but *Planorbis armigerus* Say by assumption. As subgenus of *Segmentina*

1870. *Planorbula* Dall, Ann. N. Y. Lyc. N. H., IX, p. 352. Type *Planorbis armigerus* Say. As subgenus of *Segmentina*

1870. *Segmentina* Tryon, Con. Hald. Mon., p. 213 (non Fleming). No type cited but *Planorbis armigerus* Say, listed.

1883. *Planorbula* Fischer, Man. de Conch., p. 509. Type *Planorbis armigerus* Say. As subgenus of *Planorbis*

1884. *Planorbula* Tryon, S. & S. Conch., III, p. 107. Type *Segmentina armigera* (Say). Subgenus of *Segmentina*

1886. *Planorbula* Clessin, Conch. Cab., XVII, p. 35. Type *Planorbula armigera* (Say). As genus

1899. *Planorbulina* Martens, Biol. Cent. Amer., Moll., p. 400. Clerical error for *Planorbula*. May equal *Tropicorbis* in part. For group of *Planorbis armigerus* Say

1902. *Planorbula* F. C. Baker, Moll. Chicago Area, Part II, p. 300. Radula figured. As subgenus of *Segmentina*

1905. *Planorbula* Dall, Alaska Moll., p. 97. Type *Planorbis armigerus* Say. As subgenus of *Segmentina*

1906. *Planorbula* Pilsbry and Ferriss, Proc. Acad. Nat. Sci. Phil., p. 166. As subgenus of *Segmentina*

1909. *Planorbula* Pallary, Mem. Inst. Egypt, VI, p. 59. As genus. Doubts that *Planorbula* of America is found in Egypt

1912. *Segmentina* (part) Hannibal, Proc. Mal. Soc. London, X, p. 154. A group mixture, but includes *Planorbula* of Haldeman.

1918. *Planorbula* Walker, Miscel. Papers Mus. Zool., Univ. Mich., No. 6, pp. 14, 104. Type *Planorbis armigerus* Say. Shell and radula. As subgenus of *Segmentina*

1923. *Planorbula* Germain, Rec. Ind. Mus., XXI, p. 179. Type *Planorbis armigerus* Say. As genus

1926. *Planorbula* F. C. Baker, Trans. Wis. Acad. Sci., Arts, and Lett., XXII, p. 203. Type *Planorbis armigerus* Say. As genus

1926. *Planorbula* Lindholm, Archiv. für Mollusk., 58 year, Heft 6, p. 258. Thinks it should be separate genus

1927. *Planorbula* Pilsbry and Bequaert, Bull. Amer. Mus. N. H., LIII, p. 131. Monotype *Planorbis armigerus* Say. As genus

1928. *Planorbula* F. C. Baker, Fresh-water Moll. Wis., I, p. 353. Type *Planorbis armigerus* Say. Genitalia, jaw and radula figured. As genus

1930. *Planorbula* H. B. Baker, Occ. Papers Mus. Zool., Univ. Mich., No. 210, p. 43. Monotype *Planorbis armigerus* Say. As genus

1931. *Planorbula* Thiele, Handbuch, 2 Teil, p. 480. Type *Planorbis armigerus* Say. As genus

1934. *Planorbula* Pilsbry, Proc. Acad. Nat. Sci. Phil., 86, p. 54. Form of prostate and presence of penial gland indicated

1934. *Planorbulina* Pilsbry, loc. cit., p. 54. Typographical error of von Martens for *Planorbula*. Type designated by Pilsbry *Planorbis armigerus* Say

1940. *Planorbula* Haldeman, Morrison, Nautilus, LIV, p. 65. Notes correct date of publication, Oct. 1840

Subgenus PLANORBULA SS.

Type by original designation *Planorbis armigerus* Say

Shell (plate 79, figs. 25-27). Small, ultradextral, of few closely coiled whorls, slowly increasing in diameter, with flatly rounded whorls above and a wide depression below, the body whorl usually carinate in the middle; lips more or less thickened by a varix. Aperture with six lamellae situated well within, placed as follows: a large parietal lamella, somewhat sigmoid, obliquely transverse, with a small tubercular lamella below, at the left end of the parietal lamella; four palatal lamellae (plate 76, fig. 8), a large slightly transverse basal (4), a large lower palatal (3) which is always directed upward, an upper palatal above and smaller than the lower palatal (2), also pointed upward, and a suprapalatal (1) which is usually in a transverse position. This lamella may be vestigial or absent in some forms of *Planorbula*. Only one set of lamellae occurs in each shell although the lamellae are found at a very early period in the age of the individual, the old set appearing to be absorbed before the new one is formed as the shell increases through growth.

Animal (plate 70, fig. 11). The living animal of *Planorbula jenksii* from Lake Wentworth, New Hampshire, is almost black, the foot with lighter edges. The tentacles are long and tapering, blackish in color with a light zone near the head; a blackish band borders the head and neck above the foot and velar area; the top of the head is wine-colored or reddish, the sides of the body lighter; the black eyes are placed at the inner bases of the tentacles. The mantle is blotched with dark gray dots. The stomach region is pigmented. The liver and ovotestis are yellowish. The velar area is very wide and extends beyond the foot when the animal is in motion. The shell is carried tilted to the left, at an angle of about forty-five degrees. It is sometimes carried flat, the left side lowermost.

ANATOMICAL CHARACTERISTICS

PLATE 37 (*Planorbula armigera* (Say))

GENITALIA. Male Organs (fig. 4). The seminal vesicle (SV) is about 1 mm. long and 0.5 mm. wide and is composed of a cluster of small glands or follicles. The sperm duct (SPD) is roundly enlarged at its distal end (about 0.5 mm. long and wide) tapering anteriorly to less than half this diameter under the prostate. The prostate (PRS) is about 1.5 mm. in length and less than 0.5 mm. in height. In section (figs. 1, 2), the prostate is seen to be composed of a long diverticulum to which are attached, on one side only, five or six smaller and shorter diverticula, several of which may be branched two to four times. There are about thirty rows of diverticula in the prostate. The vas deferens is of smaller diameter than the sperm duct, for the most part about half this diameter, and is 6 mm. long.

The penial complex (fig. 9) has a strikingly pyriform preputium, narrowing anteriorly to a round tube of small diameter. The preputium is less than 1 mm. long and a trifle more than 0.5 mm. in diameter at its greatest width. The vergic sac is cylindrical in form, about 0.3 mm. in diameter and as long as the preputium. There is only a slight constriction between the preputium and the vergic sac. There is one heavy retractor muscle (RM) attached to the summit of the preputium near the vergic sac. Three wide supporting muscles are attached to the upper and middle area of the preputium. There is no external penial gland duct. The penial complex of another specimen shows a more swollen preputium and a wider vergic sac (fig. 10).

Internally (fig. 11), the preputium has two heavy vertical pilasters (PL) the left one sending a transverse, thick, rounded fold or ridge across the upper part of the preputial sac to the right pilaster. There is a rounded, basin-shaped penial gland (GL), with a shallow cup, the walls of which have many vertical folds (fig. 6, GF). There is no external gland duct, but a shallow channel, open above (DC), connects the penial gland with a circular space bordering externally the high, thick, fleshy muscular ring or diaphragm between the ring and the body wall of the preputium (fig. 11, D). The verge (V) is sac-like, about 1 mm. long, and tapers to a point at its lower end (fig. 12). The sperm canal extends through the center of the verge and has a central outlet bordered by a small penial papilla (fig. 8).

Female Organs (fig. 4). The spermatheca (S) and spermatheeal duct (SD) are about 1.3 mm. long, the duct and gland of equal length and the gland swollen to more than twice the diameter of the duct. The vagina (VG) is 0.8 mm. long and 0.3 mm. wide the spermatheeal duct entering it rather high. The uterus (U) is about 2 mm. long and is but little wider than the vagina. The nidamental gland is slightly wider than the uterus and is located beneath the prostate. The oviduct (OD) is over 2 mm. long and is of the same diameter as the sperm duct. It is somewhat convoluted at the upper end where there is a large carrefour (CF) which receives the long duct from the albumen gland (fig. 3, DA, AL). The albumen gland (AL) is large, about 1 mm. in diameter, somewhat triangular in shape, and is folded for the passage of the intestine.

Hermaphrodite Organs. The ovotestis (fig. 4, OT) occupies a little more than one whorl and is composed of long, club-shaped diverticula arranged in pairs (fig. 7), each pair bending to right or left or placed in the center. There is a very short free ovisperm duct between the ovisperm duct and the seminal vesicle, and a longer, narrow duct (2 mm. long) between the seminal vesicle and the oviduct. A few vesicles extend down a part of the ovisperm duct from the seminal vesicle.

The genitalia of *Planorbula jenksii* are in most respects like those of *armigera*. The prostate has about twenty-five rows of diverticula while in *armigera* there are thirty rows.

No figures of the genitalia of *Planorbula* have been published previously, except those by F. C. Baker (1928, p. 356, figs. 153, 154). The figure of the entire genitalia (1928, fig. 153) is incorrect in several particulars, especially in the form of the prostate and the seminal vesicle. The diagrammatic figure of a secion of the penial complex (1928, fig. 154) is more nearly correct, but does not show the details of the penial gland.

Respiratory and Renal Systems. The pseudobranch (plate 37, fig. 5, P) is rounded and has a ridge extending down the middle which connects with a crest-like ridge on the rectum (R). The ridge on the pseudobranch is heavy and when bent over (as shown in the figure) causes the pseudobranch to appear folded. There is a large pneumostome (PS). The pseudobranch of *jenksii* is like that of *armigera*.

The kidney (plate 45, fig. 3) is long and narrow (5.5 mm. long, 1 mm. wide at the pericardium). The ureter is sharply recurved and is directed upward into the mantle cavity. The pericardium is about 1 mm. long. In section (fig. 13, near middle), the kidney is seen to be much flattened, with the lumen twice as wide as high and with a vein at each end. There is no ridge on the kidney.

Digestive System. The digestive organs (narrow stomach, crop, and pyloris) are similar to those in *Carinifex* and *Parapholyx*. The intestine makes a loop around the stomach, passes backward to the liver, makes another loop and runs forward to the rectum, ending in the anus over the pseudobranch. There is a conspicuous blind sac or caecum. Both *jenksii* and *armigera* have the same type of digestive system. The buccal sac is of the same form as that of *Carinifex*. The salivary glands extend half their length behind the buccal sac and form a loop.

The superior jaw of *armigera* (plate 50, fig. 2) is slightly arched, about four times as wide as high and finely, vertically striated on the anterior face. The side jaws are about as long as the width of the superior jaw and are shaped as in *Parapholyx*. The jaws of *jenksii* (fig. 3) are the same as those of *armigera*.

Radula of *armigera* (plate 65, fig. 1). The center tooth is slightly higher than wide with a bicuspid reflection which does not reach the lower margin of the base of attachment. The lateral teeth (1-8) are squarish with three long, spade-like cusps of the same shape. The intermediate teeth (9-11) have the ectocone split two or three times, the cusps sharp. The marginal teeth (12-19) are long and narrow with cusps at the lower end. The endocone at first is split into two cusps about as long as the mesocone (12-13); they then become split into four small, equal cusps (14-16). The ectoconic margin has three to four small cusps. The outer marginal teeth are shorter than the earlier marginals but have the same form (19). The radula of *jenksii* has the same form of teeth.

RADULA DATA FOR *Planorbula*

Species	*Formula*	*Locality*	*Rows*	*Source*
armigera	18-1-18	Murphy Creek, Wisconsin	160-165	Dr. C. Juday
armigera	24-1-24	Snodgrass Lake, Ontario	160-165	Dr. A. R. Cahn
armigera	18-1-18	Devil's Lake, Wisconsin	125-140	F. C. Baker
armigera	19-1-19	Douglas Lake, Michigan	125-140	Dr. F. Smith
jenksii	19-1-19	Unionville, Connecticut	145-150	F. C. Baker

The data for the material examined anatomically are as follows: *armigera*, Murphy Creek, near Madison, Wisconsin; Snodgrass Lake, Ontario; Devil's Lake, Wisconsin; Douglas Lake, Mich.; *jenksii*, Roaring Brook, Unionville, Connecticut. Five specimens from each lot of *armigera* were examined and about fifteen specimens of *jenksii*.

Geographical Distribution. *Planorbula* is wholly an American genus distributed from Great Slave Lake and Fort Smith, Mackenzie River, south to Georgia and Louisiana, and from the New England states west to Nebraska.

Species Considered as Valid. The following are recognizable as belonging to this genus:

Planorbula armigera armigera (Say)
Planorbula armigera palustris Baker
Planorbula crassilabris (Walker)
Planorbula jenksii (H. F. Carpenter)
Planorbula campestris (Dawson)
(= *christyi* Dall)

Geological Distribution. Pleistocene to Recent fauna.

Remarks. *Planorbula* is a distinct and characteristic genus of American Planorbidae. The name has been used to cover many dentate planorbids, such as *Tropicorbis* of the tropics and certain forms of north Africa belonging to *Afroplanorbis*. It is in no way related to these groups, which belong in the subfamily Planorbinae. *Planorbula* of Haldeman belongs in a separate subfamily related to Helisomatinae, having a distinct penial gland and multiform prostate and ovotestis diverticula.

The lamellae within the aperture are also different in the two groups—in *Tropicorbis* the large lower palatal lamella is always pointed downward while in *Planorbula* this lamella points upward. In *Planorbula*, the plicae are always present but in *Tropicorbis* they may be absorbed late in life and the aperture become edentulous (see remarks under *Tropicorbis*).

Planorbula has also been subordinated to *Segmentina* as a subgenus but it has no relationship to that genus, the internal organs being of a totally different character. *Segmentina* is the type genus of the subfamily Segmentininae.

The chief characteristics of the genus *Planorbula* are the ovate or rounded penial gland without an external duct but with a canal-like duct within the preputium, and the prostate with small, branched diverticula on one side of a main diverticulum. Its nearest relative is *Promenetus*, with which it agrees in general in the form of prostate and penial gland. These genera and their relatives constitute a subfamily Planorbulinae, as suggested by Pilsbry in 1934 (p. 47).

Subgenus HALDEMANINA Dall, 1905

Type by original designation *Planorbis wheatleyi* Lea

1905. *Haldemanina* DALL, Alaska Moll., p. 97. Type *Planorbis wheatleyi* Lea. As section of subgenus *Planorbula* Haldeman

1918. *Haldemanina* WALKER, Miscel. Pub. Mus. Zool., Univ. Mich., No. 6, p. 105. Type *Planorbis wheatleyi* Lea. Synonym of *Planorbula*

1923. *Haldemanina* GERMAIN, Rec. Ind. Mus., XXI, p. 181. Type *Planorbis wheatleyi* Lea. Considered synonym of *Planorbula*

1931. *Haldemanina* THIELE, Handbuch, Teil 2, p. 480. Type *Planorbis wheatleyi* Lea. As synonym of *Planorbula*

Shell (plate 79, figs. 28-30). As in *Planorbula* but with the aperture notably thickened, the lower palatal lamella within the aperture very long and curved upward as far as the upper palatal lamella.

Animal. The animal is unknown anatomically.

Geographical Distribution. Not at present known outside of the state of Alabama.

Species Considered as Valid. *Planorbula (Haldemanina) wheatleyi* (Lea), type of this subgenus, is the only species ascribed to it.

Remarks. In 1905 (p. 97), Dall instituted a section *Haldemanina* to contain the *Planorbis wheatleyi* of Lea. No particular characteristics different from *Planorbis armigera* appear in his diagnosis, except the statement 'lamellae complex.' Upon examining the lamellae of *wheatleyi*, the complexity is at once seen. The lower palatal lamella is about twice as long as in *armigera* and the upper part is bent upward almost at right angles to the transverse lower part, so that this end is on a line with the upper palatal lamella, the whole lamella being bent like an Australian boomerang (see plate 76, fig. 9, *wheatleyi;* fig. 8, *armigera*).

Authors, generally, have considered *Haldemanina* an absolute synonym of *Planorbula*, but the difference in the lower palatal lamella is persistent in all specimens of *wheatleyi* here examined and is not found in any other species or race of *Planorbula*. The writer, therefore, is disposed to accept *Haldemanina* as a subgroup under *Planorbula*. The thickening of the lip has no special significance, as this is found in several species of *Planorbula*.

Genus PROMENETUS F. C. Baker, 1935

Type by original designation *Planorbis exacuous* Say

1928. *Menetus* F. C. Baker, Fresh-water Moll. Wis., I, pp. 357, 360, 362 (non H. and A. Adams). Genitalia of *Planorbis exacuous* Say

1935. *Promenetus* F. C. Baker, Nautilus, XLIX, p. 48. Type *Planorbis exacuous* Say. As new group

Shell (plate 79, figs. 19-21). Ultradextral with a small number of whorls rapidly increasing in diameter, carinated or rounded; left side with broad spire depression exhibiting all of the whorls; right side flat, also exhibiting all of the whorls; aperture wider than high; outer lip thin.

Animal. External features similar to those of *Planorbula*. Foot very short and rounded. Color blackish.

ANATOMICAL CHARACTERISTICS

PLATE 41 (*Promenetus exacuous* (Say))

GENITALIA. Male Organs (fig. 10). The seminal vesicle (SV) is about 2 mm. long, is nearly three times the diameter of the ovisperm duct and has many small diverticula or vesicles, about as long as the diameter of the seminal vesicle, projecting from one side of the organ. The sperm duct (SPD) is about 1.5 mm. long and 0.3 mm. in diameter and appears sausage-shaped. The prostate (PRS) is 1.5 mm. long and is composed of thirteen multiple diverticula. In section (fig. 5) the prostate is seen to have four supplementary diverticula projecting from the side which lies next to the oviduct. An unusual form of prostate is shown in fig. 11, plate 42 (*P. exacuous megas*) in which the three supplementary diverticula are each branched three times at the extremity. The vas deferens (VD) is about 7 mm. long and about one third the diameter of the sperm duct, which, itself, also diminishes greatly in diameter beneath the prostate.

The penial complex (plate 41, fig. 2) is 3 mm. long, the pyriform preputium occupying half of the length, the much narrower vergic sac the other half. There is no sharp constriction between the upper and lower sacs, the preputium simply narrowing as it joins the vergic sac. There is one narrow retractor muscle (RM) and a wide group of three to five supporting muscles (SM) forming a lattice-like pattern. The vas deferens enlarges only slightly as it enters the vergic sac (VD). In fig. 1, a penial complex is shown in which the preputium is much swollen by the enlarged penial gland. The penial complex of variety *megas* does not differ from that of *exacuous*.

Internally (fig. 3), the preputium has two heavy pilasters (PL) to the upper part of the left one of which the penial gland is attached (GL). The gland appears sac-like as seen from the side and is bent crosswise in the cavity of the preputium. There is a wide projection at the end of the gland in which there is an open groove (DC) or channel connecting the gland with the muscular ring or diaphragm (D) and separating the upper from the lower cavity. In fig. 3 on plate 42, the penial gland is shown from above, the pilasters separated to show the ovate cup of the gland and the glandular folds lining the walls of the cup. A longitudinal section of the gland (plate 42, fig. 7) shows the arrangement of the vertical folds within the gland.

The verge (V) is long and narrow, usually filling the vergic sac (plate 41, fig. 3) and protruding from the diaphragm into the preputial cavity.

In fig. 12, plate 42, the verge is shown in this condition, with the penial gland (GL) extended crosswise of the preputial cavity. The end of the verge of variety *megas* is shown in fig. 13, plate 42, indicating the centrally located opening of the sperm canal with a small penial papilla placed just below and to one side of the opening. A circular ridge near the end of the verge was observed in this specimen which did not appear in others examined.

In a specimen of variety *megas* (fig. 4, plate 42), the gland was somewhat contracted but showed well the trough-like canal or channel connecting the gland with the circular canal near the diaphragm. In this specimen, the side ridges or bands of muscle connecting the two pilasters with this canal are well shown. A specimen from Winnebago Lake had the verge and penial gland extended from the male opening and lying on the neck of the animal (plate 41, fig. 9).

Female Organs (plate 41, fig. 10). The spermatheca (S) is irregularly ovate, bulging in the center, with a wide duct (SD) about as long as the spermatheca, the two parts together measuring about 2 mm. The vagina (VG) is wide and a trifle more than 1 mm. in length. The uterus (U) is the same width as the vagina and narrows only at the upper part of the oviduct (OD). The uterus and oviduct combined are about 4 mm. long. The nidamental gland (NG) is about 1.5 mm. long. The relationship of the sperm duct, oviduct, ovisperm duct, carrefour, and albumen gland duct is shown in fig. 10, plate 42 (of variety *megas*). The duct of the albumen gland is quite long and folded in an **S** form. The albumen gland (plate 41, fig. 7) is about 2 mm. long and half as wide.

Hermaphrodite Organs. The ovotestis OT, (plate 41, fig. 10) occupies a little more than one whorl (fig. 6). In section (fig. 4), it is seen to be composed of twin, club-shaped diverticula, both glands entering the ovisperm duct. Sections of variety *megas* are shown on plate 42, one near the middle of the ovotestis (fig. 8) and one near the posterior end (fig. 9). The ovisperm duct (free portion) extends about 1 mm. on each side of the seminal vesicle and is without glandular projections or swellings.

A related species, *Promenetus umbilicatellus*, formerly known as *Gyraulus umbilicatus*, shows some differences and the anatomy of this species is shown on plate 43. The seminal vesicle is about twice the diameter of the ovisperm duct (fig. 1) and is bordered on both sides by several more or less sharply pointed gland-like protuberances. Small vesicles project from the ovisperm duct for a long distance (over 1 mm.) below the seminal vesicle. The sperm duct (SPD) is short and narrow (less than 1 mm. long) and is a small tube. The prostate (PRS) is about 1 mm. long and is composed of twenty diverticula which appear very long and narrow when the prostate is in its natural position lying against the uterus. A section about midway of its length (fig. 6) shows five supplementary diverticula or six including the termination of the main diverticulum. The vas deferens (VD) is a narrow tube about 3 mm. long.

The penial complex (fig. 4) is about 1.5 mm. long and the preputium and the vergic sac are of about equal length. The vergic sac is not much narrower than the preputium, the latter having a swelling or ridge at the upper part indicating the position of the diaphragm. There is one narrow retractor muscle (RM) attached to the upper part of the preputium and a wide band of supporting muscle (SM) attached to the middle portion of the preputium. A small supporting muscle may be present on the preputium below the retractor muscle.

Internally, the penial complex is like that of *exacuous* (fig. 3). There is a large penial gland (GL) which may be folded back as shown in fig. 10. In section (fig. 11), it is like that of *exacuous*. There is an open, canal-like duct (see fig. 9). The *verge* (V) is short and wide, with a central opening of the sperm canal bordered by a distinct penial papilla (fig. 12).

In the female system (fig. 1), there is a short spermatheca (S) with a wide duct twice as long as the spermatheca (SD). The vagina (V) is wide but shorter than in *exacuous*. The uterus (U) is wide and short and there is a swollen nidamental gland (NG). The oviduct (OD) is longer than in *exacuous*. The relationship of the oviduct, sperm duct and ovisperm duct is shown in fig. 7. The albumen gland is somewhat quadrangular in form and is composed of large vesicles (fig. 5).

Of the hermaphrodite organs, the ovotestis is composed of paired diverticula. In the specimens examined, many of the diverticula were gravid (plate 43, fig. 1, OT; fig. 8). The ovisperm duct differs from that of *exacuous* by having a number of small swellings on one side of the duct for half the length of the portion between the seminal vesicle and the oviduct. A portion of the ovisperm duct between the seminal vesicle and the ovotestis is without gland-like swellings.

The penial complex of *Menetus exacuous* is figured by Baker (1928, p. 357, fig. 154). The retractor muscle is shown with an attachment to both the preputium and the vergic sac. This feature was not observed in any specimens more recently examined and this figure must be considered abnormal. All material studied, of *exacuous* and *umbilicatellus*, had a single retractor without two branches for the vergic sac and the preputium. The same criticism extends to fig. 157 on p. 362 of the work mentioned.

Respiratory and Renal Systems. The pseudobranch appears somewhat variable in form, the variation being largely due to the amount of expansion of the organ. In specimens of *exacuous* from Winnebago Lake, Wisconsin (plate 41, fig. 8), it is large and leaf-like. In an example from Wainwright Park, Alberta (plate 42, fig. 1), it is fully expanded, wide and rounded below, with the anal opening conspicuously placed on one side within the area of the pseudobranch. It is somewhat folded in the middle. In a specimen of variety *megas* from Paul Lake, British Columbia (plate 42, fig. 2), the pseudobranch is rounded, and there is a smooth ridge extending over a part of the rectum and forming a thickened border to the pseudobranch. In *umbilicatellus* (plate 42, fig. 6), the pseudobranch is rounded in one specimen and folded in another (plate 43, fig. 2). In these examples, the anal region is outside of the area of the pseudobranch. There is no decided ridge on any specimen examined and the ridge on the rectum is not like that in Helisomatinae.

The kidney (plate 46, fig. 3) of *exacuous* is 3.5 mm. long and about 0.5 mm. wide, rather long and narrow. The ureter is a long tube and turns at right angles to the long diameter of the kidney. It borders the thickened mantle margin on the inside. The pericardium is less than 1 mm. long. A cross section of the kidney near the middle (plate 46, fig. 4) shows an ovate lumen with a small vein on each side. There is no superposed ridge. The kidney of *umbilicatellus* is of the same shape and general nature as that of *exacuous*, but the ureter bends backward at a sharper angle and is directed upward into the mantle cavity.

Digestive System. The stomach is elongated with the gizzard longer than wide and with a rounded pyloris (plate 48, figs. 4, 5). There is a long blind sac or caecum (BS). The intestine (IN) makes a tight loop around the stomach, extends backward to the liver and then makes another loop and runs forward to the rectum. The buccal sac is elongated, with a rounded radular sac. The salivary glands are narrow, looped, and as long as the buccal sac.

The superior jaw is arched, wide, and low, with the face vertically striated, as in other members of the group (plate 50, fig. 8, *exacuous*). In *umbilicatellus* (plate 50, fig. 15), there is a sharp median projection on the lower edge of the superior jaw. In *exacuous*, there is only a rounded bulge at this point. The side jaws are as in other species of the subfamily.

The radula of *exacuous* has a squarish center tooth with expanded lower margins, the two wide, spade-shaped cusps not reaching the lower border of the base of attachment. The lateral teeth (1-6) are squarish, tricuspid, the mesocone longer and larger than the entocone and ectocone. All cusps are sharply pointed. The sixth lateral has a small cusp above the ectocone. Intermediate teeth begin on the seventh tooth, the entocone splitting into two long, sharp cusps and one or two small cusps appearing on the outer margin of the tooth above the ectocone (9-10). Marginal teeth (11-15) long and narrow, the entocone splitting into three to four small cusps and the outer margin of the teeth having two to three small cusps above the ectocone. The outer marginals are almost vestigial. The radula of *umbilicatellus* (fig. 2) is similar in form to that of *exacuous*.

The radula data for *Promenetus* are as follows, two to four specimens of each having been examined:

Species	*Formula*	*Locality*	*Rows*	*Collector*
exacuous	17-1-17	Winnebago Lake, Wisconsin	110-112	F. C. Baker
exacuous	16-1-16	Wainwright Park, Alberta	115	Dr. Swales
umbilicatellus	17-1-17	Wainwright Park, Alberta	138-140	Dr. Swales
umbilicatellus	18-1-18	Vermilion Lake, Minnesota	140	F. C. Baker

The material examined for the anatomical data described and figured in the preceding pages is listed below. Figures in parenthesis indicate number of specimens studied.

exacuous: Winnebago Lake, Wisconsin, collected by F. C. Baker (4); Lake Nipissing, Ontario, received from the Canadian National Museum (5); Mott Lake, Wainwright Park, Alberta, collected by Dr. Swales (4);

exacuous megas: Paul Lake, British Columbia, collected by Prof. D. S. Rawson (2).

umbilicatellus: Mott Lake, Wainwright Park, Alberta, collected by Dr. Swales (8); North Star Lake, Minnesota, collected by F. C. Baker (1); Vermilion Lake, Minnesota, collected by F. C. Baker (2).

Specimens of *exacuous* from Wainwright Park, Alberta, were heavily infested with cercariae, more abundant in the ovotestis and liver. In several specimens both of these organs were almost obliterated.

Geographical Distribution. The genus *Promenetus* has a wide distribution. It has been recorded from Maine west to Washington and Oregon and from Hudson Bay and Alaska south to New Mexico and Alabama. A single species (*imus*) is known from Bermuda.

Species Considered as Valid. Five species, in one of which two races are recognized, are attributable to *Promenetus*.

Promenetus exacuous exacuous (Say)
Promenetus exacuous megas (Dall)
Promenetus umbilicatellus (Cockerell)
Promenetus rubellus (Sterki)
Promenetus hudsonicus (Pilsbry)
Promenetus imus (Vanatta)

Geological Distribution. Pliocene to Recent fauna.

Remarks. *Promenetus*, first described as a group of the genus *Menetus*, differs so radically from *Menetus* in the form of the penial gland that it is deemed necessary to raise the group to generic rank. Its gland resembles *Planorbula* in the lack of a distinct duct and in the opening of the gland which is lengthwise instead of at the end of a cylindrical sac-like gland, as in typical *Menetus* and its subgenus *Micromenetus*. The form of the penial complex is also more like that of *Planorbula* than like this organ in *Menetus*. In other respects, the genus *Promenetus* conforms to the general characteristics of the subfamily.

The discovery that the species long known as *Gyraulus umbilicatellus* is a *Menetus* closely related to *exacuous* (Baker, 1935, p. 46) was a surprise and shows that the group *Promenetus* includes species with both rounded and sharply carinated whorls. The vas deferens in typical *Menetus* enlarges as it enters the vergic sac to form an epiphallus. In *Promenetus* and *Planorbula*, there is no such enlargement.

Genus MENETUS H. and A. Adams, 1855

Type designated by Dall in 1870, *Planorbis opercularis* Gould

1855. *Menetus* H. and A. Adams, Genera of Rec. Moll., II, p. 262. Includes several unrelated species among which is *Planorbis opercularis* Gould. (Non *Menetus* of Chenu, 1869, P. Fischer, 1883, Tryon, 1884, C. A. Westerlund, 1885, or von Martens, 1899)

1865. *Menetus* W. G. Binney, L. and FW. Sh. N. A., II, p. 125. No type cited but includes *Planorbis opercularis* and *P. exacuous* (= *exacutus*). As subgenus of *Planorbis*

1870. *Menetus* Tryon, Con. Hald. Mon., pp. 188, 206. No type cited but includes both *Planorbis opercularis* and *P. exacutus*. As subgenus

1870. *Menetus* Dall, Ann. N. Y. Lyc. N. H., IX, p. 351. Type designation, *Planorbis opercularis* Gould. As subgenus

1886. *Menetus* Clessin, Syst. Conch. Cab., XVII, p. 33. Type *Planorbis opercularis* Gould. As genus

1905. *Menetus* Dall, Alaska Moll., pp. 82, 86. Type *Planorbis opercularis* Gould. Section of subgenus *Hippeutis* Agassiz

1918. *Menetus* Walker, Miscel. Pub. Mus. Zool., Univ. Mich., No. 6, pp. 12, 94. Type *Planorbis opercularis* Gould. Section of subgenus *Hippeutis* Agassiz

1923. *Menetus* Wenz, Fossil. Cat., Pars 22, p. 1650. Genotype *Hippeutis (Menetus) opercularis* (Gould). Few of the species listed are true members of the genus *Menetus*, which is not found in Europe. They might belong in the genus *Anisus*. Subgenus of genus *Hippeutis*

1923. *Menetus* Germain, Rec. Ind. Mus., XXI, pp. 8, 156. Type *Planorbis opercularis* Gould. As subgenus of *Planorbis*

1926. *Menetus* F. C. Baker, Trans. Wis. Acad. Sci., Arts and Lett., XXII, p. 203. Type *Planorbis opercularis* Gould. Anatomy. As genus

1928. *Menetus* F. C. Baker, Fresh-water Moll. Wis., I, p. 360. Type *Planorbis opercularis* Gould. Anatomy. As genus

1929. *Menetus* J. Henderson, Univ. Col. Studies, XVII, No. 2, pp. 140-141. As subgenus of *Planorbis*

1931. *Menetus* THIELE, Handbuch, p. 481. Type *Planorbis opercularis* Gould. As section under *Hippeutis*, subgenus of *Anisus*

1934. *Menetus* PILSBRY, Proc. Acad. Nat. Sci. Phil., 86, p. 63. Type *Planorbis opercularis* Gould. Anatomy. As genus

1935. *Menetus* F. C. BAKER, Nautilus, XLIX, p. 47. Type *Planorbis opercularis* Gould. Anatomy. As genus

Subgenus MENETUS SS.

Type *Planorbis opercularis* Gould

Shell (plate 79, figs. 22-24). Small, ultradextral, of few rapidly enlarging whorls, the body whorl of large diameter compared with the inner whorls; right side flat, left side with the spire whorls deeply immersed; periphery or shoulder of body whorl more or less carinated; aperture wide, more or less expanded; outer lip usually thin.

Animal. The foot is comparatively short, the tentacles long and filiform. Color generally blackish. In general features the animal is like that of *Planorbula*.

ANATOMICAL CHARACTERISTICS

PLATES 38 AND 39

GENITALIA. Male Organs. (*Menetus opercularis*, type of the genus, plate 38, fig. 1). Seminal vesicle (SV) about 0.5 mm. long, twice the diameter of the ovisperm duct and about the same length. The vesicle proper has a few wide lobes, but the lower part (the ovisperm duct) is lined with small vesicles on the side. Sperm duct (SPD) about 1 mm. long, rather thick. Prostate (PRS) about 0.5 mm. long with about a dozen main diverticula. In section (fig. 2), the prostate shows several small diverticula projecting from a single, vertical diverticulum, there being usually five branches, one or more of which may be divided two or three times at the end (as in figs. 2, 3), or all may be single, long and club-shaped, as in *cooperi* (fig. 14). The vas deferens is 3 mm. long, about half the diameter of the sperm duct, and slightly enlarged as it enters the vergic sac.

The penial complex (fig. 10) is elongated and sac-like, about 1.5 mm. long, of which the preputium, narrowed at the male genital opening, occupies 1 mm. or two-thirds of its length. There is a slight constriction between the preputium and the vergic sac (VS). There is one narrow retractor muscle (RM) attached to the base of the vergic sac. There are four sets of supporting muscles (SM) attached to the preputium. Most of these are branched several times.

Internally (fig. 8), the preputium has two pilasters (PL). At the upper part of the preputium, there is a short penial gland which is doubled over in the normal position (GL). When expanded (fig. 6), this gland is trumpet-shaped, the bell-like cup flaring. The cup cavity is provided with vertical folds, as in other Planorbidae. There is a dependent ring or diaphragm between the preputium and the vergic sac cavity (D in fig. 8). The verge (V) is elongated and tapering and normally as long as the vergic sac.

Female Organs (fig. 1). The spermatheca (S) is ovate, about 0.3 mm. long and has a very narrow duct (SD) almost 1 mm. long, which enters the short and narrow vagina (VG). The uterus (U) is about 0.2 mm. wide and 1 mm. long. The oviduct (OD) is very short (about 0.4 mm.) and enters the ovisperm duct without notable decrease in size. There is a large carrefour (CF). The albumen gland (fig. 7) is about 1 mm. long and about half as wide as long. The vesicles are relatively large. The position of the albumen gland in relation to the other organs is shown in fig. 9.

Hermaphrodite Organs. The ovotestis (OT) is composed of rather long, club-shaped diverticula. In section (fig. 5), they are seen to be in pairs, unbranched. The ovisperm duct is not free at any portion of its length, as is the case in *cooperi* and *c. callioglyptus* and other members of the Planorbulinae, but is lined with small, rounded vesicles (SO, fig. 1).

A related, but distinct variety, *c. callioglyptus*, shows some noteworthy differences (plate 39, fig. 1). The seminal vesicle is twice the diameter of the ovisperm duct but the vesicles are longer and digitiform (SV). This is better shown in a California specimen (fig. 6), where the glands are in groups and branched. Rounded swellings or vesicles extend down the ovisperm duct some distance, but do not cover the entire length as in *opercularis*. The prostate (PRS) has 15-17 diverticula (see also fig. 13 in plate 38, a British Columbia specimen). In section, the prostate is similar to that of *opercularis* (fig. 3, plate 38) or it may be unbranched, as in fig. 14, plate 38 (British Columbia specimen).

The penial complex (plate 38, fig. 11, California specimen) is rather broader than that of *opercularis*, but the relative length of preputium and vergic sac is the same. In specimens from British Columbia (plate 38, fig. 12; plate 39, fig. 9), there is a decided enlargement at the summit of the vergic sac forming an epiphallus (EPI) as in some land snails. This was only slightly developed in *opercularis* (plate 38, fig. 10). There are five sets of supporting muscles in a California specimen (plate 38, fig. 11) but a lesser number in a specimen from British Columbia (plate 39, fig. 9). There is but one retractor muscle (RM). A penial complex from a specimen collected in British Columbia, badly infested with flukes, is shown in fig. 10, plate 39.

Internally (plate 39, fig. 7, *Menetus cooperi*), the preputium has two large vertical pilasters (PL). There is a large, sac-like penial gland (GL) with a short, narrow, tube-like internal duct (DC) which enters a canal in the muscular ring or diaphragm (D). In section (fig. 8), the gland shows a shallow cup (OC) at the outer end, lined with many vertical folds. A long duct runs through the fleshy part of the gland and connects with the short duct which emerges from the base of the gland. The penial gland of a Californian specimen of *cooperi callioglyptus* is shown in fig. 5. In this specimen, the gland was bent upward and somewhat contracted. The verge (plate 39, fig. 7, V) of *cooperi* is wide with thick walls. In section, it shows a large cavity connecting with the enlarged vas deferens (epiphallus) which narrows notably at the entrance of the vas deferens (fig. 7, EPI, VD). The end of the verge is shown in fig. 15, plate 38, indicating the centrally located exit of the sperm canal. The natural position of the penial complex beneath the female organs (vagina and uterus) is shown in fig. 3, plate 39. In the female organs, the spermatheca (plate 39, fig. 1, S) is much elongated and sac-like and the duct is narrow, widening somewhat as it enters the vagina. The duct is about as long as the spermatheca. The other organs are similar to those of *opercularis*.

Pilsbry (1934, p. 64, fig. 7a) figures the penial complex of *Menetus cooperi callioglyptus* (Vanatta) and this is similar to the figures in the present work. The verge is figured rather longer than was observed in specimens personally examined, but this organ is variable in form under different conditions. The peculiar epiphallic enlargement of the vas deferens is shown in Pilsbry's figure. The statement that the prostate alveoli (diverticula) are in a single series needs emendation, for while they appear to be in a single series when viewed in position over the nidamental gland, in a cross section they are seen to be composed of several branches, as figured on plate 38 (figs. 2, 3). The diverticula in the natural position are hidden beneath the large diverticulum (as in fig. 1 in both plates 38 and 39) and the series appears simple.

There is considerable difference between the genitalia of *Menetus opercularis* and *M. cooperi*, particularly in the penial complex, in which the form of the penial gland and the size of the epiphallus differ. This difference indicates that the two forms are distinct species. There is some slight variation between specimens from British Columbia and California, but in general the anatomical features are similar.

Respiratory and Renal Systems. The pseudobranch of *opercularis* is wide, somewhat folded or lobed and the rectum extends through the middle, the anus opening at the lower edge (plate 38, fig. 4, P, A, R). There is a large pneumostome. In *cooperi callioglyptus* (plate 39, figs. 2, 4), the pseudobranch is rounded, somewhat lobed, and with a high ridge extending over the length of the rectum (R) and running down the midde of the pseudobranch as a low ridge. The anal opening is placed at the left side of the pseudobranch. This ridge is also found in *opercularis*, but is not indicated in the figure. The two forms of pseudobranch shown in figs. 2 and 4 on plate 39 indicate the amount of variation that may take place in two individuals of the same species.

The kidney (plate 46, fig. 7) of *Menetus cooperi callioglyptus* is short and very wide (about 2 mm. long and 1 mm. wide). The ureter is a rather long, narrow tube reflexed abruptly and directed upward into the mantle cavity. The pericardium is about 1 mm. long. The lower part of the kidney is very close to the mantle margin, the ureter being in contact with it. A cross section of the kidney near the middle (fig. 8) shows the lumen to be large, ovate, somewhat wider than high, the vein leading to the pericardium much greater in diameter than the renal vein. There is no superposed ridge.

Digestive System. The stomach region is elongated, the oesophagus enlarged to form a crop, the gizzard rounded, and the pyloris rounded and diminishing to the intestine which forms a complete loop around the stomach, extends backward in the body, makes another loop around the liver, and runs forward to the rectum, ending over the pseudobranch. There is a long and narrow blind sac or caecum. The stomach region is like that of *Promenetus exacuous* which is figured on plate 48, figs. 4, 5.

The buccal sac is pyriform, with a large, rounded extension of the radula sac at the lower, posterior part. The salivary glands are about twice as long as the buccal sac and are much enlarged at the posterior end where they are attached, the whole apparatus forming a loop. The oesophagus is enlarged to twice its diameter posterior to the buccal sac.

The superior jaw of *cooperi callioglyptus* (plate 50, fig. 7) is arched, the ends attenuated. There is a central rounded bulge on the lower margin. The jaw is heavily, vertically striated. The side jaws are normal except that at the point of attachment to the superior jaw they are bent backward more than usual. The jaw of *Menetus opercularis* is similar.

The radula of *Menetus cooperi callioglyptus* (plate 67, fig. 3, from British Columbia) has a large center tooth, higher than wide, the two wide, spade-shaped cusps not reaching the lower border of the base of attachment. The lateral teeth (1-8) are squarish and tricuspid, the cusps long and spade-shaped, the mesocone the longest. The intermediate teeth (9-10) are narrower than the laterals and have one or two additional cusps above the ectocone. The entocone, mesocone, and ectocone become more nearly equal in length. The marginal teeth (11-15) are very narrow, elongated, the entocone is split into from two to four small cusps and the ectocone splits into three to four small cusps. The outer marginal teeth are very narrow and appear to be serrated with small cusps. The mesocone persists throughout the entire series of teeth and may always be identified.

DATA FOR RADULA

Name	*Formula*	*Locality*	*Rows*	*Collector*
cooperi callioglyptus	20-1-20	Quatsino, British Columbia	144-145	Mr. Arthur Peake
cooperi	20-1-20	Orcas Island, Washington	155-161	Dr. T. D. Foster

The material for the study of *Menetus* was received from the following sources: *opercularis* from Mountain Lake, near San Francisco, California, collected by Mr. H. Walton Clark, two specimens examined; *cooperi callioglyptus*, Quatsino Sound, Vancouver Island, British Columbia, collected by Mr. Arthur Peake, eleven specimens examined; mill pond at Crescent City, California, received from Dr. G. D. Hanna, four specimens studied; *cooperi*, from Orcas Island, Puget Sound, small mountain lake on Mt. Constitution, Washington, collected by Dr. T. D. Foster, fifteen specimens examined.

Specimens of *cooperi callioglyptus* from Quatsino Sound, Vancouver Island, were largely infested with cercariae of trematode worms, as many as 200 larvae occurring in one specimen. All organs were affected but the ovotestis and albumen gland were more often attacked. The parasites were most numerous over the stomach region. Specimens of *cooperi* from Orcas Island, Puget Sound, had parasites in liver, ovotestis, albumen gland, and over the stomach. In some specimens from both Washington and British Columbia all of the organs were obscured by a thick coating of mucus.

Geographical Distribution. Typical *Menetus* is distributed over the Pacific coast region from Vancouver Island south to northern California. The group does not extend far inland to the east. It is distinctively a genus of the coast region. Only a few species are known. *Opercularis* appears to be confined to California, but *cooperi* (= *planulatus*) is found from northern California northward to Vancouver Island, and within this area is quite variable. There are a number of local forms of limited distribution.

Species Considered as Valid. The following species and races are at present known for the typical subgenus of *Menetus*.

Menetus opercularis (Gould)
Menetus cooperi F. C. Baker, new name for *planulatus* Cooper, 1859, not *planulatus* Deshayes, 1824, a fossil species
Menetus cooperi callioglyptus (Vanatta)
Menetus cooperi multilineatus (Vanatta)
Menetus centervillensis (Tryon)

Geological Distribution. Pliocene to Recent fauna. Little is definitely known concerning the geological ancestry of this genus.

Remarks. Typical *Menetus* is a very distinct genus characterized by noteworthy anatomical features, chief among which are the sac-like penial gland with its short, narrow, internal duct and the epiphallus-like enlargement of the vas deferens as it enters the vergic sac. The prostate resembles that of *Planorbula* which has the same structural arrangement of diverticula. The ovotestis is also like that of *Planorbula*. The penial gland, however, is quite unlike either that of *Planorbula* or *Promenetus*. The duct is also different. The radula and jaw are like these organs in *Promenetus* and *Planorbula*.

Menetus has been subordinated to several groups as a section or subgenus. Thiele places it under *Anisus* (1931, p. 481), Dall as a section under subgenus *Hippeutis* (1905, p. 82), Germain as a subgenus of *Planorbis* (1923, p. 156). Von Martens (1899, p. 390) includes in it species now referred to *Tropicorbis*. The Adams brothers indicated no type, though one was definitely proposed by Dall in 1870 (p. 351).

F. C. Baker (1928, p. 360) and Pilsbry (1934, p. 64) have shown definitely that the group should rank as a genus. The anatomical figures herein published support this conclusion.

Subgenus MICROMENETUS F. C. Baker, New Subgenus

Genotype *Planorbis dilatatus* Gould

Shell (plate 79, figs. 13-15). Very small, ultradextral, of few rapidly enlarging whorls; right side flat or convex, left side with inner whorls submerged by the body whorl; body whorl with a more or less well-developed carina, usually placed just below the top of the right side; aperture large, somewhat dilated; lips thin.

Animal. Foot short, wide, oval on base, bluntly rounded before and behind; tentacles long and filiform, enlarged somewhat at base, attached far back on the head; eyes on small swellings at inner base of tentacles; color mottled brown and cream, whole back dark, two black lines extending down middle of head; bottom and sides of foot yellowish; tentacles transparent. Shape of foot varies during locomotion. The shell is carried at an angle of thirty to forty-five degrees or it may lie flat on the body of the animal. It is seldom carried erect as in *Helisoma* (plate 70, fig. 9).

ANATOMICAL CHARACTERISTICS

PLATE 40

GENITALIA. Male Organs (fig. 12). Seminal vesicle (SV) of *M. dilatatus* made up of a small number of relatively large vesicles placed on each side of the ovisperm duct. Anterior to the seminal vesicle, the ovisperm duct is bordered by a number of widely spaced vesicles for a distance three times the length of the seminal vesicle. Sperm duct (SPD) of small diameter, not much greater than that of the ovisperm duct. The combined free portion and that part beneath the prostate measure about 1 mm. in length, the sperm duct being a trifle longer than the prostate portion. Prostate (PRS) with relatively few diverticula, eight or nine. In cross section, the prostate shows the same multiplication of smaller diverticula on the under side as is present in *Menetus opercularis*. In an immature specimen of *cooperi*, the prostate had but five rows of diverticula. The vas deferens is a narrow tube almost as long as the sperm duct. It is slightly enlarged near the vergic sac. In *Menetus sampsoni*, the seminal vesicle (fig. 1) differs from that organ in *cooperi* in being composed of four rounded swellings. Only a few rather large vesicles occur on the ovisperm duct.

The penial complex (fig. 12) is about 0.5 mm. long, the preputium (PR) is sac-like or elongate-pyriform and is about twice as long as the ovate vergic sac (VS). In *sampsoni* (fig. 11), the vergic sac is longer and wider. There is one retractor muscle (RM) which is usually attached to the constriction between the preputium and the vergic sac (fig. 11). There are several small supporting muscles on both sides of the preputium. The penial complex was observed in several different forms in the material examined. In one (fig. 3), the vergic sac was placed on the side of the preputium, the gland being pushed upward, as occurs so frequently in the genus *Helisoma*. In another specimen (fig. 4), the preputium was much swollen and the retractor muscle was attached to the preputium some distance below the vergic sac.

Internally (fig. 5), there is a sac-like penial gland with a rather long duct. This is shown to better advantage in *Menetus sampsoni* (fig. 10), where the gland (GL) is much elongated and gradually diminishes in diameter to the round duct, which follows the wall of the preputium (DC) to the muscular ring or diaphragm separating the preputial sac from the vergic cavity. The cup containing the vertical folds is small and is placed at the end of the penial gland. There is a central duct running through the gland as in *Menetus cooperi callioglyptus*. In a Texas specimen (fig. 2), the gland was somewhat different, resembling a pipe or trumpet. This might have been abnormal. The verge (fig. 10, V) is elongated, narrowing to a point at the lower end. The sperm canal has a central outlet. See also fig. 5.

Female Organs. The spermatheca (fig. 12, S) is short and sac-like and is connected with the very wide vagina (VG) by a wide duct twice as long and half as wide as the spermatheca. The uterus (U) is wide, increasing to about twice the diameter of the vagina in the region of the prostate, where the still wider nidamental gland (NG) appears. The oviduct (OD) is short and gradually narrows to meet the sperm duct. There is a carrefour which lies between the oviduct and the albumen gland (not shown in the figure). The albumen gland (AL) is very large and wide (almost half as wide as long) and is composed of large vesicles. The intestine makes a loop beneath the albumen gland (IN).

Hermaphrodite Organs. The ovotestis (OT) is composed of relatively few large, somewhat club-shaped diverticula arranged in pairs. A single diverticulum filled with developing ova is shown in fig. 6. The diverticula vary in form, being more swollen when filled with ova ready for discharge.

Respiratory and Renal Systems. The pseudobranch of *dilatatus* (plate 40, figs. 7, 9) is about twice as long as wide and extends below the margin of the foot in preserved specimens. It is somewhat folded on the side and in a Texas specimen (*sampsoni*, fig. 8) formed a hollow cylinder. There is a fluted crest on the rectum (R) which, however, does not appear on the pseudobranch in the specimens examined. The anal opening (A) is placed at the upper end of the pseudobranch.

The kidney (fig. 5) is rather short, about 1 mm. long and 0.3 mm. wide. The ureter is very long and is folded back tightly against the lower part of the kidney. A cross section near the middle of the kidney (fig. 6) shows an oblong or ovate lumen with a small vein at each end. There is no superposed ridge. The kidney is wider than that of *exacuous* but narrower than that of *cooperi* or *c. callioglyptus*. The pericardium is very wide.

Digestive System. The digestive system is similar to that of *exacuous* (see plate 48, figs. 4, 5). The radula sac is essentially the same as in *Menetus*.

The superior jaw (plate 50, fig. 9) of *dilatatus* is wide and low with vertically striated face. The side jaws are as long as the width of the superior jaw. The jaws of *sampsoni* (fig. 6) are similar, but larger. There is a slight bulging in the center of the lower cutting edge of the superior jaw in both *dilatatus* and *sampsoni*.

The radula (plate 67, fig. 4, *dilatatus*). Center tooth squarish, not as wide as in typical *Menetus*. Lateral teeth (1-7) squarish, tricuspid, the mesocone longest, all cusps sharp and spade-shaped. Intermediate teeth (8-10) becoming narrower and developing a split entocone and one or two small cusps above the ectocone. Marginal teeth (11-14) long and narrow, the entocone with three to four small subequal cusps, the ectocone with several small cusps on the outer edge of the teeth. The marginal teeth become much smaller toward the edge of the membrane. The radula of *sampsoni* is practically of the same type as that of *dilatatus* (fig. 5).

RADULA DATA

Name	*Formula*	*Locality*	*Rows*	*Collector*
dilatatus	15-1-15	Unionville, Connecticut	125	F. C. Baker
dilatatus	15-1-15	Hyannis, Massachusetts	125	F. C. Baker
sampsoni	15-1-15	Merrimec R., Missouri	125	Leslie Hubricht
sampsoni	15-1-15	Dallas, Texas	120	E. P. Cheatum

The material examined for anatomical data has been as follows: *dilatatus*, near Unionville, Connecticut, twelve miles west of Hartford, collected by F. C. Baker (16); near Hyannis, Cape Cod, Massachusetts, collected by F. C. Baker (2); *sampsoni*, Merrimec River, near Stanton, Franklin County, Missouri, collected by Mr. Leslie Hubricht (14); small creek, six miles northeast of Dallas, Texas, collected by Dr. E. P. Cheatum (4); slough, near Trinity River, twelve miles southeast of Dallas, Texas, collected by Dr. Cheatum (2); small lake, near Hutchins, Dallas County, Texas, collected by Dr. Cheatum (2).

The cercariae or rediae of trematode worms were found in some of both species of *Micromenetus*. Of *dilatatus*, near Unionville, Connecticut, one specimen infested; *sampsoni*, Merrimec River, Missouri, nearly all specimens examined, many of the specimens being badly diseased.

Geographical Distribution. The species belonging to the subgenus *Micromenetus* are distributed over the eastern part of North America from Massachusetts west to Iowa and Missouri, and from Maine and Michigan southward to Alabama, Florida, and Texas. It is a group found east of the Rocky Mountains. One species, *Menetus uliginosus* Vanatta, is found in Bermuda.

Species Considered as Valid. There are several distinct species and races of the subgenus *Micromenetus* recognizable within the genus *Menetus*, as follows:

Menetus (Micromenetus) dilatatus dilatatus (Gould)
Menetus (Micromenetus) dilatatus pennsylvanicus Pilsbry
Menetus (Micromenetus) dilatatus buchanensis (Lea)
Menetus (Micromenetus) alabamensis alabamensis Pilsbry
Menetus (Micromenetus) alabamensis avus Pilsbry
Menetus (Micromenetus) brogniartianus (Lea)
Menetus (Micromenetus) sampsoni (Ancey)
Menetus (Micromenetus) uliginosus Vanatta

Geological Distribution. Not exactly known but certainly from the Pliocene to Recent fauna.

Remarks. The group here separated as *Micromenetus* differs from typical *Menetus* in the size of the shell which is always much smaller, none exceeding 4 mm. in diameter. The form of the shell is lenticular and there is usually a peripheral carina more or less well developed. The penial gland has a duct which is almost three times as long as the gland and is attached to the inner wall of the preputium for the greater part of its length (plate 40, fig. 10). In typical *Menetus*, this duct is short and enters the diaphragm directly without being attached to the wall of the preputium (plate 39, fig. 7). The pseudobranch in *Micromenetus* is also very long and narrow while in typical *Menetus* it is short and wide (compare plate 38, fig. 14, with plate 40, fig. 9). These are small differences, perhaps, but they appear constant. *Micromenetus* differs from both *Promenetus* and *Planorbula* in the shape of the penial gland. As far as examined the radulae of the two groups differ in formulae, that of *Menetus* being 20-1-20 while in *Micromenetus* it is 15-1-15.

Genus PLANORBIFEX Pilsbry, 1934

Type by original designation *Planorbis vanvlecki* Arnold

1934. *Planorbifex* Pilsbry, Proc. Acad. Nat. Sci. Phil., 86, p. 568. Genotype *Planorbis vanvlecki* Arnold. As subgenus of *Menetus*

1935. *Menetus (Planorbifex) vanvlecki* Pilsbry, J. Henderson, Fossil Non-Marine Moll. N. A., p. 252.

Shell (plate 81, fig. 6). Discoidal, dextral in appearance, the right side moderately convex, with the last whorl carinate, the periphery rounded; left side deeply umbilicate, the last whorl more or less flattened. Sculpture of fine, close, hair-like striae. Aperture strongly oblique, its outline excised by the preceding whorl, the receding left margin thickened within (Pilsbry).

Geological Horizon and Distribution. Basal part of the Tulare formation, Pliocene. North dome, Kettleman Hills, Kings County, California.

Species Considered as Valid. The fossil species *Planorbifex vanvlecki* Arnold, as genotype, is the only species known for this genus.

Remarks. 'Except for the narrow umbilicus, the absence of a peripheral keel, and the thickened peristome, this form resembles *Platytaphius* Pilsbry, a much larger planorb from Lake Titicaca, which has similar sculpture. *Paraplanorbis* Hanna resembles *Planorbifex* in being small and narrowly umbilicate, but it has a spire of closely coiled whorls like *Drepanotrema*. The small size and umbilicate left side are like *Menetus*, which, as Arnold thought, is probably its nearest relative; but in carinate species of *Menetus* the keel is peripheral' (Pilsbry, 1934, p. 568).

'The shell of the type species, *Planorbifex vanvlecki*, varies in the amount of flattening of the base; sometimes it is scarcely noticeable. The species was referred by Dr. Cooper to *Valvata virens*, a very different shell. It has certain resemblances to such forms as *Valvata bicarinata* Lea, but the excised outline of the strongly oblique aperture, and the thickened peristome, exclude a reference to the Valvatidae, some of which have a similar sculpture' (Pilsbry, 1934, p. 569).

As remarked under the genus *Paraplanorbis*, it appears better to regard *Planorbifex* as a separate genus related to *Menetus* rather than as a subgenus of *Menetus*. The carina in the middle of the whorl of the right side is distinctive, and is different from any known species of *Menetus* or *Promenetus*, where the carina is peripheral or just below the margin of the left side.

VIII.

GROUPS OF UNCERTAIN AFFINITIES

Subfamily CHOANOMPHALINAE Germain, 1923

Characters those of the genus *Choanomphalus* Gerstfeldt

Genus CHOANOMPHALUS Gerstfeldt, 1859

Type by original designation, *Choanomphalus maacki* Gerstfeldt

1859. *Choanomphalus* Gerstfeldt, Ueber Land und Süsswasser-mollusken Siberiens, p. 527. Type *Choanomphalus maacki* Gerstfeldt. As genus

1870. *Choanomphalus* Dall, Ann. N. Y. Lyc. N. H., IX, pp. 353, 358. Type *Choanomphalus maacki* Gerstfeldt. As genus

1875. *Choanomphalus* W. Dybowski, Die Gasteropoden Fauna Baikal-See. Mem. Acad. Sci., St. Petersburg, Ser 7, XX, p. 52. Type *Choanomphalus maacki* Gerst. As genus

1879. *Choanomphalus* Crosse and Fischer, Jour. de Conch., XXVII, p. 160. Type *Choanomphalus maacki* Gerst. As genus

1883. *Choanomphalus* Fischer, Man. de Conch., p. 508. Type *Choanomphalus maacki* Gerst. As genus

1884. *Choanomphalus* Tryon, S. and S. Conch., III, p. 105. Type *Choanomphalus maacki* Gerst. As genus

1885. *Choanomphalus* Westerlund, Fauna der paläarct. Region Binnenconchylien, V, p. 63. Type *Choanomphalus maacki* Gerst. As genus

1886. *Choanomphalus* Clessin, Syst. Conch. Cab., XVII, p. 232. Type *Choanomphalus maacki* Gerst. As genus

1909. *Choanomphalus* Lindholm, Mollusken, in Korotneff, Wissens. Ergebn. Zool. Exped. Baikal-See, IV, pp. 8, 93. Type *Choanomphalus maacki* Gerst. As genus

1923. *Choanomphalus* Germain, Rec. Ind. Mus., XXI, p. 190. Type *Choanomphalus maacki* Gerst. As genus

1925. *Choanomphalus* Dybowski and Grachmalichi, Kosmos, L, p. 877. As genus

1931. *Choanomphalus* Thiele, Handbuch, p. 482. Type *Choanomphalus maacki* Gerst. As genus

Shell (plate 81, figs. 7, 8, 9) small, pseudodextral, turbinate, of few whorls rather rapidly increasing in diameter, the spire depressed but not flat, base widely umbilicated or with a small chink; aperture rounded. The shell resembles some species of *Valvata* in form.

Animal. Similar to *Planorbis* in tentacles, jaw, and radula. Respiratory and genital openings on the left side (see Dybowski and Grachmalichi, p. 870). The eggs are laid in capsules with four to five eggs in each capsule. The jaws are three in number with a large, half-moon-shaped superior jaw and two small lateral jaws.

The radula plate measures 1.6 mm. in length and 0.3 mm. in width, and carries 175 rows of teeth. The formula of *Choanomphalus maacki* is (4)-9-5-16-1-16-5-9-(4) (69 teeth in row) or sixteen lateral teeth, five intermediate teeth, nine marginal teeth, and four outer marginal teeth without distinct form. In *Choanomphalus valvatoides* the formula is (3)-10-5-10-1-10-5-10-(3) (57 teeth in row). In *Choanomphalus bicarinatus* the formula is 4-6-20-1-20-6-4 (61 teeth in row). *Choanomphalus cryptomphalus* has the formula 5-6-20-1-20-6-5 (63 teeth in row). The smallest formula is borne by *Choanomphalus schrencki* which is 4-7-1-7-4 (23 teeth in row), the outer marginals indistinct and uncountable (op. cit., p. 871). No mention is made of the cusps of the teeth. There seems to be great uniformity in the total number of teeth but some variation in the number of lateral teeth.

The published information concerning the anatomical details is wholly insufficient for purposes of classification.

Geographical Distribution. Lake Baikal, Siberia. The different species occur at varying depths, thus *maacki* occurs at great depths, principally between 150 and 350 meters. *Valvatoides*, on the other hand, occurs in comparatively shallow water, from two to ten meters. One species is found in the Angara River, near Lake Baikal (*amauronicus*). Another species is found in Japan (*japonicus*). Westerlund includes Europe, Thessalia, between Greece and Turkey, in the distribution of the genus. This range needs confirmation.

Remarks. The genus *Choanomphalus* is a group of mollusks probably related to the Planorbidae but of uncertain status as to its proper position in the classification of the fresh-water pulmonates. Dall (1870) and Tryon (1884) placed the genus in the subfamily Pompholiginae with *Pompholyx* (*Parapholyx*) and *Carinifex*. Crosse and Fischer in 1879 compared the genus with the American group *Carinifex* and suggested its group relationship with the fossil *Valvata multiformis* (=*trochiformis*). The resemblance to *Carinifex* in both *Choanomphalus* and the Steinheim fossil (*trochiformis*) is superficial, *Choanomphalus* not having the same characteristics of anatomy found in *Carinifex* and *Parapholyx*. Westerlund, in 1902 (p. 120), placed *Choanomphalus* in the subfamily Planorbinae.

In 1909, W. A. Lindholm made a study of the Lake Baikal fauna and divided *Choanomphalus* into three subgenera, as noted below.

1. *Choanomphalus* Sensu Stricto. Type *Choanomphalus maacki* Gerstfeldt
2. *Achoanomphalus* Lindholm. Type *Choanomphalus amauronius* Bourguignat
3. *Sulcifer* Lindholm. Type *Choanomphalus schrencki* W. Dybowski

The Japanese species is placed in a separate section by Lindholm, *Choanomphalodes*, 1927; type *Choanomphalus japonicus* Preston.

Germain (1923) places the group in a subfamily Choanomphalinae. Dybowski and Grachmalicki (1925, pp. 819-881), in an exhaustive monograph, review all of the species of *Choanomphalus*, some twenty-five in number, of which fifteen are considered valid. The peculiar *Planorbis paradoxus* Sturany, from Lake Ochrida near the city of Ochrida, in European Turkey, is discussed, but its relationship to *Choanomphalus* is questioned. It has been thought to be related to *Choanomphalus* by Sturany and other European conchologists. It probably represents another peculiar form of Planorbidae and its anatomy should be examined.

The suggestion in the foregoing reference (p. 835), that *Segmentina* may be related to *Choanomphalus* is obviously erroneous because that genus has been shown to be the type of a distinct subfamily not known to have any affinities with the Baikal Lake group. A form of *Segmentina nitida* is found in Lake Baikal and is given the name of *angarensis* by these two authors.

On pages 877 to 880, Dybowski and Grachmalicki present a new arrangement of *Choanomphalus* which is made a separate family, Wladislaviidae. Six genera and some twenty-three lesser groups are designated.

The subgeneric names proposed by Lindholm in 1909 are ignored. These six genera, as listed by Thiele (1931, p. 482) with the earlier names of Lindholm and the new names proposed by Tomlin for the preoccupied names, are tabulated below.

1. *Choanomphalus* (SS). Type *Choanomphalus maacki* Gerst.
2. *Valvatomphalus* D. and G. (= *Achoanomphalus* Lindholm, 1909). Type *C. amauronicus* Bourg.
3. *Cryptomphalus* D. and G. (non Charpentier, 1837) = *Omphalocrypta* Tomlin, 1929. Type *C. cryptomphalus* W. Dybowski
4. *Biangulatus* D. and G. Type *Choanomphalus bicarinatus* Dybowski
5. *Anomphalus* D. and G. (non Meek and Worthen, 1866) = *Anomphalodes* Tomlin, 1929. Type *C. anomphalus* W. Dybowski
6. *Platybasalis* D. and G. (= *Sulcifer* Lindholm, 1909). Type *C. schrencki* W. Dybowski

The value of these generic and group names is debatable. The plate of species in the Dybowski and Grachmalicki monograph does not show variation enough to warrant any such minute division, and many of the figures suggest individual variation, such as is common among many of our North American species of *Helisoma*. Possibly the few groups and species enumerated by Lindholm can be recognized, judging from the figures in Fischer's paper (1879, plate 4, figs. 8-10) which are reproduced on my plate 81. Just why all of the Lake Baikal species of *Choanomphalus* should not be included in the one genus is not apparent from a study of the shells and what little is known about the animals.

The name Wladislaviidae can not be used because Germain in 1923 (p. 190) proposed the subfamily name Choanomphalinae two years earlier. On this page Germain also questions the value of recognizing subgenera for the different species.

Until the details of the genitalia are known, particularly the form of the ovotestis, prostate, and the internal conditions of the penial complex, it will be impossible to determine the true position of this group in the classification of the fresh water pulmonates. For the present, the group designation of Germain as a subfamily of Planorbidae should be retained. It is possible, of course, that when the anatomy is known the group might be found to be of family rank, but in that case the name of Germain must be used because it was given at an earlier date than Wladislaviidae of Dybowski and Grachmalicki.

Genus POECILOSPIRA Mörch, 1853

Type by original designation *Valvata multiformis* Zeiten

1853. *Poecilospira* Mörch, Cat. Conch. Yoldi. Type *Valvata multiformis* Zeiten (= *Helicites trochiformis* Stahl, 1824)

1879. *Poecilospira* Crosse and Fischer, Jour. de Conch., XXVII, p. 160. Type *Valvata multiformis* Zeiten. As genus

1884. *Poecilospira* Tryon, S. and S. Conch., III, p. 105. Type *Planorbis multiformis* (Zeiten). As subgenus of *Choanomphalus*

Shell (plate 81, fig. 1). Dextral, varying from flat with depressed spire, discoidal, to trochiform with greatly elevated spire, the last whorl rounded and in the same plane as the body whorl or greatly deflected. Whorls carinated, the carina placed at the upper side of the whorl in planorboid forms and forming a peripheral ridge in the forms with elevated spire. Umbilicus large and conspicuous. Aperture round or lunate, entire and separated from the body whorl, a thick callus on the parietal wall and the outer lip thickened in many specimens.

Horizon and Distribution. Miocene period. Steinheim near Heidenheim, Württenberg, Germany.

Remarks. The planorbid fauna at Steinheim has become classical for studies of variation, not only as individuals in a fauna, but also in time between the earlier and later strata. Perhaps Hyatt's studies in 1880 (pp. 1-114, plates 1-9) are the best known and show in large measure the great amount of variation which has taken place during the life of these mollusks while the Tertiary strata were being formed in the old lake bed and on its shores. Hyatt refers all species to the genus *Planorbis*.

In a later paper (1920, pp. 155-216, Taf. 10-12), Gottschick reviews what is known concerning the fossils of this locality. He postulated a cold-water fauna and a warm-water fauna, as we sometimes find in the Pleistocene faunas of the middle west. This paper is well illustrated and shows the great variation in the group of shells known as *Planorbis multiformis*. Wenz (1923, p. 1601) includes all of the Steinheim fossils in the genus *Gyraulus*. The work of Wenz also brings out clearly the fact that the fossils of this and nearby regions have been very much overnamed, for between 1824 and 1920 no less than forty-five names have been given to variations of this group.

A careful study of the works of Hyatt, Gottschick, and others shows that, while many of the so-called species appear to be referable to the genus *Gyraulus*, the forms grouped around *multiformis* (*trochiformis*) appear different from the Gyraulus-like shells, approaching *Valvata* in form, and apparently should be segregated in another group. Mörch, in 1863, recognized this difference and gave the assemblage the name of *Poecilospira*. Later authors appear to have overlooked this name which does not appear in recent monographs or check lists. It is not mentioned by Wenz (1923) in the list of fossils related to *trochiformis*.

To what group *Poecilospira* is related is not definitely clear. It is certainly not near *Gyraulus* and apparently does not belong in the subfamily Planorbinae. Also, it is not related to *Carinifex* or to any of the fossil relatives of this group. There are some features in common between *Poecilospira* and *Choanomphalus* and its true position may be with the latter group, as suggested by Tryon in 1884.

IX.

FAMILY BULINIDAE

This group has almost universally been considered a subfamily of Planorbidae. It is so treated by Pilsbry (1927, p. 132). More recently several authors have considered the group as of family rank, distinct from the Planorbidae (Germain, 1931, p. 514; Larambergue, 1939). The shell is of Physoid shape but the radula is like that of *Planorbis*. Two characteristic features of the group separate it from any known division of the Planorbidae, the fluted or lobular pseudobranch and the shape of the penial complex in the genitalia. These are so different that they would appear to be characteristics of family rank. The family is mostly exotic, distributed as far as known in Australia, Oceania, New Guinea, Celebes, Japan, India, the Ethiopian and Malagasy regions, the Mediterranean subregion as far east as Mesopotamia, and the Antilles (vide Pilsbry, 1927, p. 132). Only one species occurs in the Antillean region.

The present work was prepared to include only the groups properly belonging to the family Planorbidae, but as one species previously referred to the Planorbidae has recently been placed in Bulinidae, space is given to a discussion of this species and the data for its inclusion in a family to which it was not previously believed related.

Genus INDOPLANORBIS Annandale and Prashad, 1920

Type by original designation, *Planorbis exustus* Deshayes

1920. *Indoplanorbis* ANNANDALE and PRASHAD, Jour. Med. Res., VIII, p. 112. Type *Planorbis exustus* Deshayes. As genus

1921. *Indoplanorbis* PRASHAD, Rec. Ind. Mus., XXII, p. 471. Type *Planorbis exustus* Desh. As genus

1921. *Indoplanorbis* ANNANDALE and PRASHAD, Rec. Ind. Mus., XXII, p. 578. Type *Planorbis exustus* Desh. As genus

1921. *Planorbis (Planorbis) exustus* GERMAIN, Rec. Ind. Mus., XXI, pp. 26-41. Exhaustive account of variation and synonymy

1922. *Indoplanorbis* ANNANDALE and PRASHAD, Rec. Ind. Mus., XXIV, p. 360. Type *Planorbis exustus* Desh. As genus

1923. *Indoplanorbis* RAO, Rec. Ind. Mus., XXV, pp. 199-219. Type *Planorbis exustus* Desh. Description of anatomy. As genus

1926. *Indoplanorbis* THIELE, Handbuch, p. 479. Type *Planorbis exustus* Desh. As section of *Planorbis*

1933. *Indoplanorbis* F. C. BAKER, Jour. Morph., LV, No. 1, pp. 1-12, plate 1-2. Type *Planorbis exustus* Desh. Account of anatomy, especially genitalia and radula. As genus

1934. *Indoplanorbis* PILSBRY, Proc. Acad. Nat. Sci. Phil., 86, p. 54. Remarks on taxonomic position

1939. *Indoplanorbis exustus* LARAMBERGUE, Bull. Soc. Zool. de France, LXIV, No. 5, pp. 286-295. Anatomy and family position. As genus

Shell (plate 79, figs. 33-35). Of medium size, sinistral, with few rapidly increasing whorls, the body whorl large and greatly increasing in diameter toward the aperture; spire whorls flat, depressed below the level of the body whorl; base with small umbilical opening, the inner whorls concealed by the last two whorls; aperture usually oblique, lips simple, sharp.

Animal (plate 21, fig. 2). 'The animal is sinistral. Its foot is relatively broad and short, leaf-shaped, broadly rounded in front and pointed behind.

The head is very broad and has its lower margin expanded and flattened. The tentacles are elongate and filiform. The eyes lie at the inner base of the tentacles and are completely sessile. The mouth opens on the lower surface of the head in front of the foot' (Annandale and Prashad, 1921, p. 578). See Rao, 1923, p. 200, for a more extended account of external characteristics.

ANATOMICAL CHARACTERISTICS

GENITALIA (plate 21, fig. 3). **Male Organs.** The seminal vesicle (SV) is about 4 mm. long and nearly 1 mm. wide and is composed of small lobes or tubercles surrounding the ovisperm duct. The sperm duct (SPD) is a small tube 7 mm. long, the portion near the ovisperm duct folded or coiled. The prostate (PRS) is 3.5 mm. long and nearly 2 mm. wide, its lower end broadly rounded, its upper end narrowed to half the diameter of the lower lobe. The prostate is composed of many long, branched diverticula, all of which radiate fan-wise from the common meeting place of the sperm duct and vas deferens. In a cross section near the middle (fig. 8), there are shown eight primary diverticula each of which is branched three or four times toward the outer end, causing the outer surface of the prostate to show twenty-four or more rounded projections. Each diverticulum is branched as shown in fig. 9. The sperm duct and vas deferens meet on the lower side of the prostate, the prostate diverticula radiating outward from this junction. The prostate diverticula enter the sperm duct from which the vas deferens proceeds as a small tube less than half the diameter of the sperm duct. This condition is indicated in fig. 10.

Both Rao and Larambergue describe the prostate as ellipitical in form, but it was of the shape figured in all but one of the specimens examined and the exception was regularly elliptical. There may, obviously, be some variation in the shape of this organ. In its natural position, the prostate lies against the uterus below the nidamental gland. The vas deferens is a very long, narrow tube (about 12 mm. long).

The penial complex (fig. 3) is made up of a short, cylindrical preputium (3.5 mm. long) and a very long (17 mm.), narrow tube-like vergic sac (VS), which is five times the length of the preputium. In the figure of Larambergue (1939, fig. 3, the vergic sac is shown four times the length of the preputium. In Rao's figure (1923, p. 215), the vergic sac and the vas deferens are confused and the enlarged vergic sac is entirely too short. The figure by Larambergue (fig. 1) shows the vergic sac too short and the preputium too long as compared with the specimens personally examined.

There is a single retractor muscle (RM) attached to the vergic sac near the summit of the preputium. A heavy nerve (N) innervates this muscle. Bands of supporting muscles (SM) are attached to the preputium on both sides. In Rao's figure (1923, p. 215), the retractor muscle is shown as attached to the vergic sac far above the preputium, which position was not observed in any specimen examined. Larambergue's figure (1939, p. 288) shows the muscle attached to the vergic sac just above the preputium, which appears to be its natural position.

Internally (plate 21, fig. 1), the preputium contains two long, vertical, muscular pads or pilasters (MP) which extend the whole length of the preputial cavity. There is a small muscular ring or diaphragm between the vergic cavity and the preputial cavity. The verge (V) is a very long, narrow tube freely movable within the vergic sac (VS). This organ was entirely misunderstood by Rao and was not fully comprehended by the writer (Baker, 1933). Larambergue (1939, p. 288) correctly figures the relationship between the vergic sac (poche de pénis) and the verge (tube pénial), the latter being much longer than figured by Baker and extending the whole length of the vergic sac.

The writer figured and described a bulbous swelling within the vergic sac (plate 21, fig. 1, B) which was thought to be the termination of the verge, the tube behind this swelling being considered as a part of the vas deferens. Larambergue's figure 2 (reproduced as fig. 2 on plate 73 of this work) shows that this is not the case and that the whole tube must be considered the verge. However, this bulbous portion of the verge was present in all specimens examined and a swelling of this region is shown in the figure of Larambergue where the long line for the symbol pe is directed. It seems probable that this bulbous portion (use unknown) is found in all examples of *Indoplanorbis* but in the specimens examined by Larambergue there was less contraction than in the specimens examined by Baker. In other words, the differences may be attributable to methods of preservation.

Two specimens examined by Baker had the preputium completely everted from the male opening, the sac lying on the body of the animal, as shown in fig. 2 of plate 21. One of these specimens is shown in optical section in fig. 7 of plate 22. In this specimen, the preputium was greatly flattened so that the pilasters (MP) became two flattened muscular pads, filling the greater part of the preputial cavity. The verge (V) and vergic sac (VS) extend through the preputium nearly to the opening of the preputium (PR). The bulbous portion of the verge is conspicuous and has moved downward. The retractor muscle is attached to the vergic sac near its distal end and the large nerve lies beside it (RM, N). It is clearly evident that this muscle pulls back the male intromittent organ after copulation. A cross section of the preputium near its widest part is shown in fig. 6. The branching of the retractor muscle and the connections of the nerve are shown in fig. 5, greatly enlarged. The so-called supporting muscles of the preputium apparently become retractor muscles when the verge and the preputium are everted (fig. 5, plate 21).

Larambergue (1939, p. 293) describes and figures the penial complex in the everted position (see plate 74, fig. 6). The vergic sac is shown extended from the everted end of the preputium. The everted copulatory organ is enlarged at the distal end, being almost twice the diameter of the proximal end near the preputium. A trifle more than half of the length of the vergic sac is everted, the shorter portion remaining within the preputium and body during eversion. These drawings of Larambergue were made from freshly anesthetized specimens taken in coitus.

Observations on the specimens dissected by the author do not entirely agree with those of Larambergue. In several specimens, the verge extended from the vergic sac and protruded into the perputium for some distance (plate 21, fig. 1). Rao (1923, p. 215) figures the verge (penis) as protruding from the vergic sac into the preputial cavity. He also figures the retractor muscle as attached to the vergic sac and not to the preputium.

It has been the writer's opinion that only the verge was protruded from the end of the preputium when the latter was everted from the male opening. The retractor muscle is shown by Larambergue as attached to the upper end of the preputium, while in all specimens personally examined this muscle, distally branched, was attached to the end of the vergic sac, as shown in plate 22, fig. 7. There are muscles on the preputium which probably aid in its retraction (plate 21, fig. 5). The writer believes that the bulbous swelling (shown at B in fig. 1, plate 21, and at B in fig. 7, plate 22) has some significance, for it is also shown, although in a more lengthened condition, in Larambergue's figure on page 288. It might be that it marks the limit of the copulatory portion of the verge, as suggested by the writer in a previous paper (1933, p. 4). The schematic figures 8 and 9 in Larambergue's paper (copied on plate 74, figs. 8, 9) suggest such a condition. As observed by Larambergue, however, these differences may be largely due to the preservation of the material examined.

Female Organs (plate 21, fig. 3). Spermatheca (S) small (about 1 mm. long) pyriform, attached to the long, narrow vagina (2 mm. long) by a very short duct. The spermatheca is, in fact, almost sessile. The uterus (U) is about 5 mm. long and nearly four times as wide as the vagina. The large nidamental gland (NG) is 6 mm. long, is about as wide as the uterus and is curved about the uterus and oviduct. The oviduct (OD) is about as long as the uterus and vagina combined (about 9 mm. long). It is 1 mm. wide at the uterus end but decreases in diameter toward the albumen gland where it joins the sperm duct to form the ovisperm duct. There is a small carrefour. The albumen gland (AL), a flattened, more or less heart-shaped organ, is convex above and concave below. It has a narrow duct which enters the carrefour. The ovisperm duct (SO) is a narrow tube about 3 mm. long between the seminal vesicle and the oviduct. In the specimens examined it was entirely smooth, but Larambergue figures it as having lateral swellings, as was observed in some species of Planorbidae. A small, smooth duct about 1 mm. long joins the seminal vesicle to the ovotestis. The female organs are as figured in Larambergue's paper and also as described by Rao.

The ovotestis (OT) appears on the surface as a multilobed organ. In cross section (near the anterior end) it is seen to be made up of seven or more main diverticula which branch twice at the outer end (plate 21, fig. 7). They radiate fan-wise from the ovisperm duct. Several branched diverticula contained ripe ova at their distal ends. The ova were dark gray in color and with these there were several small, rounded bodies which were red in color, evidently undeveloped ova.

Respiratory and Renal Systems. The pseudobranch (figs. 4, 6, plate 21) is large and conspicuous and is not simply folded or leaf-like, as in all of the Planorbidae examined, but on the upper and lower surfaces of a leaf-like base are developed a number of projections with broad lobes, plaits, or folds (fig. 4) grouped together in series of three to six folds, each group of folds being separated from the other folds by a distinct depression or gap. The base of attachment of the folds is not modified by the folded series (see fig. 6). In the living animal, the folded portion of the pseudobranch is turned back against the mantle edge. The rectum (R) is on the side above the pseudobranch and the anal opening is between the pseudobranch and the pneumostome.

Rao (1923, p. 208) describes the lobes as occurring in groups of three or four, but in the specimens examined there were two groups of six each on the under side of the base and two groups of three lobes and two groups of two lobes on the upper side, as shown in fig. 6. The pneumostome (PS) is a large, thin lobe and is capable of considerable extension (fig. 4, PS). In fig. 2, it is shown turned back and spread open.

The pseudobranch is highly vascular, well-supplied with blood vessels, veins, and muscles. It more nearly resembles the molluscan branchium than the pseudobranch of any of the other fresh-water pulmonates.

The kidney is long and narrow (12 mm. long, 1.5 to 3 mm. wide). The ureter is 1.5 mm. long and is sharply reflexed against the lower part of the kidney, pointing backward and upward into the mantle cavity. In form, the kidney resembles that of *Helisoma trivolvis* figured on plate 44 (fig. 2). The reflexed ureter in the specimens examined is not so long as figured by Rao (1923, p. 206). A cross section near the middle (plate 45, fig. 19) shows a high, thick, wide ridge. The lumen is rounded and shows internal folds or septa. A large vein lies on each side of the lumen. The cross section somewhat resembles that of the kidney of *Planorbarius corneus* (plate 45, fig. 18). The kidney of *Indoplanorbis* is noteworthy for the size and width of the superposed ridge, which resembles some of the large *Helisoma* species (as *Helisoma pilsbryi*, plate 44, fig. 12).

Digestive System. The stomach resembles that organ in *Australorbis glabratus* (plate 48, figs. 9, 10). The intestine first makes a loop around the stomach, passes backward to the posterior part of the liver, then makes another loop and passes forward to the enlarged rectum, which has its exit in the anus above the pseudobranch. There is a narrow, low ridge on the rectum which ends near the pseudobranch. There is a large caecum or blind sac near the pyloric portion of the stomach.

The buccal sac is short, wide, and high. Viewed from above, it is roughly heart-shaped. The radula sac is represented by a wide, flatly rounded bulge at the lower posterior extremity of the buccal sac. The two salivary glands are rather long, about one and a half times as long as the buccal sac when fully extended. In the natural position, the posterior portion of the salivary glands (somewhat less than half the length) is doubled backward beneath the anterior portion, which is wider with larger glandular lobules. The ducts are short and narrow. The salivary glands are joined behind as in *Helisoma* and other planorbids.

The jaws (plate 50, fig. 10) consist of a wide and low superior jaw, striated on its outer face, slightly bent downward at the ends. The lateral jaws are in the form of a question mark, are very narrow and about as long as the width of the superior jaw. The jaws of *Indoplanorbis* do not differ notably from the jaws of the subfamily Helisomatinae.

The center tooth of the radula (plate 66, fig. 1) is higher than wide, rather narrow, the reflection broadly bicuspid and reaching nearly to the lower margin of the base of attachment. Lateral teeth (1-5), squarish, tricuspid, the mesocone the longest, the ectocone the shortest and placed high up on the reflection, all cusps wide and spade-shaped. Intermediate teeth (6-11) narrower, differing from the typical laterals in having a second small cusp above the ectocone. The tenth intermediate tooth has two small cusps above the ectocone. Marginal teeth (12-26) narrow, about three times as long as broad. The entocone is split into three to five small, subequal cusps, the mesocone is larger and distinct, and the ectocone is smaller with two to three small cusps above it on the outer margin of the tooth. The outer marginal teeth (27, 32) are still narrower and the lower edge of the reflection is minutely denticulated. The extreme outer marginal teeth are very small (33).

The radula formula of *Indoplanorbis* is 33-1-33 with 140 to 150 rows of teeth. There is some variation among the different rows of teeth, principally in the number of accessory cusps in the marginal teeth. The radulae examined were remarkably uniform. The radula figured on plate 66 agrees with that described by Rao (1923, p. 204).

The material examined consisted of six specimens from Hsipaw, North Shan State, Burma, collected by Dr. B. N. Chopra and Dr. H. S. Rao. The specimens were received from Dr. B. Prashad of the Zoological Survey of India.

Geographical Distribution. The genus as represented by the type species, *Planorbis exustus* Desh., occurs throughout the plains of the Indian Empire east of the Indus, in Siam, the Malay Peninsula, French Indo-China, and Sumatra (vide Annandale). For a more detailed account of the distribution of this group see Germain (1921, pp. 28, 29).

The number of species or races referable to *Indoplanorbis* is in doubt. Germain (1921, p. 27) places almost everything under *exustus* as synonyms of that species. *Planorbis coromandelicus* Sowerby and *Planorbis indicus* Clessin have been thought to be distinct by some conchologists. A careful study of all names in connection with a large series of specimens from various localities might establish several recognizable forms.

Remarks. The systematic position of Deshayes' *Planorbis exustus* has been a matter of interest for a number of years. It is the largest planorbid in India and the shell closely resembles certain species of the American genus *Helisoma*. An examination of its anatomy led Annandale and Prashad (1920) to consider it a new genus and Rao's investigations (1923) strengthened the view of its distinction as a generic group. Baker (1933) stated that it was 'one of the most distinct groups of the Planorbidae, its male complex exhibiting characters not shared by any other group at present known.' Pilsbry (1934, p. 54) suggests its resemblance to *Tropicorbis,* particularly in the form of the penial complex.

More recently Larambergue (1939, pp. 291, 294) argues that the genus *Indoplanorbis* is a group of the family Bulinidae. Little is known concerning the anatomy of the majority of the species of this family. Two species have been rather carefully studied, *Bulinus contortus* of Europe by Larambergue (1939) and *Isidora globosa* from Portuguese East Africa by Connolly. In both of these species, the genitalia are similar to those of *Indoplanorbis,* especially in the form of the penial complex and the prostate (see plate 71, fig. 3 and plate 75 of this work). The most convincing characteristic is the pseudobranch, which is lobed in Bulinidae (Germain, 1931, p. 514). In *Isidora globosa* the lobed condition is well shown in Connolly's figure (plate 71, fig. 5, of this work.)

The anomaly of a distinctly planorboid shell in a group made up almost exclusively of physoid shells is no greater than is shown in the American subgenus *Seminolina* where one species, *Helisoma duryi seminolina,* contains all shapes of shell from distinctly physoid to normally planorboid. The shell of *Indoplanorbis exustus* is distinctly sinistral, particularly so in the young and immature stages of growth.

The writer agrees with Larambergue in the statement that the group *Indoplanorbis* is a distinct genus of the family Bulinidae, the deciding features being the lobulated pseudobranch and characteristics of the male genitalia, particularly the penial complex.

X.

GENERA WRONGLY REFERRED TO PLANORBIDAE

Genus NAUTILINUS Mousson, 1872

Type by original designation, *Hyalina clymene* Shuttleworth

1872. *Nautilinus* Mousson, Neue Denksch. Allg. Schweiz. Gesell., XXV, p. 19. Type *Hyalina clymene* Shuttl. As subgenus of *Hyalina*

1921. *Nautilinus* Thiele, Archiv. für Mollusk., LIII, p. 111. Type *Hyalina clymene* Shuttl. Radula and generic position

1931. *Nautilinus* Thiele, Handbuch, Teil 2, p. 481. Type *A. (N.) clymene* (Shuttl.). As subgenus of *Anisus*

This genus, based on a supposed land snail from Garachico, Ténérife, Canary Islands, is scarcely a member of the family Planorbidae, although so considered by Thiele. The figures given by Mousson (his plate 1, figs. 28-30, natural size, figs. 31-33 enlarged) do resemble some forms of *Gyraulus*. The shell is very small, only 2 mm. in diameter. Tryon (in Man. Conch., II, p. 172, 1886) places it in Zonitidae and says 'Its habitat is different from the Hyalininae generally, living in wet moss, associated with *Physa*, *Ancylus*, and *Hydrocena*, etc.' Pilsbry (Man. Conch. IX, p. 24) lists it among the land shells. Wollaston (1878, p. 324) says 'I am extremely doubtful whether this curious little Planorbis-like shell should be associated with *Hyalina*.'

In 1921 (p. 111), Thiele extracted a dried radula from a shell of this species and briefly described the teeth. The formula is 20-1-20. The center tooth is small and has one indistinct cusp. The side teeth (laterals and marginals) have four sharp cusps. The single cusp of the center tooth removes *clymene* from the Planorbidae in which the center tooth always has two cusps. The form of the shell is distinctly unlike any form of the family Lymnaeidae, in which the center tooth of the radula is unicuspid. The radula resembles some groups of Ancylidae and *Nautilinus* might prove to be related to this family, perhaps in a similar manner to the American genus *Neoplanorbis* Pilsbry, in which the shell is particularly Planorbis-like. Only an examination of the anatomy of the animal, especially the genitalia, will definitely settle the question of the taxonomic position of *Nautilinus*.

Genus PALAEORBIS Beneden and Coemans, 1867

1867. *Palaeorbis* Beneden and Coemans, Bull. Acad. Belgique, ser. ii, XXII, pp. 385, 390

The only recent reference to this group, so far as known to the writer, is in Zittel's Grundzüge der Palaontologie (Palaozoologie), Abth. I, Invertebrata, p. 424, where the following comment is made: 'Hierher dürfte wohl auch die *Planorbis* sehr ähnliche Gattung; die zierliche *Palaeorbis* Bened. et Coemans em. Reis aus oberkarbonischen und permischen Ablagerungen von Europa und Nordamerika gehören.' The name does not occur in any other edition of Zittel's work.

The group is believed to include fossil Vermes, possibly Polychaetes. It does not appear to be referable to any mollusk, centainly not to the Planorbidae, which are unknown in both the Carboniferous (Mississippian and Pennsylvanian) and Permian periods of America. The generic name does not appear, as far as known to the writer, in any American work on fossil pulmonates. It is probable that some Planorbidae will eventually be found in Palaeozoic strata, since the family is so well developed in Mesozoic time.

XI.

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THE MOLLUSCAN FAMILY PLANORBIDAE

PART II

THE PLANORBIDAE INHABITING NORTH AND SOUTH AMERICA AND THE WEST INDIES*

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*It was Mr. Baker's plan that Part II should contain full morphological and taxonomic descriptions together with comprehensive illustrations of the shells of all species of the Planorbidae known for North and South America and the West Indies. His voluminous working notes were not near enough objective organization at the time of his death to permit their being edited for publication. Any attempt at preparation of these notes by another hand could not ensure the reflection of Mr. Baker's matured judgment and ultimate intent in the casting of specific descriptions, in the portrayal of individual variability, and in the discussion of geographical distribution and ecological relationships. However, at the time of his death, he had completed fifty-four of the plates intended for this section and had prepared typewritten copy for them. In his desk were found plainly-marked photographic prints of other species sufficient to prepare six additional plates and pencil manuscript for descriptions of the figures had been written out. The entire group of sixty plates (82-141) is included as a supplement to Part I, even though the six plates at the end of this series represent working copy in which he might have desired to make some final alterations. For convenience of arrangement and reference, the plates of Parts I and II are presented in a single undivided series at the end of this monograph.

In addition to the plates for Part II, descriptions have been prepared for nine new species and seventeen new varieties.

The foreword was written by Professor Harley Jones Van Cleave, who also assembled and edited the descriptions of the new forms and edited the explanations of the plates.—H.E.C.

XII.

FOREWORD

FOR ALMOST A QUARTER OF A CENTURY, Frank Collins Baker had been engaged in the preparation of detailed descriptions of the species and critical evaluation of the synonymy of the Planorbidae of the Western Hemisphere. This study was the natural outgrowth of the long years of detailed morphological studies which led him to the evaluation of anatomical detail as expressed in the broader phases of taxonomy in the main body of the present volume. The second volume in this series was to have treated the species of the Planorbidae in a manner similar to his treatise on another large and important family of fresh-water snails, the Lymnaeidae. Though published in 1911, his volume on the Lymnaeidae of North and Middle America after more than thirty years still stands as the leading taxonomic and distributional study of the lymnaeid snails of the Western Hemisphere.

Though such a program of study involved intimate familiarity with the voluminous, scattered literature and wise interpretations of matters of disputed priority and synonymy, these labors paled into insignificance when compared with the self-imposed task of dissecting and microscopically studying representatives of all the species available through the well-recognized repositories of collections. To these customary sources were added large quantities of material from individuals throughout the world with whom kindly cooperation had established intimate personal and professional contacts. Large numbers of dissections and long series of shells gave opportunity for bridging the gap between the earlier field of Conchology and the newer science of Malacology to both of which Mr. Baker had made notable contributions. As he reached final decisions on the validity and synonymy of the species in the various genera, he prepared photographs of the shells or of original drawings of the type specimens when shells were not available. These photographs he arranged as plates and for each he prepared a detailed descriptive legend. He had completed plates illustrating the shells of the genera *Helisoma*, *Carinifex*, *Parapholyx*, *Planorbula*, *Menetus*, *Drepanotrema*, *Tropicorbis*, and *Taphius*. In his office at the time of his death were hundreds of photographic prints of other genera and species intended for use in this monograph. Some of these he had so marked and keyed with numbers that it has been possible to assemble six additional plates which are included at the end of the series. With this inclusion, all of the genera which he apparently intended to figure are included though many of the species are not portrayed in the detail which he established in those earlier parts which he had completed. The explanations of plates 136 to 141 are compiled from rough pencil notes and must be accepted as the author's tentative arrangement of work in progress which might have been changed somewhat in the final editing.

Some of the species not included in the plates of the appendix have representative shells figured on plates 72 to 81 of the illustrations for the body of the monograph. However, these figures are usually of only the type species in each genus and do not carry out the plan of comprehensive comparisons set for the second section of the monograph as originally projected by the author.

In the sixty plates included in this appendix (plates 82 to 141), many type specimens and other critically determined materials are figured, and information as to the present whereabouts of these critical materials is made available. In the members of the family Planorbidae, where synonymy has been so involved and where intergradations in shell characters have been so confusing, the interpretation of range of individual variability by one who has devoted years to the study and had the singular advantage of access to all the important collections, will be appreciated by all naturalists who have the need for studying snails.

For convenience of reference, the plates in the appendix are numbered in direct continuation with the series of plates in the body of the monograph. In the explanation of the plates, the repository of the figured specimens is usually indicated by the following abbreviations:

A.N.S.—Academy of Natural Sciences of Philadelphia
B.—Frank Collins Baker Collection
C.A.S.—California Academy of Sciences
M.C.Z.—Museum of Comparative Zoology, Harvard University
U.C.—University of Colorado Museum
U.I.—University of Illinois, Museum of Natural History
U.M.—University of Michigan Museum
U.S.N.M.—United States National Museum

In connection with the foregoing list of repositories, it should be here recorded that the Frank Collins Baker collection of fresh-water snails and the specialized library accompanying it, after his death, was deposited in the United States National Museum. This was in keeping with his expressed desire. It should be further explained that the collections attributed to the University of Illinois are designated by two series of letters. Those 'U.I.' entries having the letter 'Z' preceding the accession numeral are in the zoological research collections of the Museum of Natural History in the University of Illinois. Paleontological specimens, indicated by insertion of the letter 'P' immediately before the accession number, are now deposited in the Paleontological Collections of the Illinois State Geological Survey, in Urbana, Illinois.

Citations of magnification in the explanation of the plates are usually only approximate. In final preparation of the cuts, it was in many instances unavoidably necessary to make slight modification of the author's indicated amount of reduction from the original plates so as to conform to the available page size.

In listing the names of the species in the explanation of plates in the appendix, Mr. Baker placed the name of the author of the species immediately after the specific name and frequently gave no indication by the use of parentheses in instances where the specific name was recombined with a generic name other than that to which the species was originally ascribed. It should be recalled that the preliminary draft which he prepared was never finally edited by him. Through the very generous cooperation of a number of the most widely recognized American authorities in the study of the Mollusca, the use of parentheses for author names has been carefully checked. Some errors or inconsistencies may yet be found because the literature is extremely scattered and there are no comprehensive check lists of the species of Planorbidae.

As previously explained, the manuscript for the section in which Mr. Baker had expected to provide full descriptions of all species and varieties of the Planorbidae of the New World had never been completed. In the voluminous long-hand notes which he left in unfinished form, there were included the preliminary drafts of descriptions of many new species and new varieties intended for incorporation in Part II. After it had been decided that the plates for Part II should be included as an appendix to the morphological studies, it was discovered that the legends for these plates made frequent reference to previously unpublished specific and varietal names. His manuscript descriptions for many of the new species and new varieties were so well organized that there could be no doubt regarding his intention. Consequently, his preliminary descriptions have been edited and are included as a separate section of Part II. A few of the varieties and species which he tentatively considered as new could not be found in his files. For these it is assumed that he had never prepared definite descriptions. In order to avoid nomenclatorial difficulties, these names have been deleted to prevent their becoming *nomina nuda*. In each such instance the undescribed and unnamed form has been referred to under its proper genus as a questioned species or questioned variety.

XIII.

DESCRIPTIONS OF NEW SPECIES AND NEW VARIETIES

AS EXPLAINED in the foreword, the following technical descriptions of new species and new varieties were edited from longhand notes prepared by Mr. Baker. During the past quarter of a century he examined every important collection of Planorbidae housed in the museums of America and received extensive field collections from many private collectors as well. In the handling of this huge quantity of material he came to recognize fundamental likenesses and differences at varying levels. In addition to his study of the shells, his intensive work on the morphology of the snails gave him a broad background for the recognition of natural groups. On the one side, he expressed his conclusions in the broad new classification of the Planorbidae as set forth in Part I of this volume. There he evaluated the characteristics on which families, subfamilies, genera, and subgenera may be recognized with safety. On the other side, his attention to the limits of individual variation in characteristics of the shell furnished the basis for the detailed recognition of specific and varietal boundaries. The descriptions of new forms and the redescription of all known species were to have been the final goal of Part II of this study.

From his incomplete notes the following descriptions include only those for which he had prepared tentative definitions. On other species and varieties, which he obviously thought of as new, he had not committed himself through the preparation of manuscript notes and in the assembly of illustrations.

The descriptions of nine new species and seventeen new varieties are arranged in the same sequence of genera and subgenera as outlined in Part I (see pages xiv and xv of the Contents).

All tabular arrangements of shell measurements are expressed in millimeters.

GENUS *Tropicorbis*

Tropicorbis shimeki, New Species

Plate 134, figs. 12-14, 28

Shell solid, small, of three and one-half whorls. Upper surface showing three and one-half whorls which are subangulate above, sutures very deep. Lower surface showing three and one-half whorls which are subangulate in the middle, sutures very deep. Whorls rounded on the periphery. Apical whorls sunken on both surfaces. Whorl slightly deflected at aperture. Aperture lunately rounded, outer lip thick with callus. A callus on parietal wall connecting the extremities of the outer lip. Sculpture of coarse growth lines with fine spiral lines. Apertural lamellae six, those of sigmoid form extremely short and thick, only slightly more than half the length of those found in *obstructus*.

Shell Height	*Greater Diameter*	*Lesser Diameter*	*Aperture Height*	*Aperture Diameter*	
1.5	4.0	3.2	1.1	1.0	Holotype
1.6	3.8	3.1	1.1	1.1	Paratype
1.5	3.4	2.8	1.1	1.0	Paratype

Type Locality. Ometope, Nicaragua.

Type Material. Collected by B. Shimek in 1893. Four specimens deposited in United States National Museum, Accession no. 534290. The holotype is shown on plate 134 as fig. 12; figs. 13, 14 are paratypes.

Tropicorbis shimeki resembles *albicans* but is smaller, has a greater axial height, and has subcarinate whorls. The parietal lamellae are distinctly shorter and thicker than in other forms of the genus. *T. shimeki* is smaller than *declivis* and its axial height is greater; it also has deeper sutures than are found in *declivis*.

Additional representatives of *T. shimeki* were collected by Orcutt in Coatzocoales, Mexico (United States National Museum, Accession no. 219696).

This species is named in honor of Professor B. Shimek.

GENUS *Helisoma*

Helisoma anceps anticostianum, New Variety

Plate 96, figs. 18-22

Shell differs from typical *anceps* in the low axial height, the wide and shallow spire depression with bluntly angular carina, and the shallow and wide umbilical region of the new variety. The aperture is but slightly expanded. Whorls about four, evenly and regularly coiled, with faint spiral lines.

Shell Height	*Greatest Diameter*	*Aperture Height*	*Aperture Diameter*	
4.7	10.0	3.7	3.0	Holotype
6.0	12.5	4.8	3.6	Paratype
4.8	9.5	3.7	2.9	Paratype

Type Locality. English Bay, Anticosti Island, Quebec, Canada.

Type Material. Collected by W. S. Brooks, September 15, 1919. The holotype is shown on plate 96 as fig. 18; paratypes as figs. 19 to 22. Deposited in the collection of the Museum of Comparative Zoology, Harvard University, Accession no. 48285.

H. anceps anticostianum, a Pleistocene fossil, is similar in appearance to *striatinum* from Milwaukee, but differs in the fact that the new variety has wider and shallower spire depression, has general lower axial height, and lacks distinct angulations above and below. All of these features are marked in *striatinum*. The whorls are likewise flatter above in the new form than in *striatinum*. Spiral lines are not notably distinct. Some specimens have evidence of a former campanulate lip.

Helisoma anceps bartschi, New Variety

Plate 83, figs. 19-22

Shell compressed, with four whorls. Periphery rounded. Spire depression wide, a wide cone with flat sides; shallow, bordered by a well defined carina. Base with flattened whorls, the carina sharp and placed near the outer edge. Surface of shell shining, growth lines very fine; occasionally white varices on whorls. Sculpture of very faint spiral lines. Aperture inverted ear-shaped, forming a sharp V above and a broad V below. Outer lip thickened and expanded, white, bordered by reddish band inside. Parietal wall with white callus.

Shell Height	*Maximum Diameter*	*Aperture Height*	*Aperture Diameter*	
6.5	11.7	5.5	3.3	Holotype
6.1	12.0	5.1	3.0	Paratype
6.6	11.6	5.5	3.3	Paratype

Type Locality. Brook at Great Falls, Virginia. Collected by Soelner.

Type Material. Holotype and seven paratypes, deposited in the United States National Museum, Accession no. 227858. Holotype figured on plate 83, fig. 19; paratypes figs. 20-22.

This variety may be distinguished by its small axial height, depressed shape, wide and shallow spire depression, flat basal whorls with carina near periphery. It resembles the variety *politum* from Canada, but that variety has rounded basal whorls without marked carina, its spire depression is wide with more flat-sided whorls, and dorsal carina is more acute. The basal part of the aperture is rounded or almost flat in *politum*, but has sharp, wide angle in *bartschi*.

Bartschi differs from *sayi* in lower axial height, less sharply angled basal whorls (with carina not near edge as in *sayi*); shallow and wide spire depression.

Bartschi differs from *anceps* in lower relative axial height (compared with diameter); wider spire depression; basal whorls flatter; carina nearer periphery (near center in *anceps*).

Helisoma anceps bartschi is apparently a common form in the Potomac drainage.

Helisoma anceps idahoense, New Variety

Plate 84, figs. 26-28
Plate 101, figs. 11, 12

Spire with carina in center. Base concave, basal whorls flat to sutures which are well marked. Whorls four. Spire depression deep and funnel-shaped, the whorls flat-sided. Carina well marked. Whole shell is cone-shaped, the whorls sloping upward to the spire carina. Color yellowish horn. Sculpture of regular growth ribs crossed by distinct spiral lines. Aperture auriform (reversed), sharply angled above, flat or flatly-rounded below. Lip sharp. Distinct columellar callus. Color of aperture whitish or slightly purplish. A callus often within the lip edge.

Shell Height	*Maximum Diameter*	*Aperture Height*	*Aperture Diameter*
11.0	18.0	9.5	6.0
8.5	15.6	7.5	6.0
9.5	15.5	8.6	6.2

There is considerable variation in width and depth of spire depression. Base rarely rounded, without carina. Carina always near center of base. Some variation in shape of aperture. It may form a sharp V below (as in the holotype) or it may be rounded and flattened at this point. This variety is nearest to *latchfordi*, differing in the less angular basal portion of the aperture and also in the more distinct and heavier spiral sculpture in *idahoense*.

Type Locality. Pend Oreille River, Sand Point, Idaho.

Type Material. Holotype (plate 84, fig. 26) and paratypes in F. C. Baker Collection, no. 1863, now deposited in United States National Museum.

H. anceps idahoense is apparently common in Idaho and Montana. In some places it occurs on muddy sand or on old logs.

Helisoma anceps politum, New Variety

Plate 83, figs. 16-18

Shell flattened, wider than high, spire deeply sunken, showing three and one-half to four whorls, the depression widely cone-shaped rising to a vaguely defined, rounded carina. Umbilical region flattened, showing three and one-half to four whorls, the front half of the body whorl with a faint ridge about in the center of the whorl. Ridge disappears on the last third of the body whorl which is rounded. Sculpture of fine, thread-like riblets, often raised into slight ridges, especially toward the aperture. Color of shell pale yellowish to dark brown. Surface polished in living specimens. Fine impressed spiral lines present in all specimens examined. Aperture ovate, higher than wide, obtusely angled above, straight or but slightly curved below. Outer lip thickened, bordered within by a reddish-brown band. The lip edge is white on the outside.

Shell Height	*Maximum Diameter*	*Aperture Height*	*Aperture Diameter*	
8.1	15.0	7.0	4.4	Holotype
8.1	14.0	7.0	4.0	Paratype
8.0	14.2	7.0	4.0	Paratype

Type Locality. Honeywell Creek, Carleton Co., Ontario, Canada. Collected by F. R. Latchford.

Type Material. Deposited in United States National Museum, Accession no. 367426. Holotype figured on plate 83, fig. 16; figs. 17, 18 are paratypes.

H. anceps politum is related to *unicostatum* but the new variety has a wider and shallower spire depression, a more compressed shell, and a distinct carina on the basal whorl, besides having the surface of the shell polished. Latchford identified this material as *unicarinatum*.

Helisoma binneyi randolphi, New Variety

Plate 94, figs. 1-8

Shell differing from typical *binneyi* in being of less axial height, the carina surrounding the spire depression is obsolete or faintly developed; the basal whorls are rounded, not angulated. Sculpture is fine with the ribs close together, both being very much finer and closer together than in *binneyi*. The lip is only slightly expanded. Mature shells have four whorls.

Shell Height	*Maximum Diameter*	*Aperture Height*	*Aperture Diameter*	
11.8	20.8	10.2	7.3	Holotype
11.0	20.8	10.3	6.5	Paratype
9.1	17.1	8.5	5.0	Paratype
9.2	15.9	8.2	5.5	Paratype
7.6	12.4	7.0	4.1	Immature

Type Locality. Lake Washington, Seattle, Washington.

Type Material. Collected by P. B. Randolph, deposited in United States National Museum, Shimek Collection, Accession no. 504360. Holotype figured on plate 94, fig. 1; paratypes, figs. 2-4; immature, fig. 5.

Helisoma caribaeum cubense, New Variety

Plate 119, figs. 22-25

Shell differing from that of typical *caribaeum* in having the spire depression much narrower, the whorls, especially the body whorl, increasing more rapidly in diameter. Five full whorls. Sutures not impressed as in *caribaeum*, the spire whorls flattened, not rounded, and there is often a carina at the edge of the whorls. Nuclear and first whorl rounded as in *caribaeum* and of the same size. Basal whorls rounded, the umbilical region concave, umbilical opening distinct. Axial height somewhat greater than in typical *caribaeum*, the body whorl flattened near the spire depression, not evenly rounded as in typical *caribaeum*. Aperture more nearly auriculate than in *caribaeum*, the lip sometimes (as in the holotype) thickened by a heavy callus. Sculpture as in *caribaeum*.

Shell Height	*Greater Diameter*	*Lesser Diameter*	*Aperture Height*	*Aperture Diameter*	
8.7	19.1	16.0	6.0	4.0*	Holotype
7.0	16.0	13.5	6.2	4.0	Paratype
6.1	14.0	12.0	4.5	3.0	Paratype
6.0	14.1	11.1	4.3	3.1	Paratype

*Aperture contracted in holotype by thickened lip.

The form of the whorls increases like that of *tenue*, especially like that of *tenue sinuosum*, but inner whorls are like those of *caribaeum* in that they are rounded, and are not like those of *tenue* which are flat and carinated at the edges. Some living Cuban specimens have a somewhat narrower spire than the typical form here figured but these lack the greatly increased diameter of the body whorl characteristic of *cubense* and the aperture is not auriculate or thickened by a callus as in mature and nearly mature specimens of *cubense*. The basal whorls are more concave than in *caribaeum*. Sutures are not as deep as in *caribaeum*. Evidently a Pleistocene fossil.

Type Locality. Zapata Swamp, Cuba, in marl between layers of peat.

Type Material. Eight specimens, collected April 19, 1927, by H. H. Bennett, are deposited in the United States National Museum, Accession no. 404719. Of these, the holotype is figured on plate 119 as fig. 22, and three of the paratypes are shown as figs. 23-25.

Helisoma columbiense, New Species

Plate 119, figs. 16-21

Shell with four to four and one-half whorls, rapidly enlarging. Spire depression flattened, the inner whorls bordered by a sharp carina which becomes distinctly central in position on the last whorl. The sides of the depression slope sharply downward. Base of shell concave, broadly funnel-shaped, the last whorl with a more or less sharp carina or ridge. Sutures well marked. Sculpture of coarse riblets, widely spaced, as in typical *sub-*

crenatum. Aperture ovately rounded, the lip rim thickened and broadly reflected. A callus on the parietal wall renders the aperture continuous. There is usually a border of dark chestnut or reddish brown within the aperture. The aperture may be rounded above or there may be a sharp V-shaped angle, depending upon whether the dorsal carina is sharp or rounded. There is normally an indication of angulation at this point. The basal part of the aperture is flatly rounded. Several old lip expansions may show on the body whorl back of the aperture. Color whitish, tinged with chestnut in some specimens.

*Shell Height**	*Shell Height at Aperture*	*Greater Diameter*	*Lesser Diameter*	*Aperture Height*	*Aperture Diameter*	
8.5	10.5	18.5	14.6	8.5	6.5	Holotype
10.0	10.5	19.0	15.5	9.3	6.2	Paratype
9.5	11.0	19.0	15.5	10.0	6.5	Paratype
9.5	10.0	17.6	13.6	9.0	6.5	Paratype
9.1	11.0	17.0	13.1	8.1	6.0	Paratype

*Measurement taken behind the expanded lip.

Type Locality. Lac La Hache, Cariboo District, British Columbia.

Type Material. Fifteen specimens, collected by H. and R. D. Svihla, are deposited in the Museum of Comparative Zoology of Harvard University, Accession no. 93710. The individual selected as holotype is shown on plate 119 as fig. 16; paratypes as figs. 17-21.

Helisoma columbiense shows relationship to the *binneyi* group in its sculpture and the carination of its whorls. It differs from the members of that group in that it is of smaller size, has less relative axial height, its rib striae are less widely spaced and the whorls are usually more angulate.

It differs from the *subcrenatum* group in having more regular and less widely spaced rib striae, in its angulated base and spire depression, and in the shape of the aperture.

Helisoma kennicotti, New Species

Plate 89, figs. 13-17

Shell in four whorls, rapidly increasing in diameter. Body whorl axially very high. Sculpture of evenly spaced, rather heavy, rib-like growth lines becoming more widely spaced on the last half of the body whorls. Spire depression concave, widely cone-shaped, flat-sided, bordered by a strong, sharp carina, extending to the aperture. Base showing three whorls, the umbilicus deep, with a small perforation; only slight indication of a carina in adult, but distinct and sharp in immature specimens. Aperture auriform, sharply angled above, flatly rounded and effuse below, the outer lip expanded. Parietal wall with a thin wash of callus which connects the extremes of the lip. Color light, yellowing horn, brownish or bluish in some specimens.

Shell Height	*Greater Diameter*	*Height at Expanded Lip*	*Diameter at Expanded Lip*	*Aperture Height*	*Aperture Diameter*	
12.5	19.0	14.2	20.2	12.0	6.6	Holotype
12.0	17.1	14.0	18.5	11.5	6.5	Paratype
12.5	18.1	14.2	19.4	12.0	5.5	Paratype
7.5	11.0	9.0	12.0	7.0	4.0	Immature
8.0	11.0	9.0	12.0	7.0	4.1	Immature

Helisoma kennicotti is a very distinct species. It differs from *infracarinatum* in its smaller size, greater relative axial height, as compared with diameter. Expressed in percentages of height to diameter, *kennicotti* is sixty-five per cent and *infracarinatum*, fifty-six per cent. The spire depression is much smaller, narrower, and deeper in *kennicotti*, the shell forming an inverted cone. The base of the new species is likewise narrower, and the whorls dip into the umbilicus at a sharper angle, only one and one-half turns before entering the umbilicus. In contrast, in *infracarinatum* there are two full turns visible.

Type Locality. Lake Isle la Crosse, English River, Canada.

Type Material. Deposited in United States National Museum, Accession no. 29231, bearing the label of the old Binney collection no. 9272 and there recorded as *Planorbis trivolvis*. Figures on plate 89; holotype as fig. 15; paratypes as figs. 16, 17; 13, 14 immature shells.

Helisoma pilsbryi preblei, New Variety

Plate 91, figs. 6 to 8

Helisoma pilsbryi preblei differs from typical *pilsbryi* in its greater relative height in comparison with diameter of the shell. The whorls in *preblei* are more tightly coiled, the body whorl increasing more rapidly in diameter, causing the spire depression and umbilical region to appear smaller than in *pilsbryi* in which the whorls are rounded more regularly. The aperture is widely expanded to form a reflected lip. This is not true of *pilsbryi*. Whorls, four and one-half. Sculpture as in *pilsbryi*. *H. p. preblei* differs from *subcrenatum* in absence of all indication of a carina on the umbilical side. The whorls of the spire depression are subangulated, not sharply angled as in *infracarinatum*.

Shell Height	*Greater Diameter*	*Height at Expanded Lip*	*Diameter at Expanded Lip*	*Aperture Height*	*Aperture Diameter*	
14.0	24.5	17.0	27.0	13.0	7.0	Holotype
14.0	25.0	16.0	26.0	13.0	7.5	Paratype
11.5	19.0	....*	....	9.5	5.6	Paratype*

*Broken specimen with four and one-fourth whorls, the last one-half whorl broken away.

Type Locality. Knee Lake, Manitoba, Canada.

Type Material. Three specimens, collected by E. A. Preble in the 'North West Territory, Knee Lake, Keewatin,' deposited in United States National Museum, Accession no. 180279. Figured on plate 91, holotype as fig. 6; paratypes as figs. 7, 8.

The type material was previously called *infracarinatum* but it is nearer to *pilsbryi*. It differs from the latter in its expanded lip and more tightly coiled whorls of the umbilical region. Differs from *infracarinatum* in the absence of a basal carina and in having a narrower and more sunken spire depression.

Helisoma subcrenatum perdisjunctum, New Variety

Plate 96, figs. 13-17

Shell small, horn colored; whorls three and one-half to four, discoidal, evenly rounded; 3 whorls below. Whorls slowly increasing in diameter, rounded above and below, not carinated. Sculpture of distinct growth lines, finer than in *disjunctum*. Aperture rounded above and below, slightly expanded where it joins the body whorl. A distinct callus on the parietal wall, often making the aperture and lip continuous. A slight thickening inside outer lip, bordered by brown band.

Shell Height	*Greater Diameter*	*Aperture Height*	*Aperture Diameter*	*Number of Whorls*	
4.0	8.5	3.7	2.6	4.0	Holotype
4.6	9.2	4.1	3.0	3¾	Paratype
5.0	9.0	4.7	3.2	3½	Paratype
5.2	10.5	4.9	3.2	4.0	Paratype

Type Locality. Yellowstone Lake, Wyoming.

Type Material. Five specimens, collected by Dr. Curtis, deposited in the United States National Museum, Accession no. 30207a. Holotype here shown as fig. 13 on plate 96; paratypes as figs. 14-17 on same plate.

H. s. perdisjunctum is similar to *disjunctum* but is much smaller, about the size of *oregonense*, but lacks the characteristic shape of the aperture of the last named form. The dorsal carina and the more uniformly and evenly coiled whorls, without rapid increase in size distinguish it from *oregonense*. Appears at first like immature *disjunctum* but is uniformly smaller; never has the axial height of *disjunctum*. Many specimens have lost the epidermis, exposing white, chalky shell.

Helisoma trivolvis marshalli, New Variety

Plate 87, figs. 11-15

Shell compressed, whorls four and one-half, rapidly increasing in diameter, the body whorl notably expanding toward the aperture. Sutures well marked above and below. Sculpture of coarse lines of growth, thread-like; spiral lines very indistinct or wanting. Spire depression small, narrow, shallow (less than one-half the width of whorl), its border rounded, without carina in adult specimens, carina slightly developed in young and immature specimens. Spire flat in young individuals. Ventral surface flattened, the whorls coiled in one plane in mature specimens, three whorls visible, the umbilical whorls with a more or less acute carina. Sutures deep. In young and immature individuals the carina is sharp and the basal whorl about the umbilicus is raised to form an inverted V; whorls rounded ventrally in half grown and immature specimens. Aperture wider than high, long oval, the dorsal margin forming an inverted V near junction with body whorls; the ventral margin flat, straight, extending well beyond the position of the dorsal margin on the body whorl. Outer lip sharp, with slight thickening within, margined by reddish line. Surface of shell light or dark horn.

Shell Height	*Greater Diameter*	*Lesser Diameter*	*Aperture Height*	*Aperture Diameter*	
5.9	14.8	11.5	5.0	4.7	Holotype
6.0	13.0	10.8	5.0	4.1	Paratype
5.8	14.0	11.9	4.9	4.5	Paratype
5.4	11.0	8.6	4.8	3.5	Immature
4.9	10.2	8.0	4.2	3.3	Immature

Helisoma trivolvis marshalli differs from *fallax* in that the new variety has the body whorls more expanded toward the aperture; the dorsal depression is smaller; color is light or dark horn, not greenish; the aperture is wider and more ovate.

Type Locality. Washington, D. C.

Type Material. Collected by Foreman, deposited in United States National Museum, Accession no. 124989. Holotype on plate 87 as fig. 13; paratypes as figs. 11 and 12; figs. 14 and 15 of immature shells.

In addition to the type locality, *H. t. marshalli* has been identified in collections from various localities in Maryland, New York, New Jersey, and Virginia.

Helisoma campanulatum dalli, New Variety

Plate 111, figs. 12, 13, 15, 16

Shell resembling *michiganense* in the low axial height, but the body whorl is irregularly coiled and overlaps the penultimate whorl. Five whorls, upper whorls irregular; blunt carina on upper whorls. Four whorls showing on base, base 'reamed out' similar to that of *rudentis*, and whorls irregular. Umbilicus much smaller than in *rudentis* and also smaller than in *michiganense*. Lower whorls rounded. Sculpture and aperture as in *michiganense*.

Shell Height	*Maximum Diameter*	*Lesser Diameter*	*Aperture Height*	*Aperture Diameter*	
6.2	15.0	11.6	5.5	4.0	Holotype
5.4	14.1	11.0	4.7	4.0	Paratype
5.5	14.1	11.5	5.0	3.6	Paratype
6.1	14.9	11.6	5.3	4.0	Paratype

Type Locality. Anticosti Island, Quebec, Canada.

Type Material. Collected by Dr. J. Schmitt, deposited in United States National Museum, Accession no. 162724. Holotype, plate 111, fig. 12; paratypes, figs. 13, 15, 16, five others not figured.

Differs from other varieties in irregularly coiled body whorl which conspicuously overlaps the preceding whorls. Base is not excavated, but whorls are irregularly coiled as in spire. Axial height less than in *rudentis*.

Helisoma campanulatum dalli is known only from marl deposits.

Helisoma campanulatum pleistocenicum, New Variety

Plate 110, figs. 21-26

Shell small, whorls four, the inner spire whorls tightly coiled and gradually increasing in diameter, the last whorl rapidly increasing in diameter. The spire depression occupies about thirty per cent of the greater diameter of the shell while in *campanulatum campanulatum* it occupies about forty per cent of the greater diameter of the shell. Sutures well impressed. Base with two to two and one-half whorls visible, the whorls tumid. Umbilicus large for the size of the shell. Aperture strongly campanulate, the campanulation beginning a considerable distance back of the aperture.

The small diameter of the spire depression and the rapidly enlarging body whorl serve to distinguish this variety from all other forms of *campanulatum*. This form is distinctly different from the Pleistocene *campanulatum* of the middle west.

Type Locality. White Pond, Marlsboro, Warren Co., New Jersey.

Type Material. Holotype (figured on plate 110, fig. 21) and eight paratypes (five shown on plate 110, figs. 22-26) are in the Lea Collection in the United States National Museum, Accession no. 121195.

Helisoma campanulatum rideauense, New Variety

Plate 109, figs. 21-24

Shell very large, of five whorls, spire flattened, the inner whorls raised slightly above the body whorl; sutures deeply marked. Base with three to four whorls visible, rounded, in same plane, not reamed out as in *dalli* and *rudentis;* sutures well marked and whorls rounded. Umbilicus small, deep. Aperture as in *campanulatum*. Sculpture of heavy, evenly spaced riblets, but not as heavy as in *wisconsinense;* about as in some individual shells of *campanulatum*. In the following table the measurements were taken just behind the aperture, which is constricted and then dilated.

Shell Height	*Greater Diameter*	*Lesser Diameter*	*Aperture Height*	*Aperture Diameter*	
6.5	19.6	15.0	6.5	6.0	Holotype
7.0	18.5	14.1	6.5	5.1	Paratype
7.0	18.0	14.0	6.3	5.1	Paratype
6.8	17.5	13.0	6.3	5.4	Paratype

H. c. rideauense differs from *michiganense* in the former's larger size, smaller umbilical opening, and greater axial height. Surface is dull, not shiny, caused by the heavy sculpture. Color bright horn. The aperture is more distinctly campanulate than in *michiganense*.

Type Locality. Rideau River, Ottawa, Canada.

Type Material. Five specimens, collected by F. R. Latchford, deposited in the United States National Museum, Accession no. 346627. The holotype is shown on plate 109, fig. 21; paratypes, figs. 22-24.

GENUS *Parapholyx*

Parapholyx effusa dalli, New Variety

Plate 115, figs. 27-30

Three whorls, rounded. Color greenish horn. Spire slightly raised, sutures well marked, deep on last whorl. Sculpture of strong, erect, membranous ribs, thirteen to fifteen on body whorl, equidistant or widely spaced. Very fine lines of growth between ribs, spiral lines obsolete. Ribs usually absent on spire whorls. The ribs produce spaced, vertical depressions inside aperture. Aperture rounded, acute below. Columella narrow, concave, either completely closing the umbilicus or leaving a small narrow and long chink. A thin wash of callus on the parietal wall.

Shell Height	*Greater Diameter*	*Lesser Diameter*	*Aperture Height*	*Aperture Diameter*	
4.9	5.0	4.8	3.9	3.3	Holotype
5.0	5.0	5.0	4.0	3.3	Paratype
5.0	6.0	5.0	4.1	3.2	Paratype

Parapholyx effusa dalli differs from all other forms of the genus in the presence of membranous ribs which stand up, either at an angle or vertically, as leaf-like frills, very thin and easily broken off. The ribs in *costata* and other costate forms of the genus (as costate specimens of *klamathensis* from Klamath Falls) are simply rounded ribs, enlargements of the lines of growth. These do not affect the inside of the aperture. In *dalli*, on the contrary, the ribs appear as vertical creases on the inside of the aperture. Some individuals of *costata* may have slightly membranous ribs, but these are never like those of *dalli*.

Type Locality. Klamath Falls, Oregon.

Type Material. Seventeen specimens, collected by Henshaw, are deposited in the United States National Museum, Accession no. 219749. The holotype is figured on plate 115 as fig. 27; paratypes as figs. 28-30.

Parapholyx klamathensis sinitsini, New Variety

Plate 123, figs. 2-10

Shell similar to that of *klamathensis* but smaller, more globose; the shell thicker and more solid. Spire more elevated than in typical *klamathensis*; aperture rounder, not as effuse; columella callus heavier, more tightly appressed to the columella. The umbilicus usually closed, rarely having a small chink. Color brownish horn, never greenish. Sculpture heavier than in *klamathensis*, growth lines more distinct, in a few specimens rib-like. Interior of aperture reddish-brown. Lip bordered internally by a white margin which in old specimens forms a thickened callus. In contrast, *klamathensis* of typical variety has a thin lip without a callus. Columellar callus white. Whorls three. Some specimens with diagonal markings like pores. Aperture angulate below, as in *klamathensis*, but not markedly angular in some specimens.

Shell Height	*Greater Diameter*	*Lesser Diameter*	*Aperture Height*	*Aperture Diameter*	
6.4	7.0	5.0	4.5	4.0	Holotype
5.6	7.1	4.4	4.3	4.3	Paratype
7.1	8.2	6.0	5.0	4.8	Paratype
5.6	6.8	4.5	4.0	3.6	Paratype
5.6	6.6	5.4	3.8	3.8	Paratype

Type Locality. Bercley Spring, fourteen miles north of Klamath Falls, Oregon.

Type Material. Five specimens, of which one is designated as holotype and the four others as paratypes, are deposited in the United States National Museum, Accession no. 531029. The holotype is shown on plate 123 as fig. 2; two paratypes on the same plate as figs. 3 and 4. A series of specimens from the same locality, collected by Mrs. L. Sinitsin, are accessioned in the United States National Museum, no. 531064. The individuals of this last named series are designated as locotypes of the new variety.

Parapholyx klamathensis sinitsini is a form smaller than the typical *klamathensis*. The two forms have the same columella and angular base of aperture. The new variety has a higher spire than the typical form and the shell is more globose. Some individuals with diagonal ridges resemble *diagonalis* from Crater Lake but in that form the columella is wider, more concave and flatter and the aperture is more effuse. The spire of the new variety varies from flat to elevated depending upon the deflection of the aperture. *Sinitsini* has about the same size as *Parapholyx solida optima* but that form has a flat spire and a different aperture, especially in the region of the columella.

This variety is named for Mrs. L. Sinitsin.

Parapholyx pusilla, New Species

Plate 117, figs. 1-6

Shell small, with three whorls, scalariform, the second whorl standing on the body, turban-shaped; sutures distinct. Aperture roundly ovate, lips simple, lower lip rounded at base. Columella callus narrow, not expanded, separated from the columella region where it often projects leaving a distinct umbilical chink. Aperture continuous by the presence of a parietal callus. Sculpture coarse, often costate.

Shell Height	*Maximum Diameter*	*Aperture Height*	*Aperture Diameter*	
4.0	5.0	2.3	2.3	Holotype
4.5	4.3	2.5	2.1	Paratype
4.5	4.5	2.4	2.4	Paratype

Type Locality. Six miles west of Pyramid Lake, Washoe County, Nevada.

Type Material. One hundred twenty-five specimens taken from a Pleistocene deposit by Elbert Howard, are deposited in the United States National Museum, Accession no. 308925. The individual from this lot chosen as holotype is shown on plate 117 as fig. 1. Figures 2 to 5 on the same plate are of paratypes.

Parapholyx pusilla differs from *Parapholyx nevadensis* in that the new species has a more rounded shell, with elevated and turban-shaped second whorl and the lower portion of the aperture lacks the sharp angle caused by the columellar callus in *nevadensis*. The new species differs from *P. solida* in the form of the spire, aperture and base of lip.

This is apparently an extinct species.

GENUS *Planorbula*

Planorbula smithii, New Species

Plate 118, figs. 11-12; plate 119, figs. 10-12

Shell resembling that of *wheatleyi* but larger, of five whorls, the spire whorls in the same plane and not so sunken toward the nucleus as in *wheatleyi;* no dorsal ridge as is developed in *wheatleyi;* umbilical opening with the whorls rounded, not flat sided and without the sharp carina distinctive of *wheatleyi*. Crest behind aperture not as heavy or as thickened as in *wheatleyi*. Sculpture of distinct spiral lines. Apertural lamellae as in *armigera* not as in *wheatleyi*.

Shell Height	*Greater Diameter*	*Lesser Diameter*	*Aperture Height*	*Aperture Diameter*	
3.0	7.1	5.5	2.0	1.3	Holotype
2.8	7.0	5.0	1.7	1.0	Paratype
2.9	6.9	5.8	1.5	1.0	Paratype

Type Locality. Jackson County, Alabama.

Type Material. Fifteen specimens, collected by H. H. Smith, are deposited in the United States National Museum, Accession no. 321196. The holotype is figured on plate 119, as fig. 10; paratypes on the same plate as figs. 11 and 12.

Externally *Planorbula smithii* resembles *wheatleyi* but the newly recognized species is readily distinguishable by the absence of the L-shaped second labial lamella. *Smithii* is larger than *crassilabris* and has a much heavier lip callus. It somewhat resembles *indianensis* but lacks the axial height of that race and the latter also lacks the lip callus of *smithii*.

Planorbula smithii is named for Herbert H. Smith.

GENUS *Menetus*

Menetus coloradoensis, New Species

Plate 122, figs. 23-25

Shell acutely lenticular, flattened, with three whorls. Color blackish brown. A rounded carina on the periphery which is impressed both above and below the periphery a short distance from the edge. The carina is not acute (excepting in immature specimens) but is bluntly rounded. Upper surface flattened, with deeply impressed sutures. The whorls tumid near the sutures. Base convex near the suture but flattened toward the periphery. Basal whorls separated by deep sutures. Sculpture ranging from coarse growth lines to evenly spaced ribs, spiral lines very fine. Some specimens begin with coarse growth lines and end with ribs. Aperture triangular, upper and lower lips arching downward and upward to meet the periphery which is not sharp but is narrowly rounded. Upper lip projects just above the periphery and is flat, but lower lip has a long columellar region and is convex. Aperture much wider than high, purplish within and somewhat pearly. Umbilicus rather wide and deep.

Shell Height	*Greater Diameter*	*Lesser Diameter*	*Aperture Height*	*Aperture Diameter*	
1.1	4.0	3.6	1.0	1.6	Holotype
1.0	4.6	4.0	0.9	1.8	Paratype
1.0	4.1	3.6	0.9	1.5	Paratype

Type Locality. Swamp at head of Eldora Lake, near Eldora, Colorado.

Type Material. Deposited in the University of Colorado Museum, Accession no. 10114. Holotype shown as fig. 25 on plate 122; two paratypes as figs. 23 and 24 on same plate.

Menetus coloradoensis differs from *exacuous* in the pinched nature of the periphery, the swollen or tumid base near the suture, and the heavy (in some instances, costate) sculpture. *Menetus exacuous megas* has a pinched periphery, but in this variety the base and sculpture are as in typical *exacuous*. The new species is nearest to *kansasensis* but differs in having a more tumid base and a different type of rib-sculpture.

Menetus cooperi crassilabris, New Variety

Plate 121, figs. 19-21; plate 122, fig. 13; plate 123, fig. 26

Specimens like *cooperi* but with heavy callus just within lip. Shell of four whorls. Heavy spiral sculpture. Whorls usually rounded but with slight indication of carina at shoulder as in *cooperi*. Several spiral ridges below shoulder, and base often malleated as in *cooperi*. Umbilicus with rounded edges. Aperture rounded, not usually modified by carina. Most shells are smaller than *cooperi*.

Shell Height	*Greater Diameter*	*Lesser Diameter*	*Aperture Height*	*Aperture Diameter*	
2.1	5.4	4.0	1.6	2.0	Holotype

Type Locality. Seattle, Washington.

Type Material. Twenty-four specimens are in the United States National Museum bearing Accession no. 214590, one of which is selected as holotype and the remaining specimens become paratypes. Holotype is shown on plate 121 as fig. 20; and one paratype as fig. 19.

Of the twenty-four specimens in the type lot all but one had a callus, this one being doubtfully referred to *cooperi*. The original labels of some lots in the National Museum carried identification as *oregonensis*. Evidently this was based upon the presence of a lip callus. However, *crassilabris* lacks a peripheral carina and cannot be allied with *oregonensis*. Other collections have been determined as *centervillensis*, but the umbilicus is distinctly different in *crassilabris*.

Menetus cooperi crassilabris has been identified in collections from Colma, San Mateo County, California; Oakland, California; Portland, Oregon; Lake Washington at Seattle, Washington; and mountain swamps at Olga, Washington. The last named were erroneously identified as *Menetus cooperi calioglyptus*. One collection from Oakland was associated with typical *cooperi*.

Menetus cooperi planospirus, New Variety

Plate 122, figs. 3-6

Shell with three whorls, of yellowish horn color. Upper surface flat, the whorl bordered by a raised revolving ridge at the edge. Spire whorls sunken below general level. Base convex. Umbilicus deep, about one-fourth the diameter of the shell. Peripheral ridge stands out and elevated above the shell as a cord. Aperture modified by carina. Sculpture of rather coarse growth lines, crossed by heavy spiral lines.

Shell Height	*Greater Diameter*	*Lesser Diameter*	*Aperture Height*	*Aperture Diameter*	
3.3	8.0	7.0	3.0	3.0	Holotype
3.0	6.5	5.6	2.6	3.0	Paratype
2.6	5.9	5.0	2.0	2.0	Paratype
2.5	5.9	5.0	2.2	2.4	Paratype

Type Locality. Orcas Island, Puget Sound, Washington.

Type Material. A collection of thirty-six specimens, taken by W. H. Souther, is deposited in the Museum of Comparative Zoology, Harvard University, Accession no. 31583. One of these, designated as holotype, is shown on plate 122 as fig. 5, and three paratypes are shown on the same plate as figs. 3, 4, and 6.

Menetus cooperi planospirus is characterized by its very flat spire and the presence of a raised carina placed at the upper edge of the whorl. It differs from *Menetus cooperi multilineatus* in the position of the carina, and in having a flat rather than a convex spire.

Menetus dalli, New Species

Plate 140, figs. 22-24

Shell small, lenticular, with a bluntly angular periphery. Upper surface flatly convex, three whorls visible, sutures deeply incised. Lower surface flatly convex, the umbilical or spire region small, occupying one-sixth of the diameter of the shell. The lower surface is swollen over the umbilicus. The lower surface has a somewhat pinched appearance, with an indistinct, impressed line bordering the periphery. Sculpture of coarse growth lines radiating from the periphery. At regular intervals there are larger rib-like projections, with four to six of the smaller ribs between. All the ribs extend into the spire cavity, which is deep. The sculpture is more conspicuous on the base of the shell. The umbilical (upper) side has the fine riblets more regularly spaced without the larger ones. This sculpture is most apparent on the large holotype specimen. There are likewise fine, impressed spiral lines. Aperture triangular, wider than high. Columella almost vertical. Lip thickened by callus, which includes the columellar and parietal walls. The right side of the aperture is acute and pinched.

Shell Height	*Greater Diameter*	*Lesser Diameter*	*Aperture Height*	*Aperture Diameter*	
1.5	4.0	3.2	1.1	1.6	Holotype
1.4	3.2	2.7	1.0	1.5	Paratype
1.2	2.9	2.2	0.9	0.9	Paratype

Type Locality. Caloosahatchie River, Florida.

Type Material. Pliocene fossils, collected by W. H. Dall, deposited in the United States National Museum, Accession no. 112556. Holotype figured on plate 140 as Fig. 22; paratypes as figs. 23, 24.

Menetus dalli differs from *alabamensis* in the former's smaller and deeper spire depression and its heavier growth lines forming riblets. It was identified by Dall (after whom the new species is named) as *exacuous*. It was associated with *dilatatus* and *alabamensis arus*.

Menetus dilatatus floridensis, New Variety

Plate 123, figs. 20-22

Shell small, of three whorls, slowly increasing in diameter. Color light horn. Body whorl forms a rounded obtuse angle as in *dilatatus*. Base flatly rounded. Spire depression wide, shallow, showing all of the whorls. Sculpture of fine growth lines crossed by fine spiral lines. Aperture rounded, not flaring. Outer lip thin. No callus on parietal wall.

Shell Height	*Greater Diameter*	*Lesser Diameter*	*Aperture Height*	*Aperture Diameter*	
0.9	2.5	2.1	0.8	1.0	Holotype
0.8	2.3	2.0	0.7	0.8	Paratype
0.8	2.0	1.6	0.7	0.7	Paratype

Type Locality. St. Johns River, Palatka, Florida.

Type Material. Collected by W. H. Dall. Deposited in the United States National Museum, Accession no. 37585. Holotype shown on plate 123 as fig. 20; paratypes as figs. 21 and 22.

Menetus dilatatus floridensis differs from typical *dilatatus* in the fact that the new variety has a smaller aperture which is rounded, not flaring; has rounded body whorl, without trace of angulation; and has wider, shallower spire depression, showing all of the whorls.

Menetus labiatus, New Species

Plate 121, figs. 9-11

Whorls three, rounded. Spire flattened, apex sunken. Base rounded, umbilicus broad and shallow, one-sixth the diameter of the shell. Whorls and umbilicus rapidly increasing in diameter. Aperture ovately rounded, the lip with a heavy internal rim of callus which joins a distinct parietal callus, making the lip in some specimens continuous. Umbilicus varies in depth. Sculpture of fine growth lines, crossed by fine spiral lines, although the latter may be absent in some specimens.

Shell Height	*Greater Diameter*	*Lesser Diameter*	*Aperture Height*	*Aperture Diameter*	
1.0	2.6	2.1	0.5	0.5*	Holotype
0.9	2.3	2.0	0.5	0.5	Paratype
1.1	3.1	2.6	0.6	0.5	Baker Coll., 2100
1.2	3.0	2.3	0.8	0.8	Baker Coll., 2100

*A heavy callus reduces the size of the aperture.

Type Locality. Terminal Island, Los Angeles County, California.

Type Material. Three specimens, collected by Eastman, are in the United States National Museum, Accession no. 190021. Designated holotype and paratypes illustrated on plate 121 as figs. 11 and 9, 10, respectively.

The type material was labelled as *centervillensis*. Taken in various southern California localities. Some large individuals of this species were collected from peat deposits by S. S. Berry, in Orange County, California. Two of these individuals, which have a heavy lip callus, are included as the third and fourth items in the above tabulation of shell characters (Baker Coll., no. 2100).

Menetus labiatus differs from *centervillensis* in the shape of the umbilicus and the aperture.

Menetus portlandensis, New Species

Plate 121, figs. 12-18

Shell less elevated than in *centervillensis*, the body whorl depressed, rounded on the periphery, not angled as in *centervillensis*. Spire flat, three and one-half whorls, sutures impressed. Color blackish to light horn, usually in the same shell. Base flatter than in *centervillensis;* the umbilicus wider, about one-fourth of the diameter of the shell. Aperture transversely ovate, wider than in *centervillensis* and not as nearly round. Slight callus on parietal wall. Sculpture of coarsely impressed spiral lines, distinct in all specimens examined.

Shell Height	*Greater Diameter*	*Lesser Diameter*	*Aperture Height*	*Aperture Diameter*	
1.4	4.0	3.3	1.1	1.2	Holotype
1.3	3.5	3.0	0.8	1.0	Paratype
1.1	3.3	2.6	0.8	1.0	Paratype

Type Locality. Tanner Creek, Portland, Oregon.

Type Material. A large collection of one hundred shells, collected by J. E. Benedict, is deposited in the United States National Museum, Accession no. 184182. The holotype is shown on plate 121 as fig. 12; six paratypes on the same plate as figs. 13 to 18.

The chief distinguishing characteristics of *Menetus portlandensis* are that the umbilicus is wider and shallower and the spiral lines on the shell are heavier than in other species of the genus.

This new species has also been taken in the vicinity of San Francisco, California, and at Astoria, Oregon. In the latter instance it was associated with specimens of *cooperi*.

ILLUSTRATIONS OF THE ANATOMY AND OF SHELLS

ANATOMICAL SYMBOLS USED ON THE PLATES

A, anus
AG, abdominal ganglion
AL, albumen gland
AO, aorta
AP, pulmonary vein
ARM, anterior retractor muscles
AU, auricle
B, bulbous termination of verge
BG, buccal ganglion
BP, buccal pouch
BR, buccal retractor muscle
BS, blind sac or caecum
BV, blood vessel
BW, body wall of gland
C, canal
CF, carrefour
CG, cerebral ganglion
CL, cilia
CM, columella muscle
CMC, cut portion of mantle collar and columella muscle
CR, crop
D, diaphragm
DA, duct from albumen gland
DC, duct of gland
DG, duct of preputium
DV, duct entering vergic sac
E, eye
EPI, epiphallus-like swelling
EUD, external opening of vas deferens
F, foot
FL, flagellum
FO, female opening
FOV, diverticula of ovotestis
FPR, diverticula of prostate
G, accessory gland
GA, gland appendage
GF, folds in wall of gland cavity
GL, penial gland
GN, ganglion
GR, growth lines
GW, wall of preputial sac
GZ, gizzard
H, head
HT, heart
IC, cavity of gland connecting with gland duct
IN, intestine or space for intestine on surface of albumen gland
J, jaw
K, kidney
L, lung
LJ, lateral jaw
LV, liver
M, mantle
MC, mantle collar
MO, male opening
MN, muscle of neck
MP, muscular pads or pillars in preputium (pilasters)
MR, muscular ridge or diaphragm
MS, suspensary muscles of verge
MT, mouth
N, nerve
NA, section through neck
NG, nidamental gland
NS, new shell forming
OC, outer cup of gland
OD, oviduct
OE, oesophagus
OLV, opening of liver duct into stomach
OT, ovotestis
P, pseudobranch
PA, vergic appendage
PC, pericardium
PD, duct of prostate
PF, prostate diverticula
PG, pedal ganglia
PL, pilasters
PP, papilla in preputium
PR, preputium
PRM, posterior retractor muscle
PRS, prostate
PS, pneumostome
PY, pyloris
R, rectum
RA, renal vein
RD, ridge
RK, ridge on kidney
RL, radula
RM, retractor muscle
S, spermatheca
SB, sarcobelum
SC, sperm canal
SD, spermatheeal duct
SG, salivary gland
SCO, opening of sperm canal
SJ, superior jaw
SH, shell
SK, saccular part of kidney
SM, supporting muscle
SO, ovisperm duct
SP, spermatophore
SPD, sperm duct
ST, stylet
STM, stomach
SV, seminal vesicle
T, tentacle
TK, tubular part of kidney
U, uterus
UO, external opening of ureter
UR, ureter
V, verge
VC, vergic sac
VD, vas deferens
VDV, vas deferens in vergic sac
VF, folds in vergic sac
VG, vagina
VGL, visceral ganglion
VL, velum
VM, muscle to vergic sac
VN, vein
VO, opening between vergic sac and preputium
VP, vergic papilla
VS, vergic sac
VT, ventricle
X, canal in penial gland

PLATE 1

Planorbis planorbis (Linn.)

From a pond 25 miles southeast of Warsaw, Poland; from A. Jankowski.

1. Entire genital system spread out. The dark spaces are folds in the anatomical preparation.
2. Penial complex with muscles.
3. Head and foot showing form of pseudobranch.
4. Vertical section through penial complex to show small size of verge.
5. Section through verge and vas deferens.
6. Junction of oviduct and vas deferens to form ovisperm duct and connection with albumen gland and carrefour.
7. Section through prostate, oviduct, and vas deferens showing a prostate canal separated from the vas deferens.
8. Section through ovotestis.
9. Section through ovotestis showing diverticula embedded in the liver cells.

Line near figure indicates 1 mm. in length

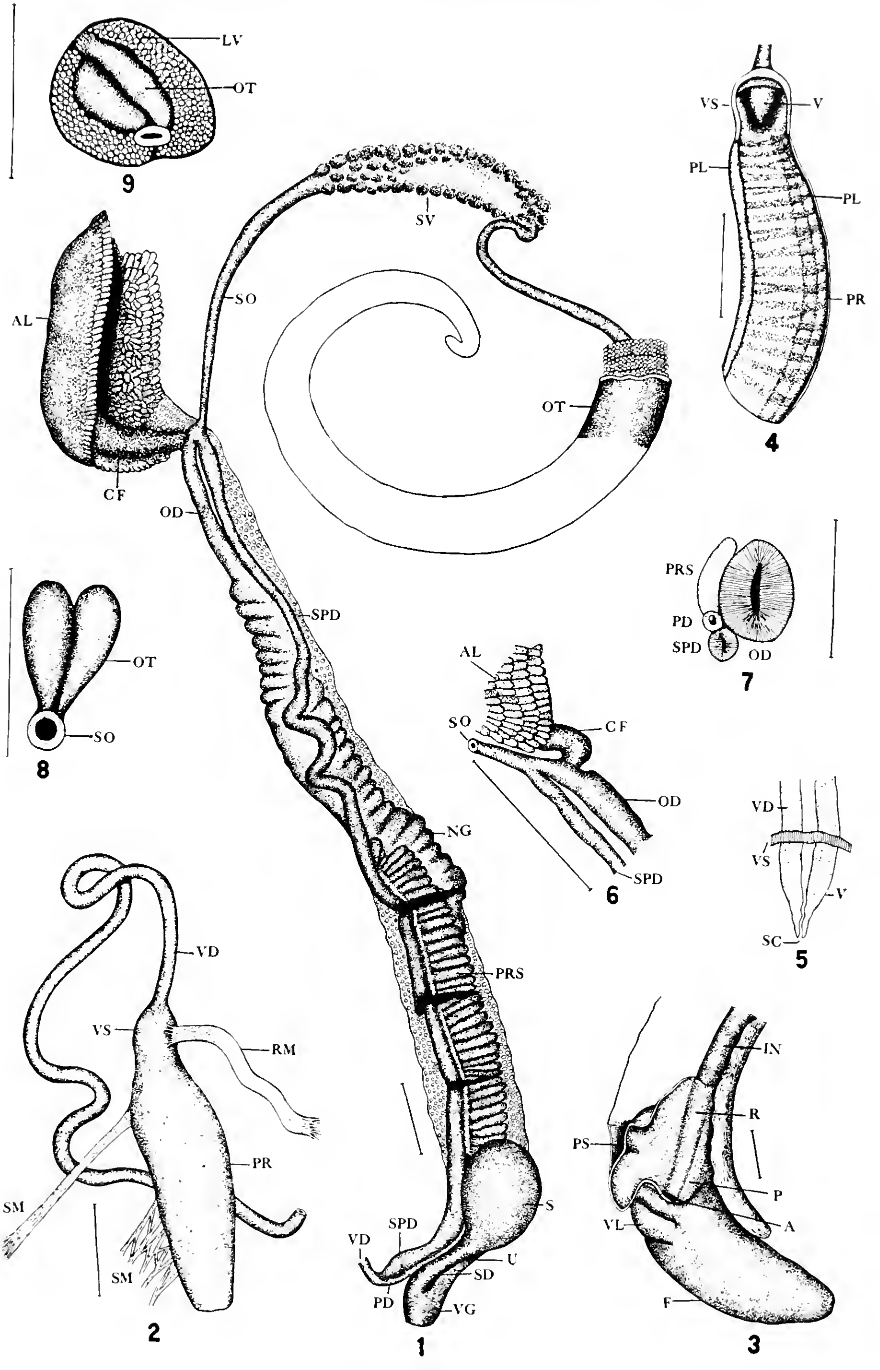
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PLATE 1

PLATE 2

Segmentina and *Hippeutis*

1–6. *Segmentina nitida* (Müller). From swamps on a meadow near Warsaw, Poland; from A. Jankowski.

1. Cross section of pilaster to which appendage is attached.
2. Vertical section of preputium showing position of gland-like appendage.
3. Upper view of cup of gland or appendage.
4. Vertical section of gland or appendage.
5. End of verge showing position of vergic appendage.
6. End of verge showing vergic appendage and outlet of sperm canal.

7–15. *Hippeutis complanatus* (Linn.). From pool in meadow in Jabtonna, 16 km. north of Warsaw, Poland; collected by A. Jankowski.

7. Two diverticula of ovotestis.
8. Cross section of prostate showing two canals, one for prostate (PD) and one for sperm duct (SPD).
9. Gland or appendage in preputium.
10. Outline of albumen gland (from above).
11. Upper part of vergic sac showing two flagella and the vas deferens.
12. Vertical section of penial complex showing relationship of verge, gland, or appendage, and flagella.
13. Head of animal showing form of pseudobranch and pneumostome.
14. Penial complex from the outside.
15. General dissection of genitalia omitting the penial complex.

Line near figure indicates 1 mm. in length. Line at left of fig. 12 also indicates size of figs. 3, 4, 5, 8, and 9. Figures 6 and 11 are greatly enlarged. Figure 14 has same magnification as fig. 15.

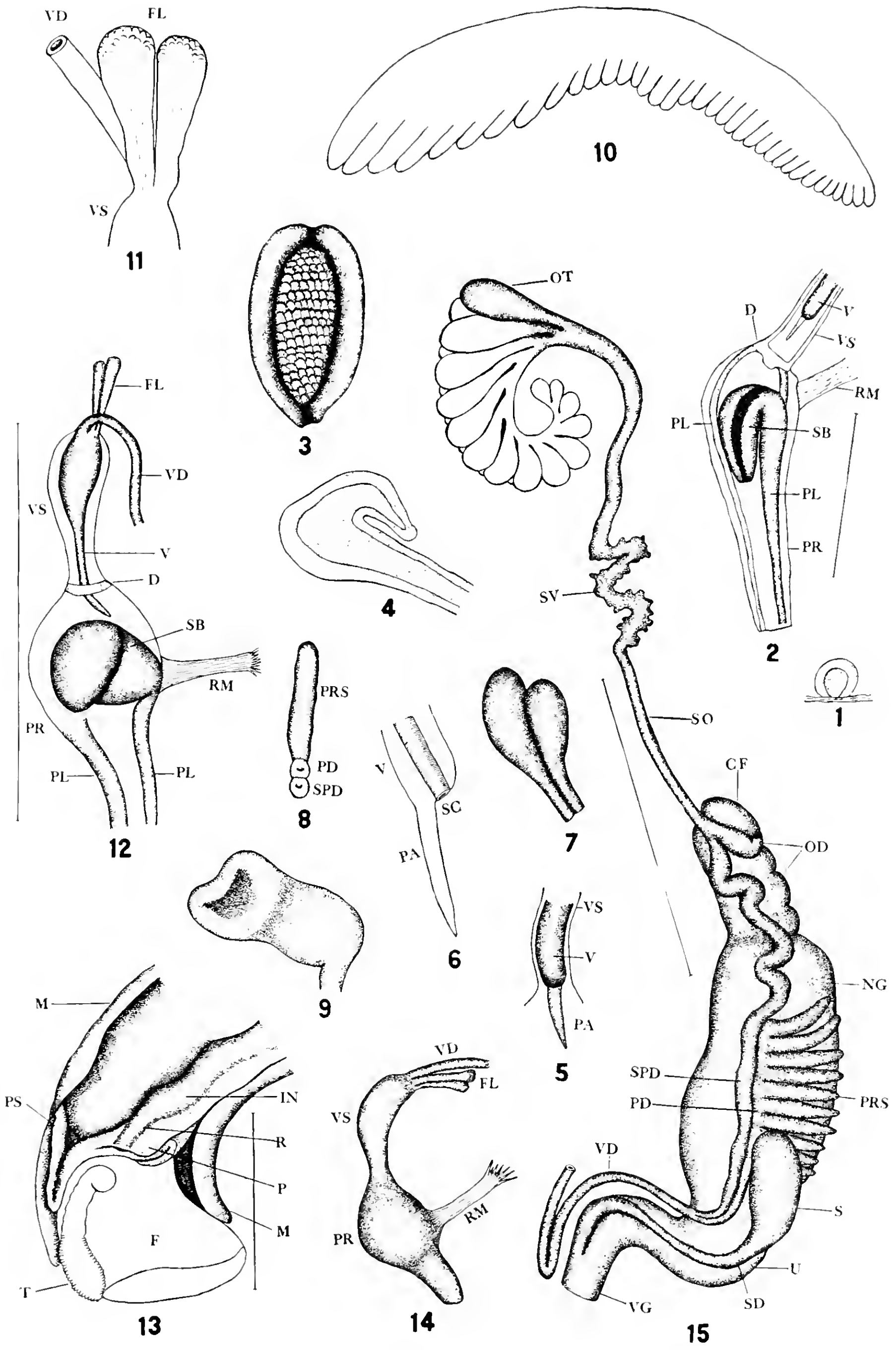
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PLATE 2

PLATE 3

Segmentina and *Bathyomphalus*

1–4. *Segmentina nitida* (Müller). From meadow near Warsaw, Poland; from A. Jankowski.

1. External view of penial complex.
2. Hermaphrodite complex.
3. Cross section of prostate and ducts of prostate and vas deferens.
4. Head showing position and form of pseudobranch.

5–10. *Bathyomphalus contortus* (Linn.). From Drewnica, a turfy ground 4 km. northeast of Warsaw, Poland; collected by A. Jankowski.

5. Head showing position and form of pseudobranch.
6. Pseudobranch showing position of rectum.
7. Cross section of ovotestis.
8. Cross section of prostate showing prostate duct separate from sperm duct.
9. Penial complex from the outside.
10. Hermaphrodite complex dissected and spread out.

Line near figure indicates 1 mm. in length. Line at left of fig. 7 also represents size of figs. 3 and 8. Figure 9 is same magnification as fig. 10.

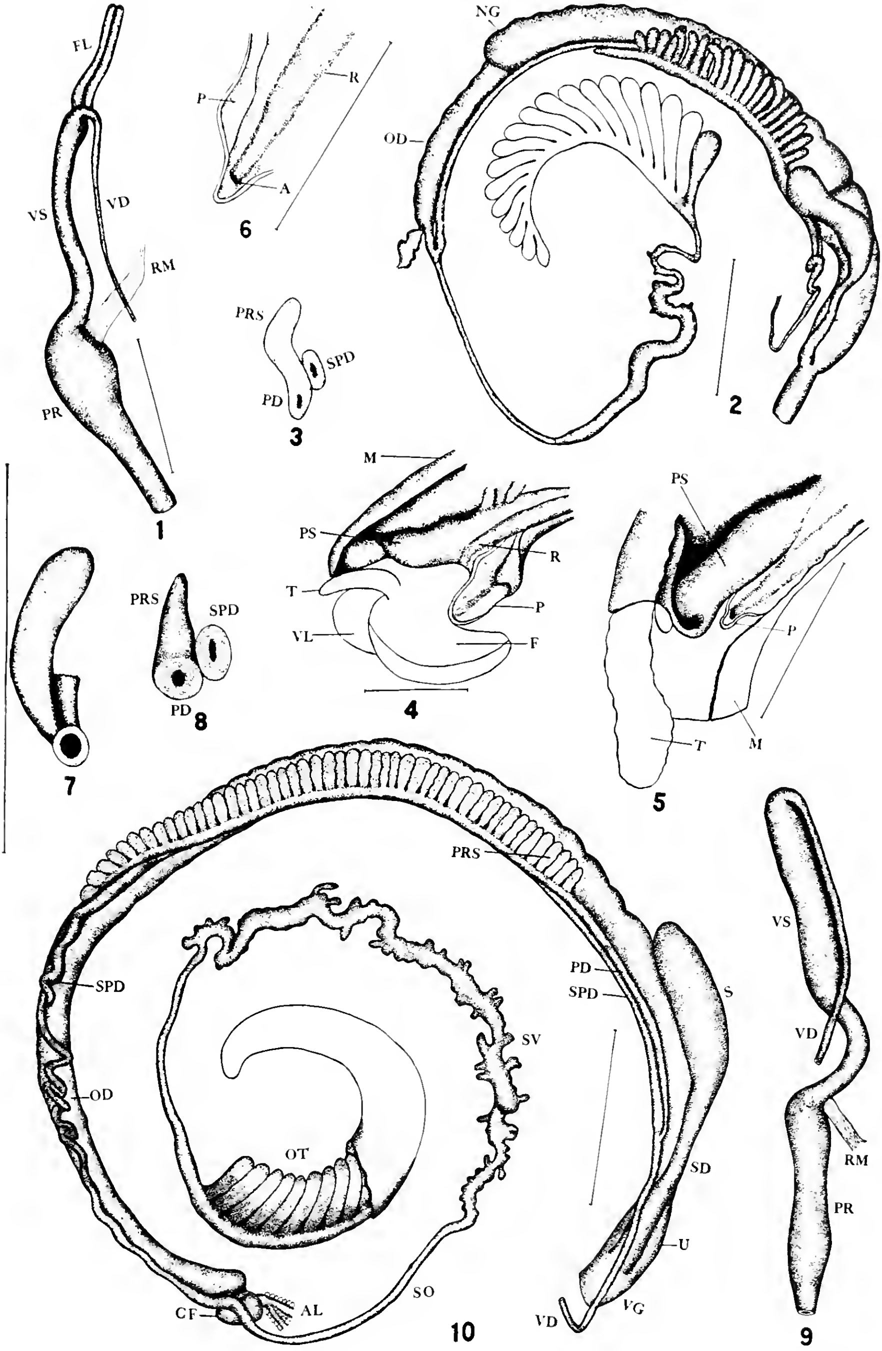
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PLATE 3

PLATE 4

Pingiella peipinensis (Ping and Yen). New genus

Peiping, China; from Fan Memorial Institute, Peiping, China.

1. Albumen gland showing position of stomach.
2. Portion of penial gland showing position of ducts.
3. Terminal end of penial gland, under side.
4. Terminal end of penial gland, view from side showing internal canal.
5. Penial complex showing long duct of penial gland and long and peculiarly formed appendages.
6. Preputium cut open to show penial gland.
7. Preputium cut open to show penial gland and relationship of long duct.
8. Verge in vergic sac.
9. General dissection of genitalia, the organs separated and extended.

Line near figure indicates 1 mm. in length. Figures 3 and 4 are greatly enlarged.

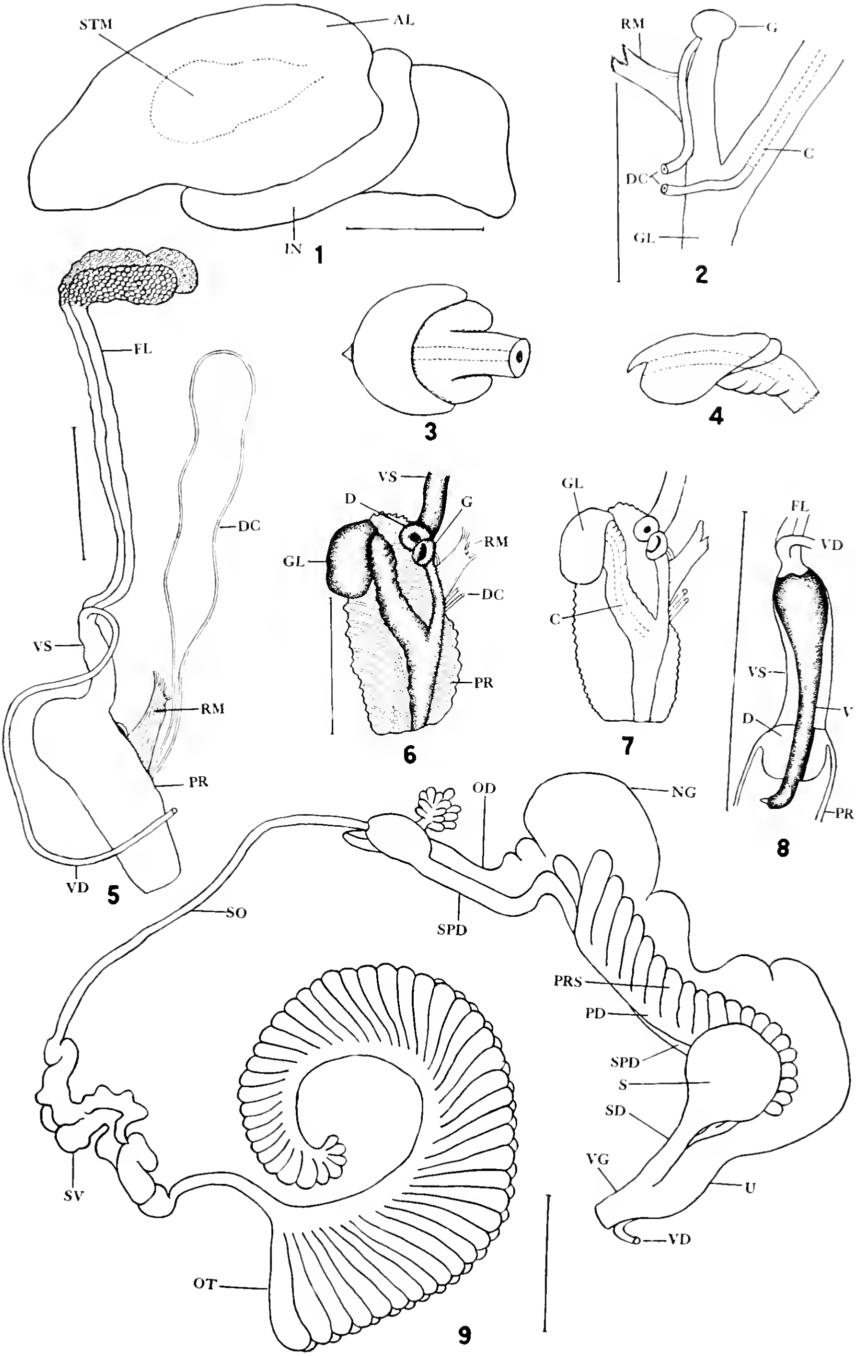
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PLATE 4

PLATE 5

Pingiella and *Polypylis*

1, 5. *Pingiella peipinensis* (Ping and Yen), new genus. Peiping, China.
  1. Region of the pseudobranch.
  5. Spermatheca of different shape.

2–4, 6, 7. *Polypylis hemisphaerula* (Benson). Peiping, China; from Fan Memorial Institute.
  2. Outline of albumen gland.
  3. Region of the pseudobranch.
  4. Section through prostate and ducts.
  6. Distal end of verge showing outlet of canal at the side.
  7. Entire genitalia dissected and organs separated.

Line near figure indicates 1 mm. in length. Figure 6 is greatly enlarged.

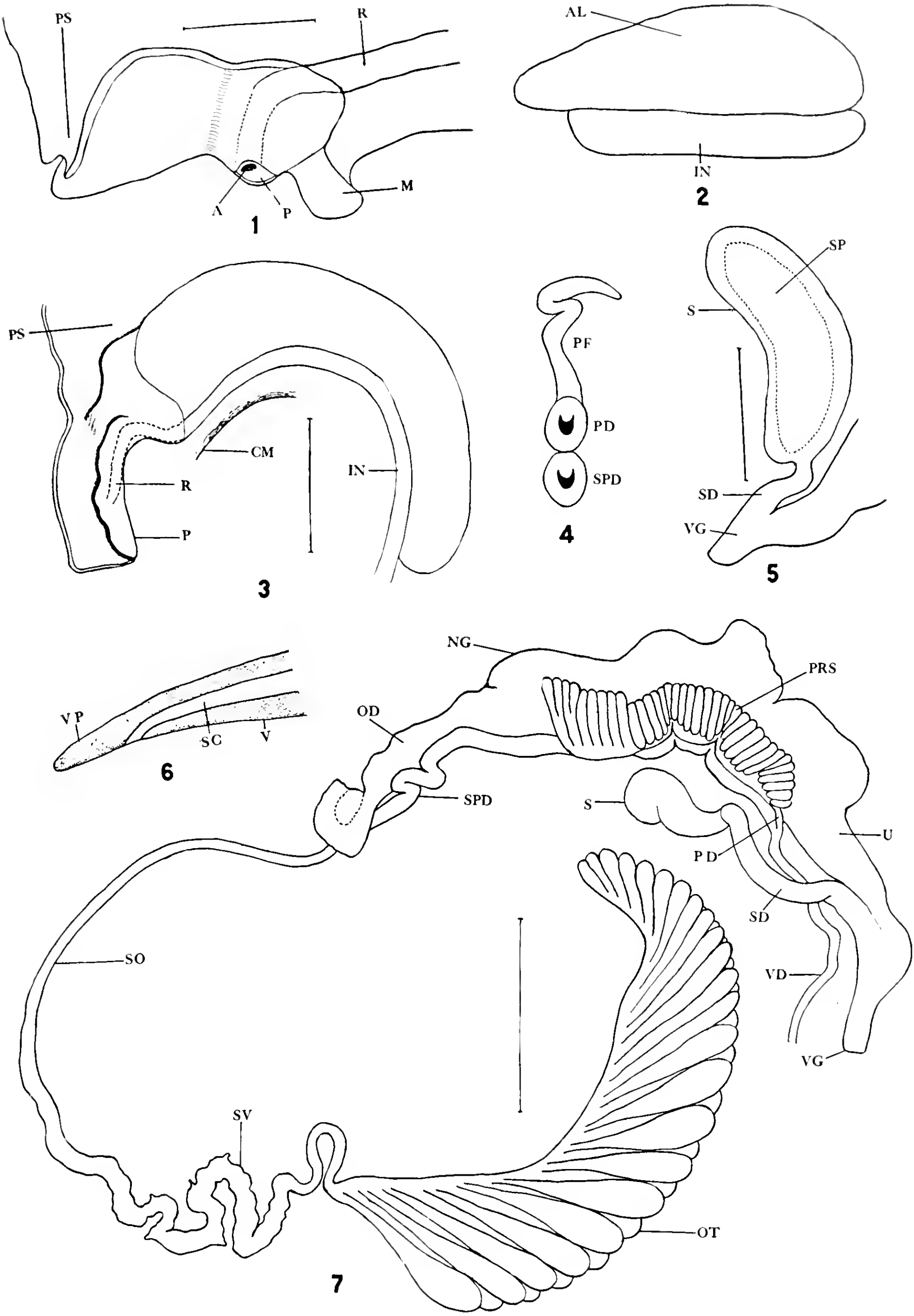
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PLATE 5

PLATE 6

Anisus vortex and *Anisus spirorbis*

1–4, 6. *Anisus vortex* (Linn.). From stream in meadow in Jabtonna, 18 km. northeast of Warsaw, Poland; collected by A. Jankowski.

1. Penial complex showing long and narrow vergic sac.
2. Stylet, dry and somewhat crushed.
3. Section through prostate and sperm canal showing two ducts.
4. Section through upper portion or preputium and vergic sac, showing papilla in preputium, stylet and outlet of sperm canal at the side of the verge.
6. Pseudobranch showing relationship to rectum.

5, 7–13. *Anisus spirorbis* (Linn.). From a trench in Struga, 12 km. northeast of Warsaw, Poland; collected by A. Jankowski.

5. Stylet at end of verge with outlet of sperm canal at side of verge.
7. Two diverticula of ovotestis.
8. Cross section through prostate and oviduct.
9. Albumen gland, upper part.
10. Penial complex in vertical section showing stylet, muscular papilla, and pilasters.
11. Foot, pseudobranch, and pneumostome.
12. Entire genitalia dissected and separated.
13. Penial complex of specimen with vergic sac shortened and club-shaped.

Line near figure indicates 1 mm. in length. Figures 2 and 5 are greatly enlarged.

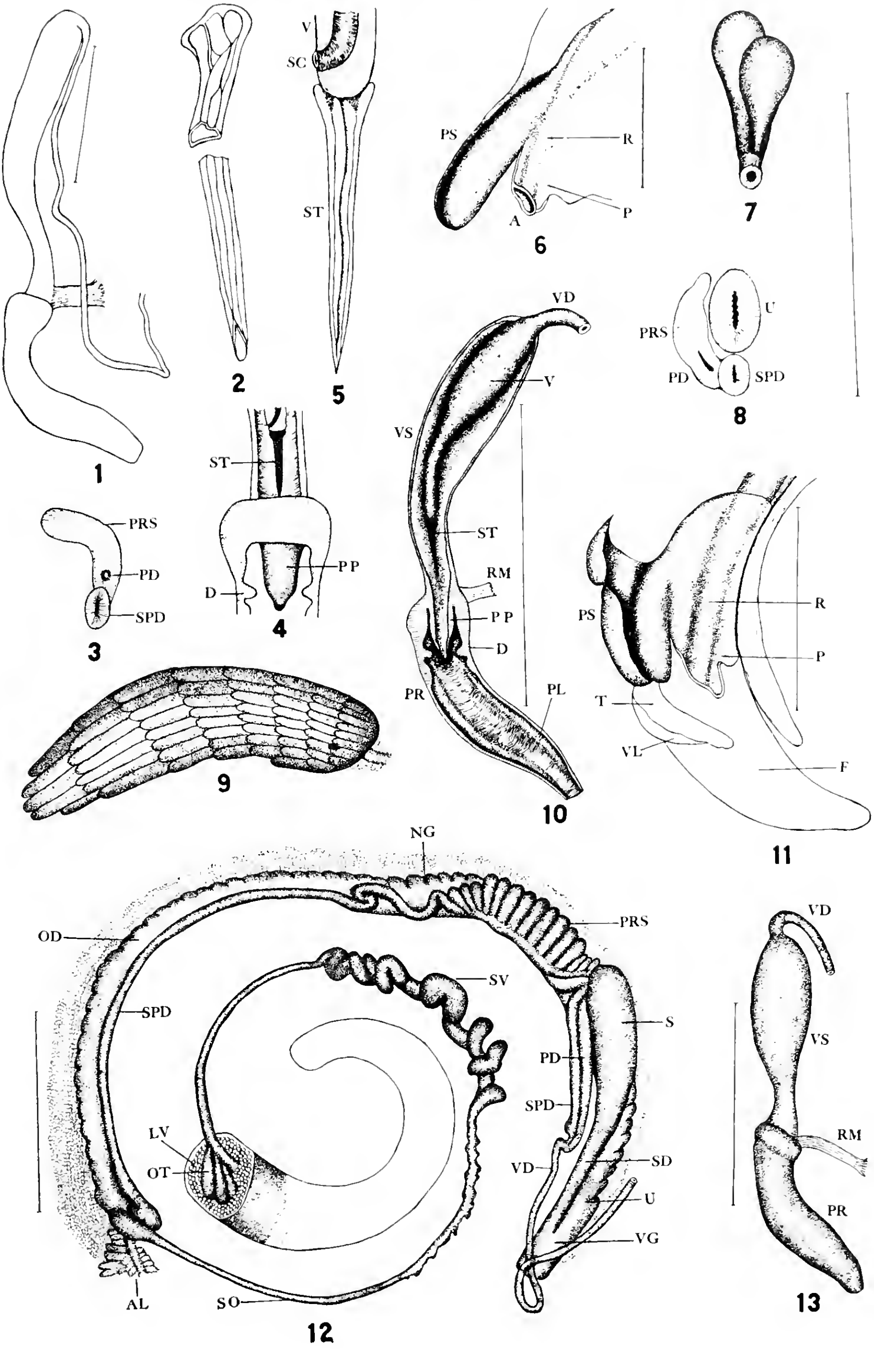
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PLATE 6

PLATE 7

Anisus leucostomus and *Anisus septemgyratus*

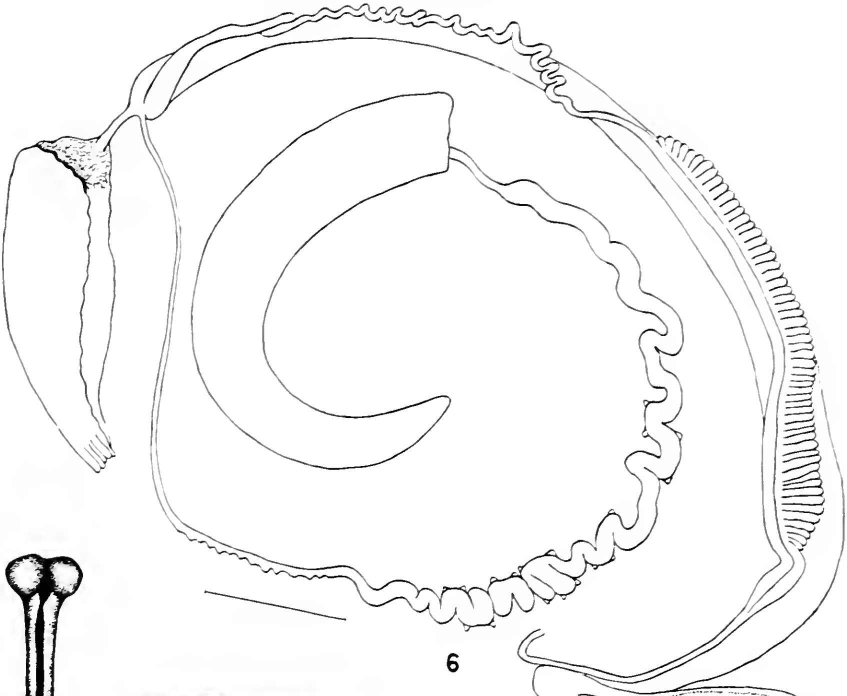
1–5. *Anisus leucostomus* (Millet). From small pond in Bielany Park, Warsaw, Poland; collected by A. Jankowski.

1. Foot, pseudobranch, and pneumostome.
2. Genitalia dissected and the organs separated. Figure under seminal vesicle shows this organ stretched out.
3. Muscular ring or diaphragm in upper part of preputium showing papilla with stylet protruding.
4. End of oviduct and vas deferens showing where ovisperm duct joins the oviduct and vas deferens.
5. Stylet.

6. *Anisus septemgyratus* (Ziegler). From turfy meadow in Drewnica, 4 km. northwest of Warsaw, Poland; collected by A. Jankowski.

6. Outline of genitalia exclusive of the penial complex.

Line near figure indicates 1 mm. in length. Line at left of fig. 5 is only for size of figs. 3 and 4.



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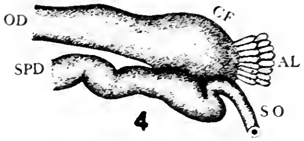

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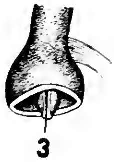

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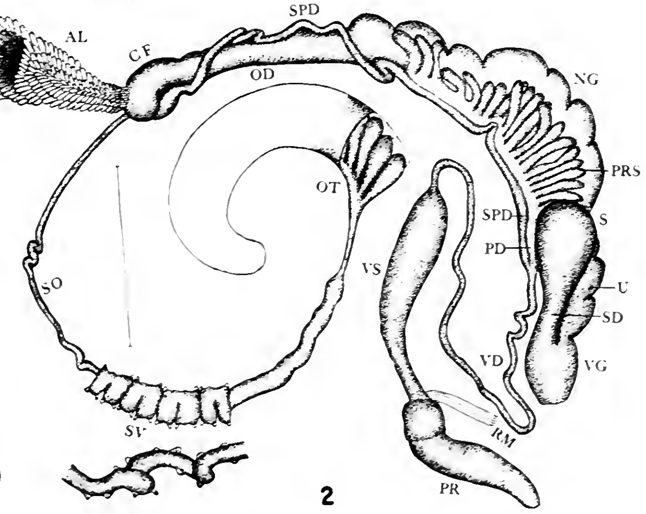

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PLATE 7

PLATE 8

Intha and *Polypylis*

1–8, 11. *Intha capitis* Annandale. From Inle Lake, South Shan State, Burma, India; collected by Dr. N. Annandale.

- 1. Outline of albumen gland.
- 2. Pseudobranch and rectum.
- 3. Head of animal showing tentacles and eyes.
- 4. Distal end of verge.
- 5. A spermatophore.
- 6. Penial complex, dorsal view.
- 7. Cross section of penial gland.
- 8. Vertical section of penial complex showing verge, gland, and duct.
- 11. Ventral view of entire genitalia, showing the large size of the flagella.

9, 10. *Polypylis hemisphaerula* (Benson). Peiping, China; from Fan Memorial Institute.

- 9. Section of penial complex cut open to show verge, diaphragm and pilasters.
- 10. Penial complex, ventral view. Small figure at right shows insertion of vas deferens at junction of vergic sac and flagellum. Dorsal view.

Line near figure indicates 1 mm. in length. Figures 1, 5, 6, and 7 have same magnification as fig. 11. Figure 4 is greatly enlarged.

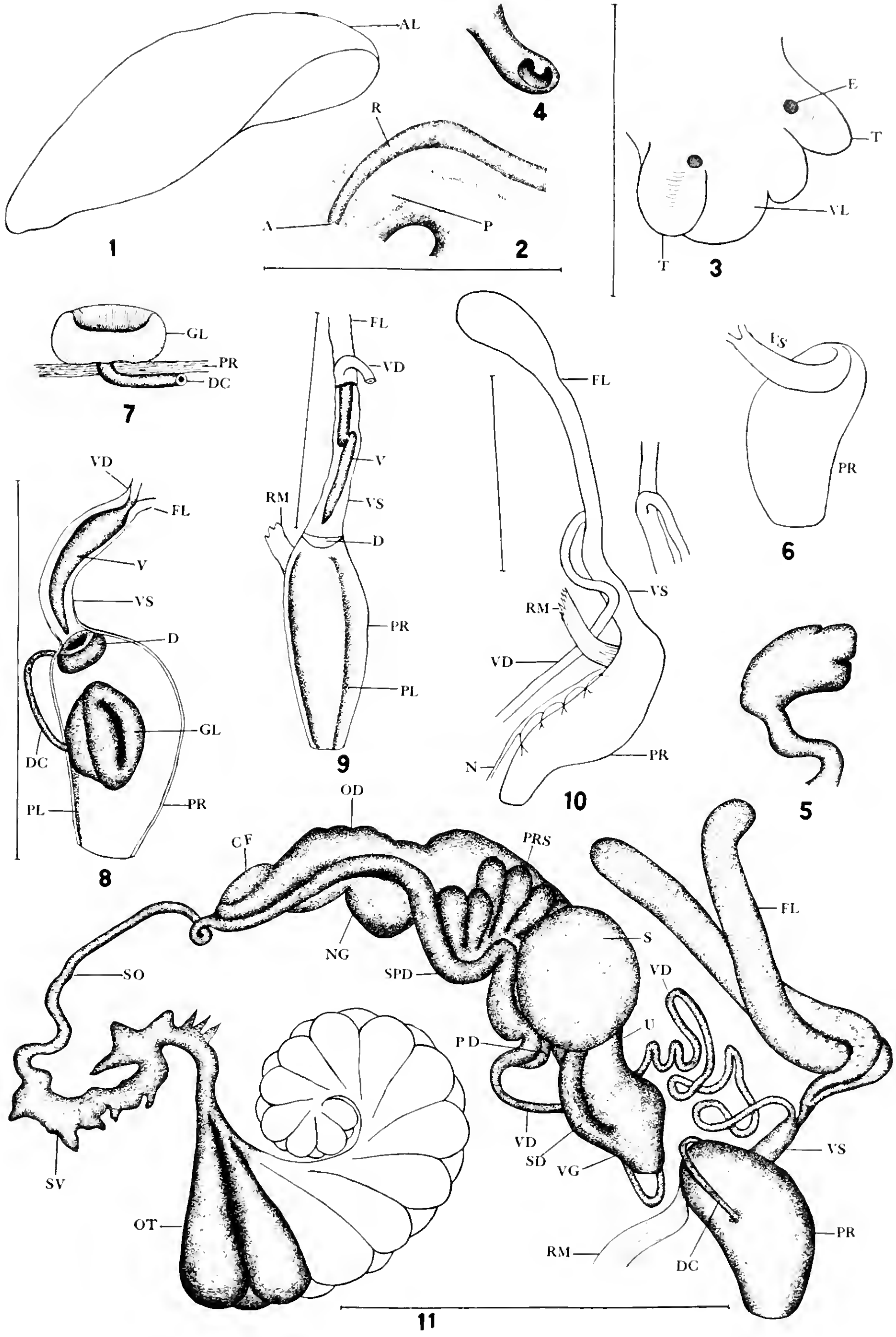
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PLATE 8

PLATE 9

Drepanotrema and *Australorbis*

1–3. *Drepanotrema anatinum* (Orbigny). From Viejo, Puerto Rico; from Dr. W. A. Hoffman.
  1. Penial complex showing form of flagellum.
  2. Genitalia dissected and organs separated. Note the small number of prostate diverticula.
  3. Head and foot showing form of pseudobranch.

4–10. *Australorbis glabratus* (Say). From Lares, Puerto Rico; from Dr. W. A. Hoffman.
  4. Cross section of portion of ovotestis to show multiple branched diverticula.
  5. Distal end of verge showing opening at center.
  6. One diverticulum of prostate showing multiple branching at end.
  7. Pseudobranch and pneumostome.
  8. Outline of albumen gland showing depression occupied by intestine.
  9. Section of penial complex showing long and narrow verge and vergic sac.
  10. Entire genitalia dissected and organs separated. Note branched form of prostate diverticula and multiple nature of ovotestis diverticula.

Line near figure indicates 1 mm. in length. Line near
left of fig. 1 is also for fig. 3.

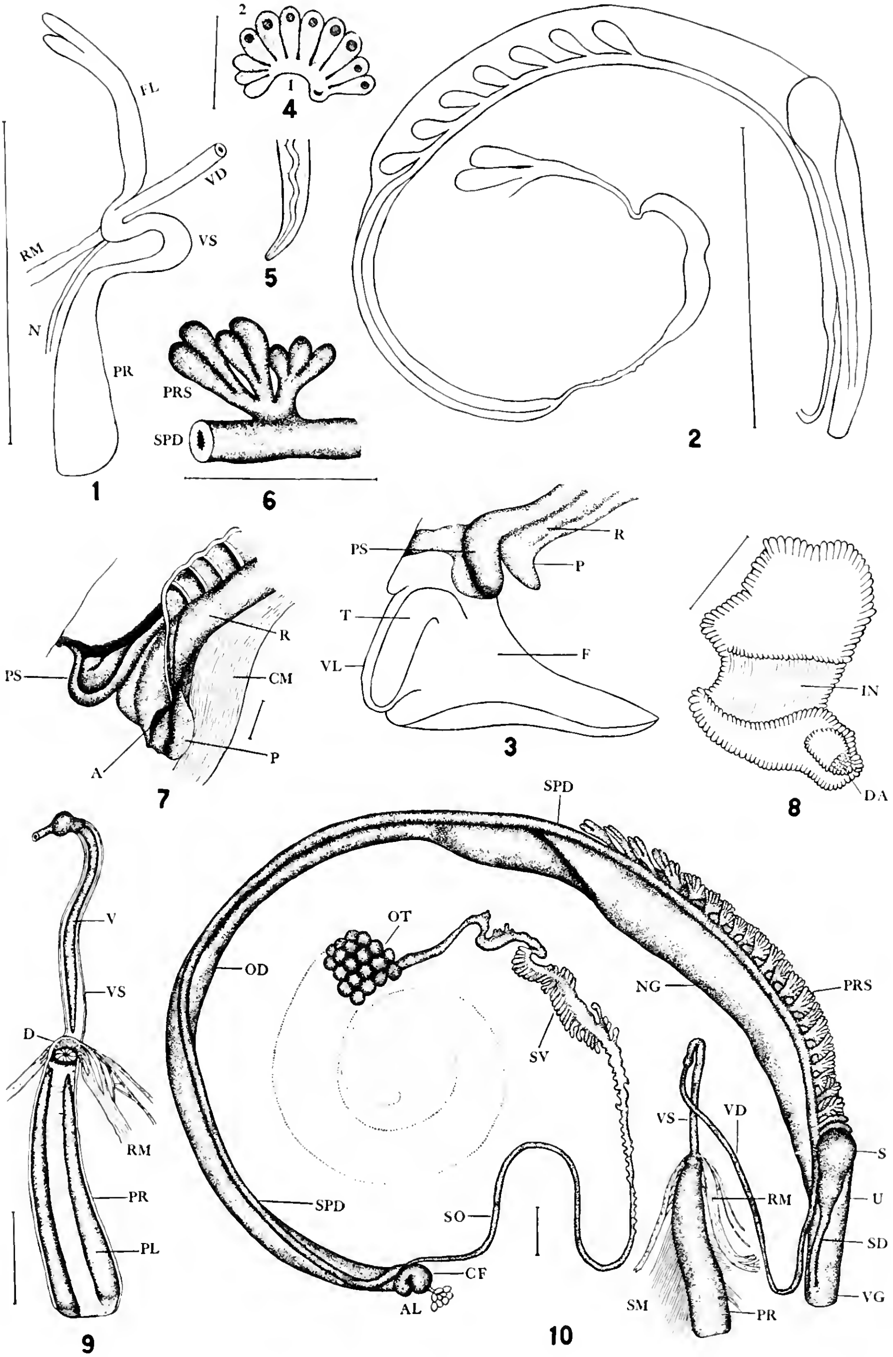
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PLATE 9

PLATE 10

Drepanotrema hoffmani F. C. Baker

From Isabela, Puerto Rico; collected by Dr. W. A. Hoffman.

1. Animal removed from shell showing pigmentation of mantle, shape of head and tentacles, and position of stomach (STM) in body.
2. Genitalia dissected and organs separated.
3. Fore part of body showing head, pseudobranch, etc.
4. Albumen gland showing attachment of ducts.
5. Penial complex showing attachment of short flagellum, vas deferens, etc.
6. Section of penial complex showing verge, pilasters, vas deferens, flagellum, etc.
7. Upper part of penial complex showing relationship of flagellum, vas deferens, vergic sac, retractor muscle, etc.
8. Penial complex of another specimen.
9. Distal end of verge showing central outlet of sperm canal.

Line near figure indicates 1 mm. in length

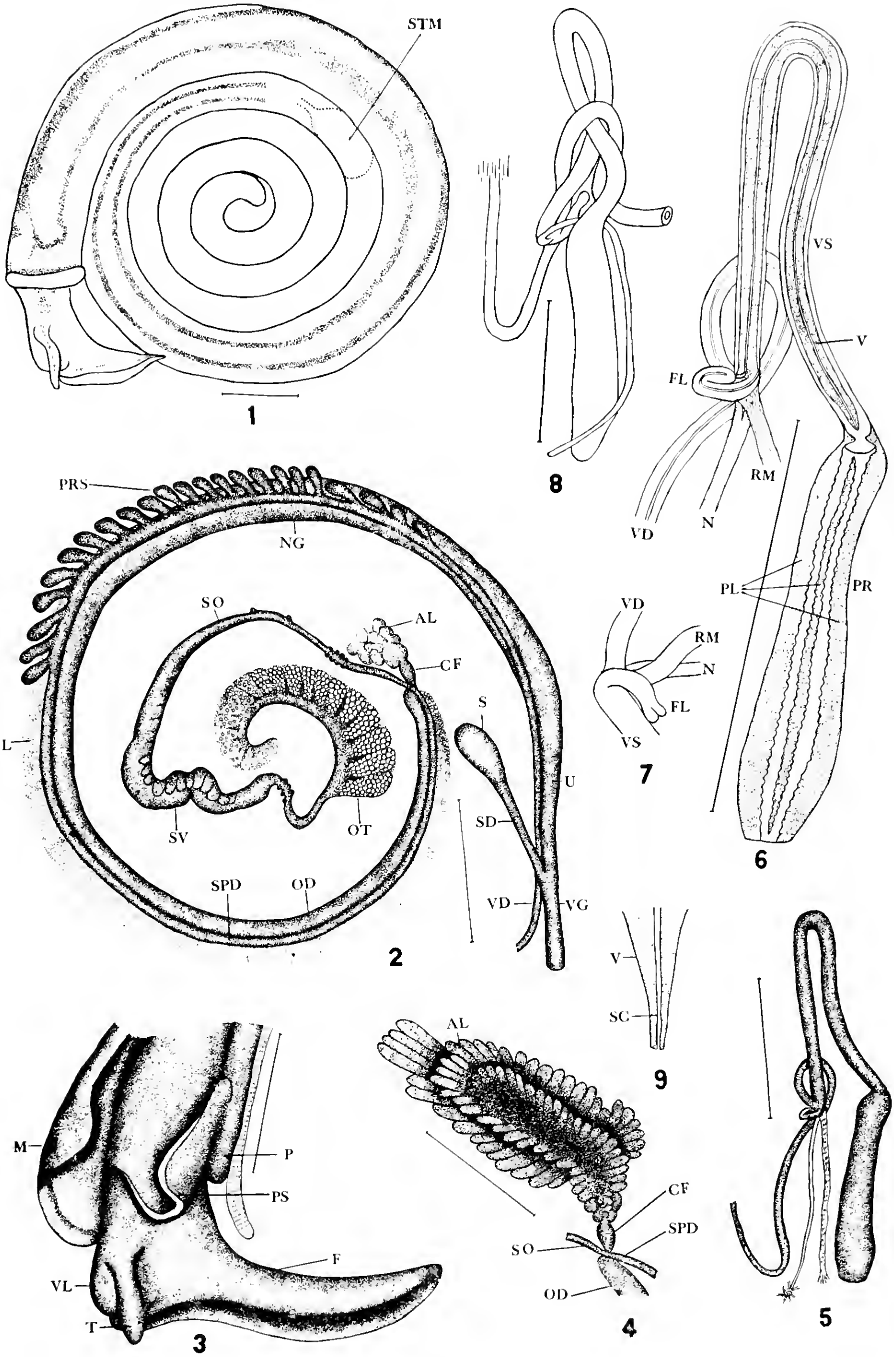
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PLATE 10

PLATE 11

Drepanotrema lucidum (Pfeiffer)

From Havana, Cuba; collected by Dr. C. G. Aguayo.

1. Head and foot with preputium and verge extended from male genital opening. The pseudobranch and rectum are also shown.
2. Head and foot with only preputium extended from male genital opening.
3. Genital system dissected and organs separated.
4. Penial complex showing flagellum, vas deferens, etc.
5. Penial complex with very long flagellum.
6. Diagram of penial complex showing preputium and verge extended from male genital opening.
7. Relationship of vas deferens, flagellum, retractor muscle in body of animal in specimen with preputium and verge extended from male opening.

Line near figure indicates 1 mm. in length

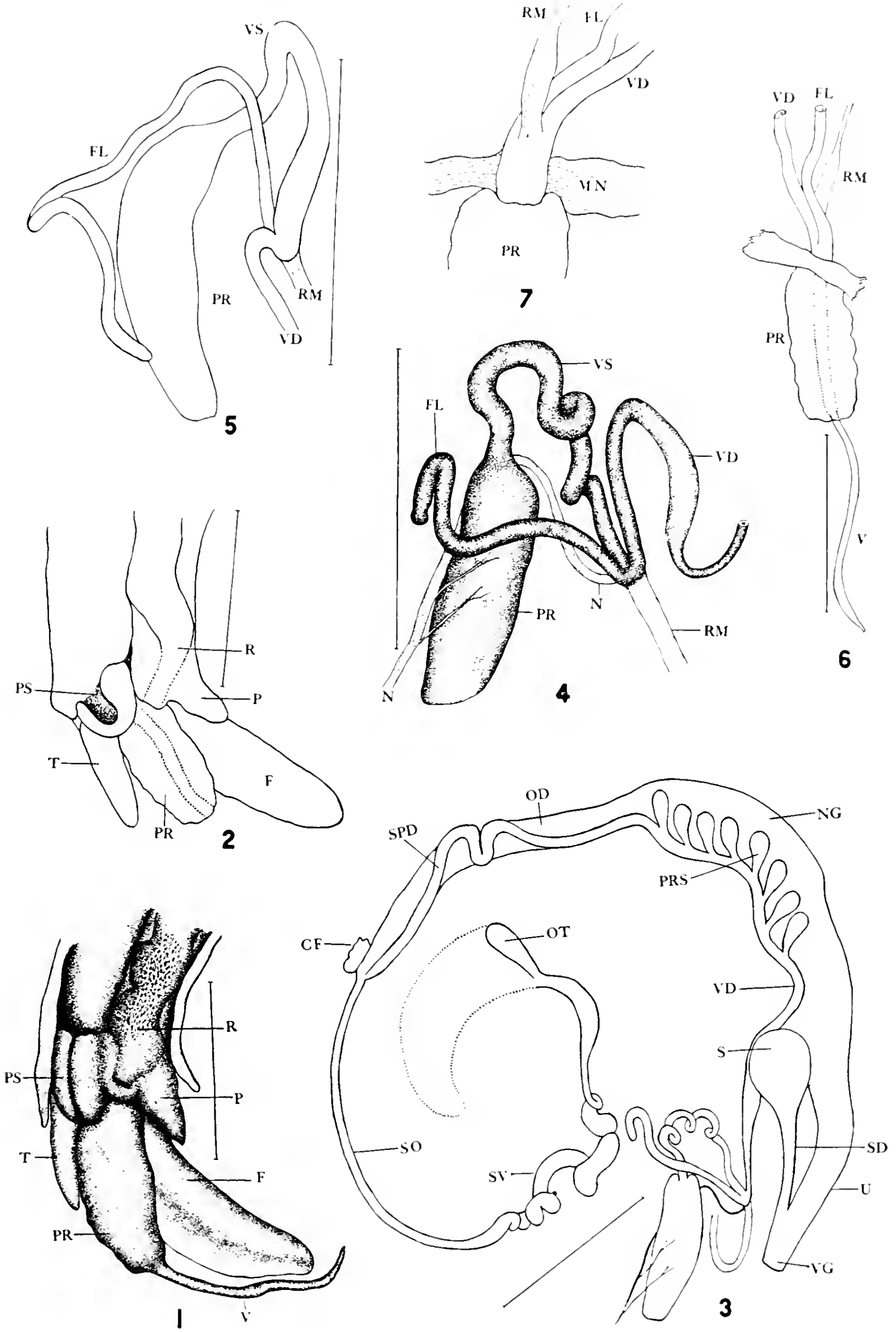
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PLATE 11

PLATE 12

Tropicorbis havanensis (Pfeiffer)

From New Orleans, La.; collected by Dr. E. Carroll Faust.

1. Penial complex in section to show verge and pilasters in vergic sac.
2. Muscular ring or ridge between vergic sac and preputium (diaphragm).
3. Distal end of verge showing central opening of sperm canal.
4. Body of snail showing pseudobranch, pneumostome, rectum, and frilled ridge or crest over rectum.
5. Body of snail showing pigmentation of mantle.
6. Albumen gland from above.
7. Portion of genitalia at junction of oviduct and sperm duct with ovisperm duct. Also entrance of albumen duct into carrefour and thence to oviduct. From below.
8. Same as fig. 7, from above.
9. Single diverticulum of prostate showing canal distinct from that of sperm duct.
10. Penial complex showing enlargement of preputial sac.
11. Genitalia dissected and the organs separated, showing relationship of all organs.

Line near figure indicates 1 mm. in length. Line at left of fig. 1 is also for figs. 7, 8, and 9. Line at left of fig. 11 is also size for fig. 6.

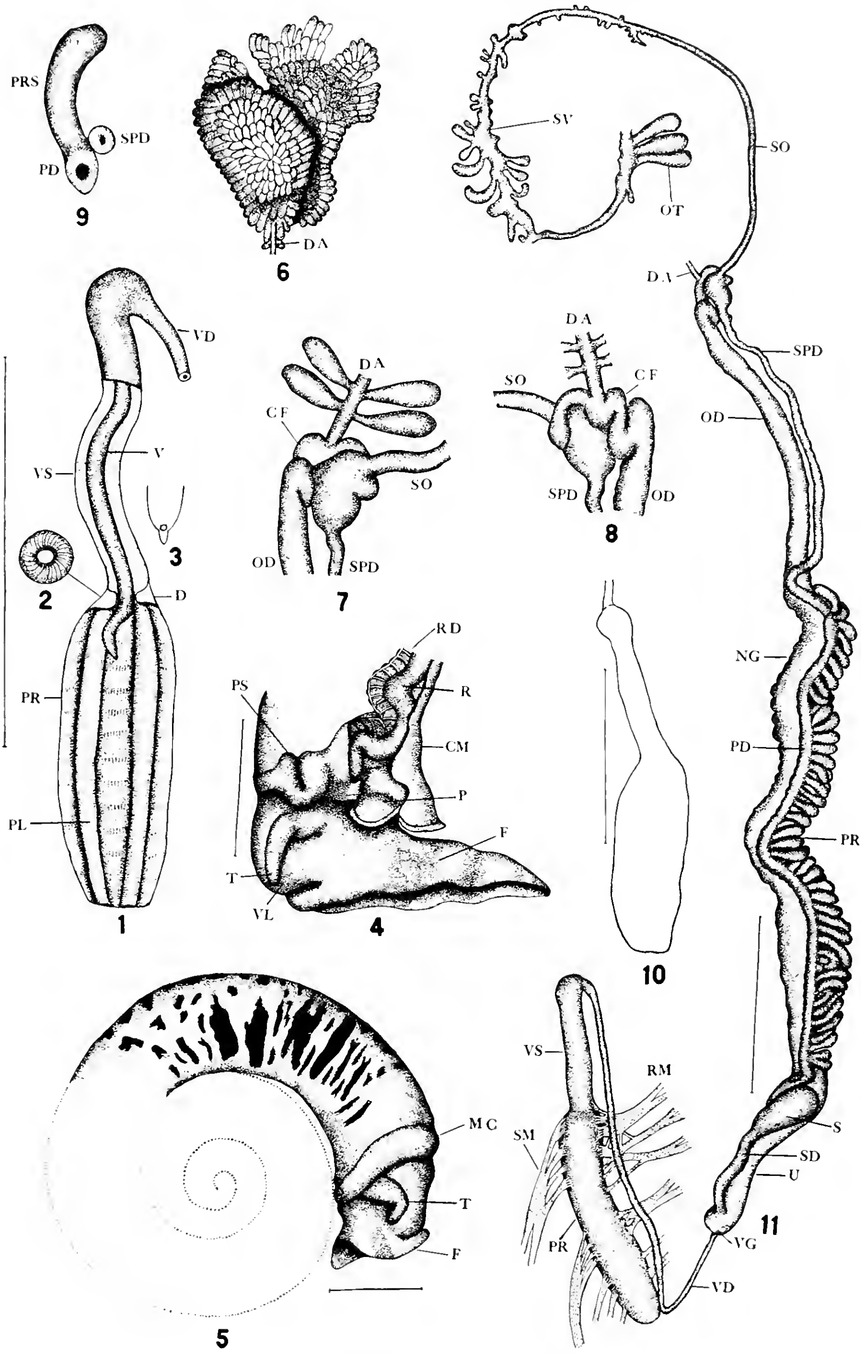
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PLATE 12

PLATE 13

Tropicorbis

1–3. *Tropicorbis obstructus* (Morelet). From New Orleans, La.; collected by Dr. E. C. Faust.

1. Genitalia dissected and organs separated.
2. Cross section of ovotestis in non-gravid stage.
3. Cross section of ovotestis in gravid stage with ova in diverticula. Line at right indicates 0.5 mm. in length.

4–10. *Tropicorbis riisei* (Dunker). From Lares, Puerto Rico; from Dr. W. A. Hoffman.

4, 5. Cross sections of prostate diverticula showing bending at end. Also presence of prostate duct distinct from sperm duct.

6. Penial complex, external view.
7. Albumen gland from below showing duct (DA).
8. Vas deferens showing branching to form sperm duct and prostate duct (greatly enlarged).
9. Portion of genitalia dissected and organs separated. Organs as in fig. 1.
10. Head of animal showing pseudobranch and pneumostome as well as ridge over rectum.

Line near figure indicates 1 mm. in length. Line at left of figs. 4 and 5 is for both figures.

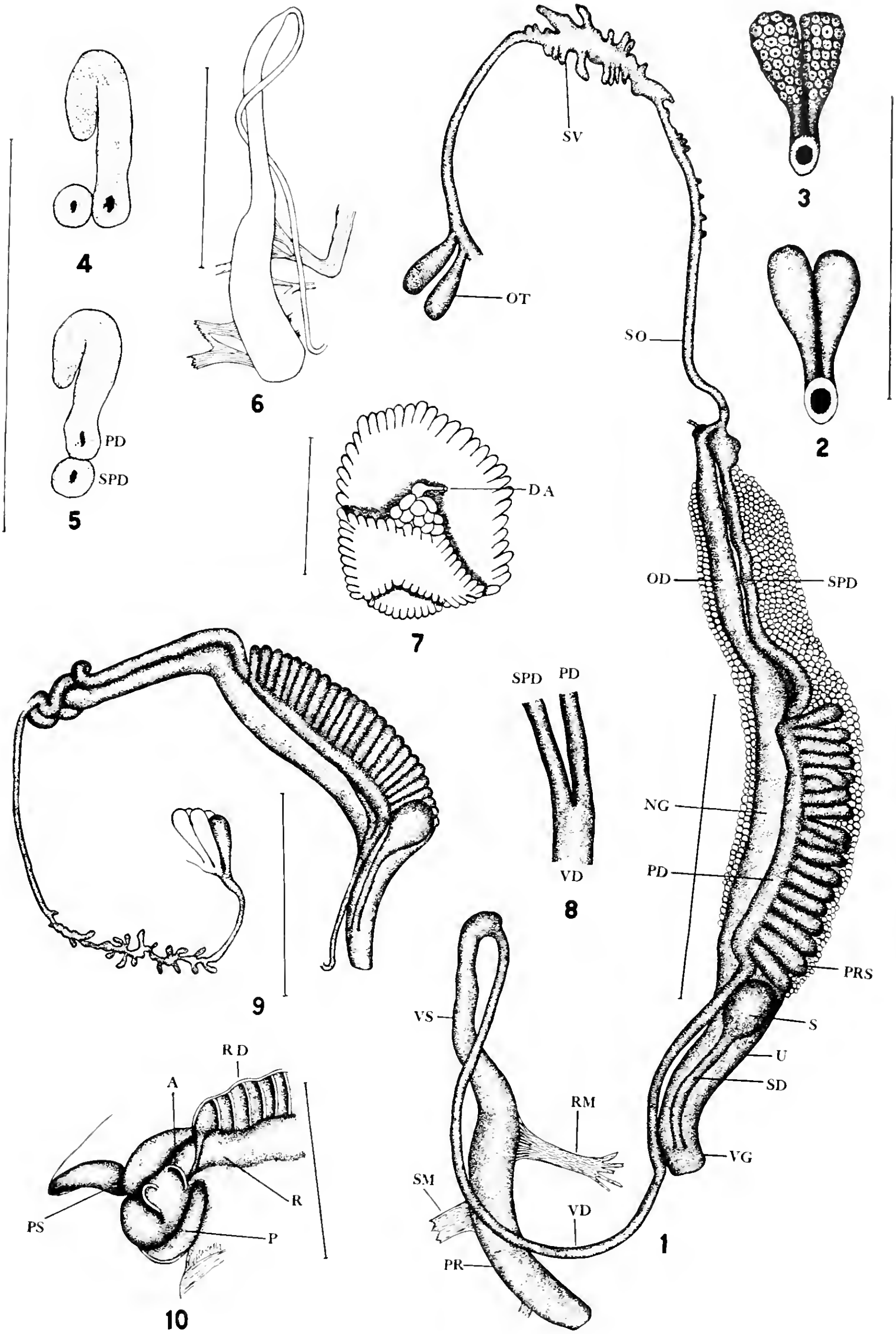
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PLATE 13

PLATE 14

Gyraulus albus (Müller)

From pond in Krolikania, a suburb of Warsaw, Poland; from A. Jankowski.

1. Penial complex sectioned to show verge, stylet, etc.
2. Penial complex, external view.
3. Fore part of animal showing pseudobranch and pneumostome.
4. Fore part of animal showing pseudobranch, pneumostome, and venation of some of these organs.
5. Albumen gland from below.
6. Portion of genitalia showing attachments of albumen gland duct, oviduct, sperm duct, and general relationship of these and other organs.
7. Genitalia dissected and organs separated.
8. Stylet at end of verge with sperm canal outlet at side of verge.
9. Section of prostate showing distinct canals for prostate and sperm duct. Three diverticula are shown.
10. Section through ovotestis near front end.
11. Distal end of ovotestis showing grouping of diverticula.

Line near figure indicates 1 mm. in length. Line at lower right corner of plate is for figs. 5, 6, 7, 9, 10, and 11. Figure 8 line is one-sixth of 1 mm. in length.

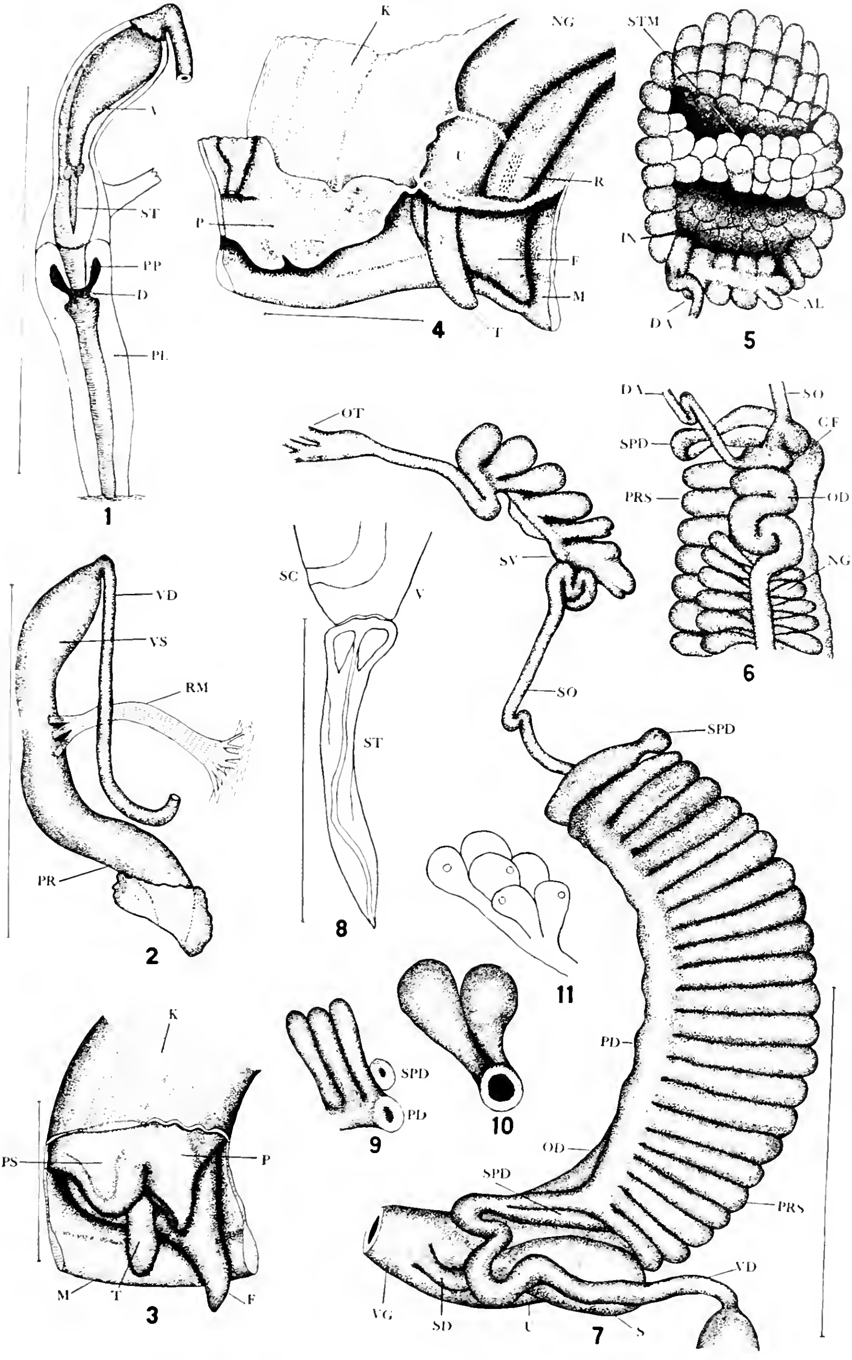
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PLATE 14

PLATE 15

Gyraulus

1–7. *Gyraulus hirsutus* (Gould). From Bass Creek, Lake Nipissing, Ontario, Canada; received from A. LaRocque.

1. Genitalia dissected and organs separated. A portion of the intestine is shown beneath the albumen gland.
2. Penial complex, external view.
3. Fore end of body showing pseudobranch, pneumostome, rectum, etc.
4. Distal end of genitalia showing connection of various ducts. From right side.
5. Same as fig. 4, from left side.
6. A single diverticulum of the prostate with duct separate from the sperm duct.
7. Two diverticula of the ovotestis.

8–10. *Gyraulus vermicularis* (Gould). From Stone Lake, Golden Gate Park, San Francisco, California; from Dr. G. D. Hanna.

8. Fore end of body showing pseudobranch.
9. Distal end of genitalia showing relationship of ducts.
10. Genitalia dissected and organs separated.

Line near figure indicates 1 mm. in length. Line in upper left corner of plate is for figs. 4, 5, 6, and 7.

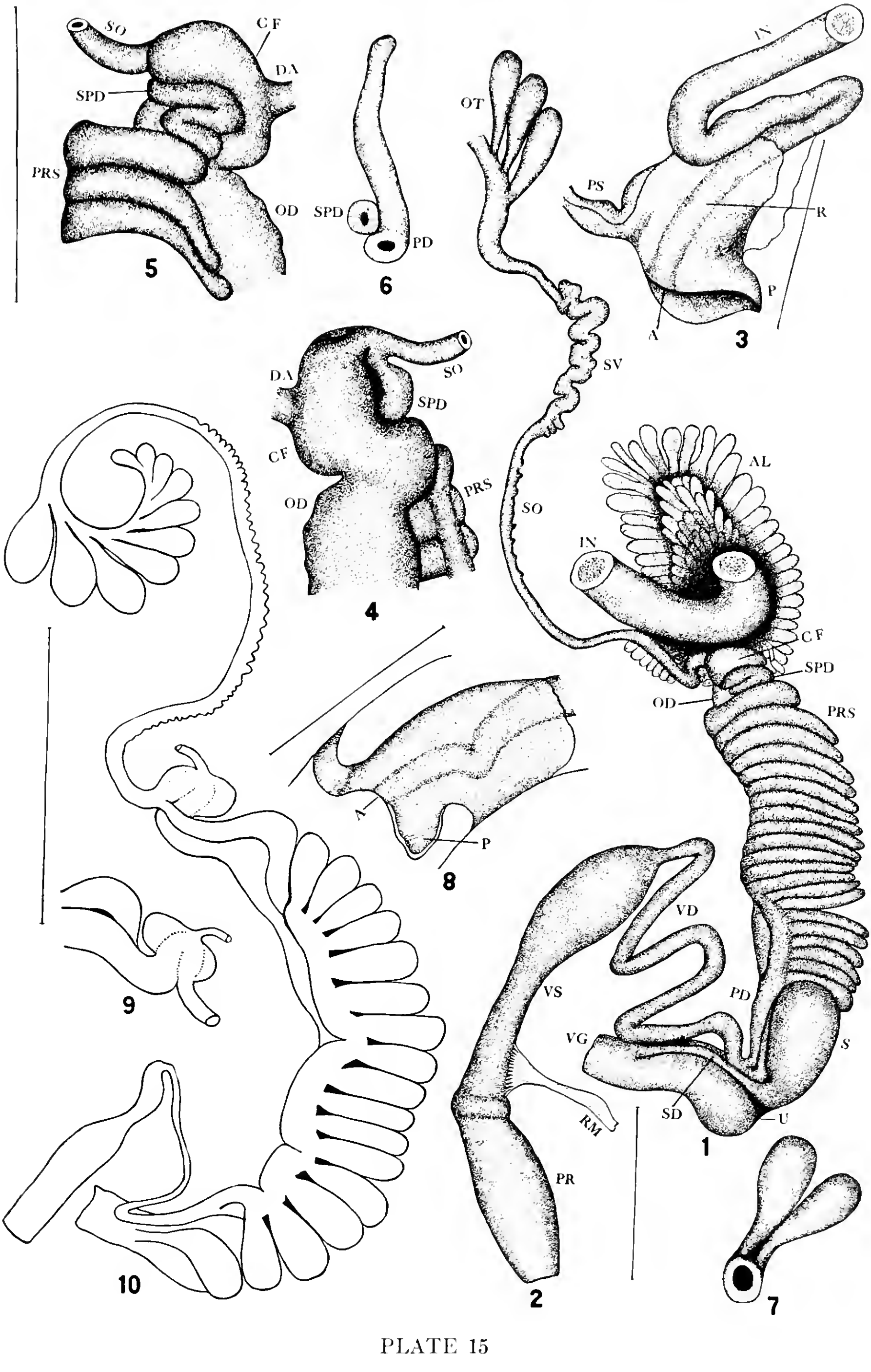
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PLATE 15

PLATE 16

Gyraulus deflectus obliquus (DeKay)

From Taylor Lake, Masham, Quebec, Canada; collected by A. LaRocque.

1. Penial complex in vertical section.
2. Penial complex of specimen with bulbous termination of vergic sac.
3. External view of penial complex showing relationship of parts. Also male opening behind tentacle.
4. Genitalia dissected and organs separated.
5. Section through portion of penial complex at junction of vergic sac and preputial sac to show thickened portion with papilla.
6. Stylet. Distal end of verge shows sperm canal outlet at side.
7. Terminal diverticula of ovotestis, showing developing ova.
8. Terminal diverticula of ovotestis from left side.
9. Section through diverticula of ovotestis.
10. Distal end of genitalia showing position of sperm duct, oviduct, albumen duct, etc.
11. Section of prostate near middle.
12. Section of prostate six diverticula from front end.
13. Body and foot of animal showing pseudobranch, etc.
14. Pseudobranch showing network of blood vessels.
15. Another form of pseudobranch.

Line near figure indicates 1 mm. in length. Line at middle left of plate indicates size of figs. 5, 6, 7, 8, 9, 11, and 12.

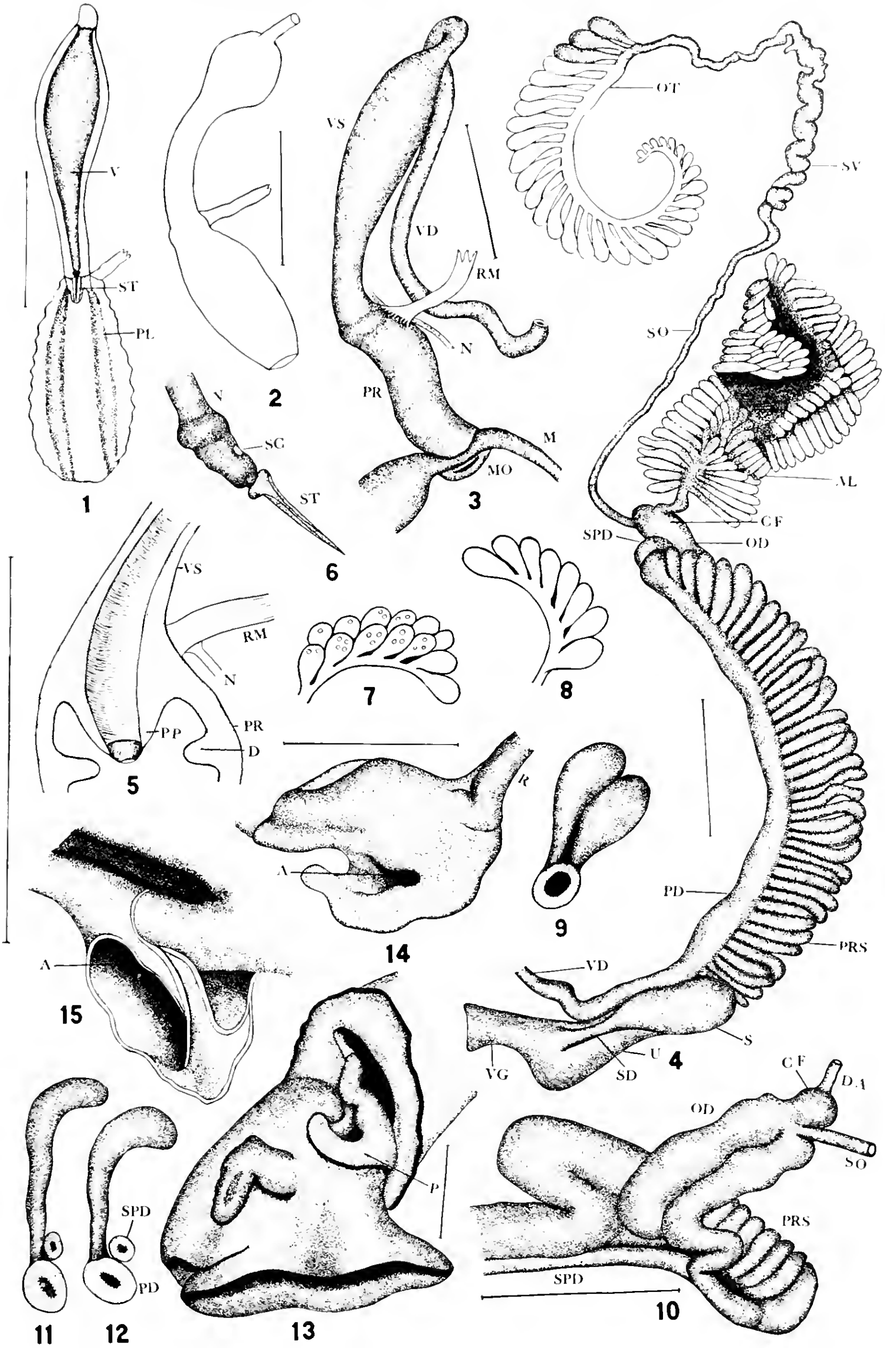
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PLATE 16

PLATE 17

Gyraulus

1–5. *Gyraulus circumstriatus* (Tryon). From Wainwright Park, near Mott Lake, Alberta, Canada; collected by Dr. Swales.

1. Genitalia dissected and organs separated. Outline. Penial complex in natural position.
2. Distal end of genitalia showing duct connections. From left side.
3. Pseudobranch and pneumostome.
4. Animal removed from shell showing position of several organs.
5. Two diverticula of ovotestis in gravid condition.

6–12. *Gyraulus parvus* (Say). From Winnebago Lake, near Oshkosh, Wisconsin; collected by F. C. Baker.

6. Genitalia dissected and organs separated.
7. Distal end of genitalia, from left side.
8. Portion of fore end of animal showing pseudobranch, etc.
9. Albumen gland showing attachment of oviduct.
10. Three diverticula of prostate with prostate duct below and sperm duct at the side.
11. Two diverticula of ovotestis.
12. Penial complex opened to show verge, stylet, papilla, etc.

Line near figure indicates 1 mm. in length. Figures 5, 10, and 11 have same magnification as fig. 12.

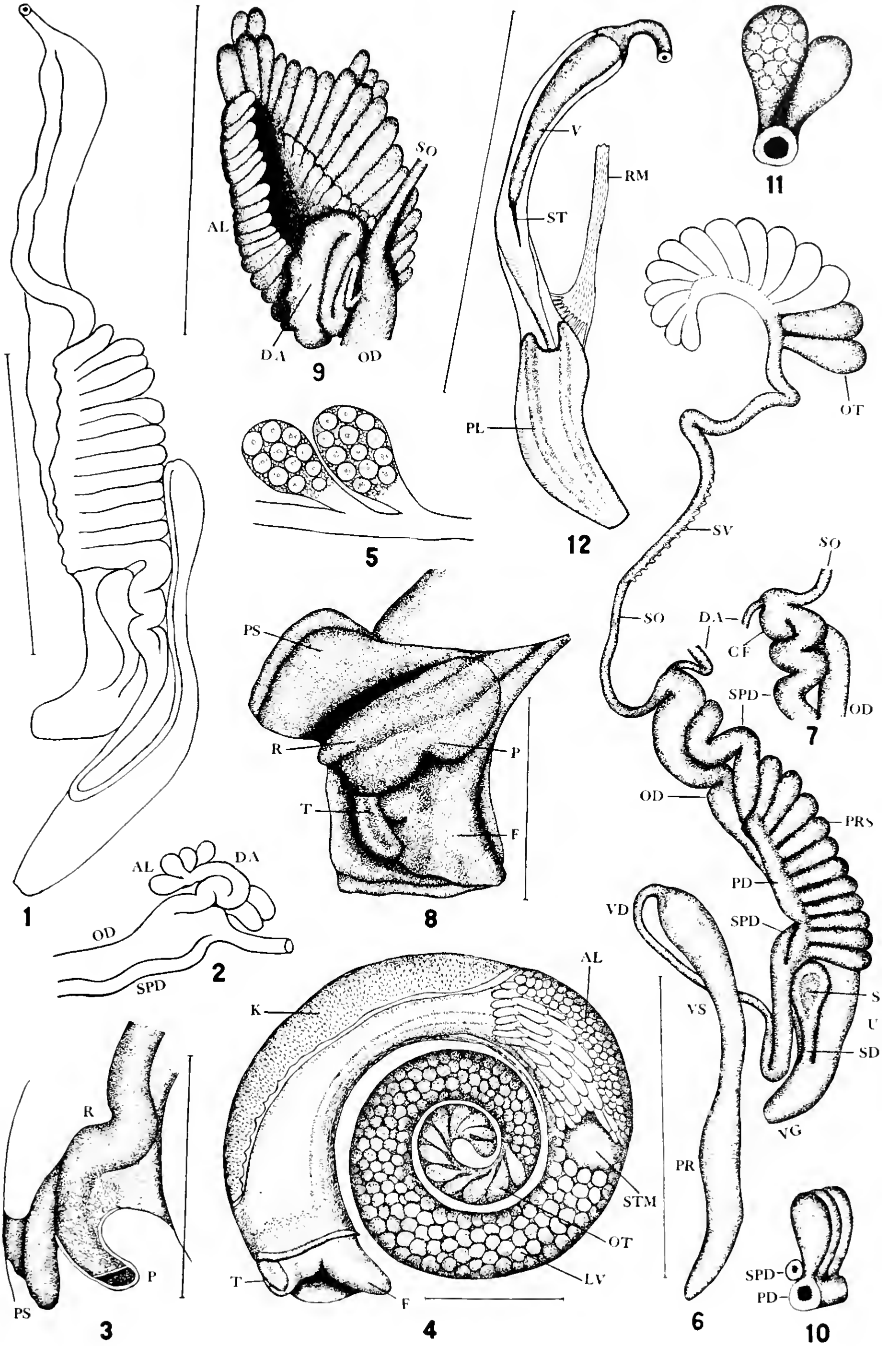
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PLATE 17

PLATE 18

Gyraulus and *Armiger*

1–5. *Gyraulus similaris* (F. C. Baker). From Smartweed Lake, near Tolland, Colorado; collected by Dr. Frank Smith.

1. Genitalia dissected and organs separated.
2. Distal end of genitalia showing arrangement of ducts.
3. Penial complex in section showing verge, stylet, and preputium.
4. Stylet. Outlet of sperm canal is shown at side of verge.
5. Head and foot of animal showing pseudobranch.

6–11. *Armiger crista* (Linn.). From pond in Krolikarnia, a suburb of Warsaw, Poland; collected by A. Jankowski.

6. Head showing form of pseudobranch.
7. Genitalia dissected and organs separated.
8. Albumen gland from side.
9. Penial complex in section showing verge without stylet.
10. End of verge showing absence of stylet and presence of a fleshy papilla. Sperm canal with outlet in center of verge.
11. End of verge from side showing relationship of papilla and canal.

Line near figure usually indicates 1 mm. in length. Line at left of fig. 4 measures one-fifth of 1 mm. Line in center of fig. 7 is also for fig. 8. Same line equals 0.5 mm. for fig. 9.

Figures 10 and 11 are much enlarged.

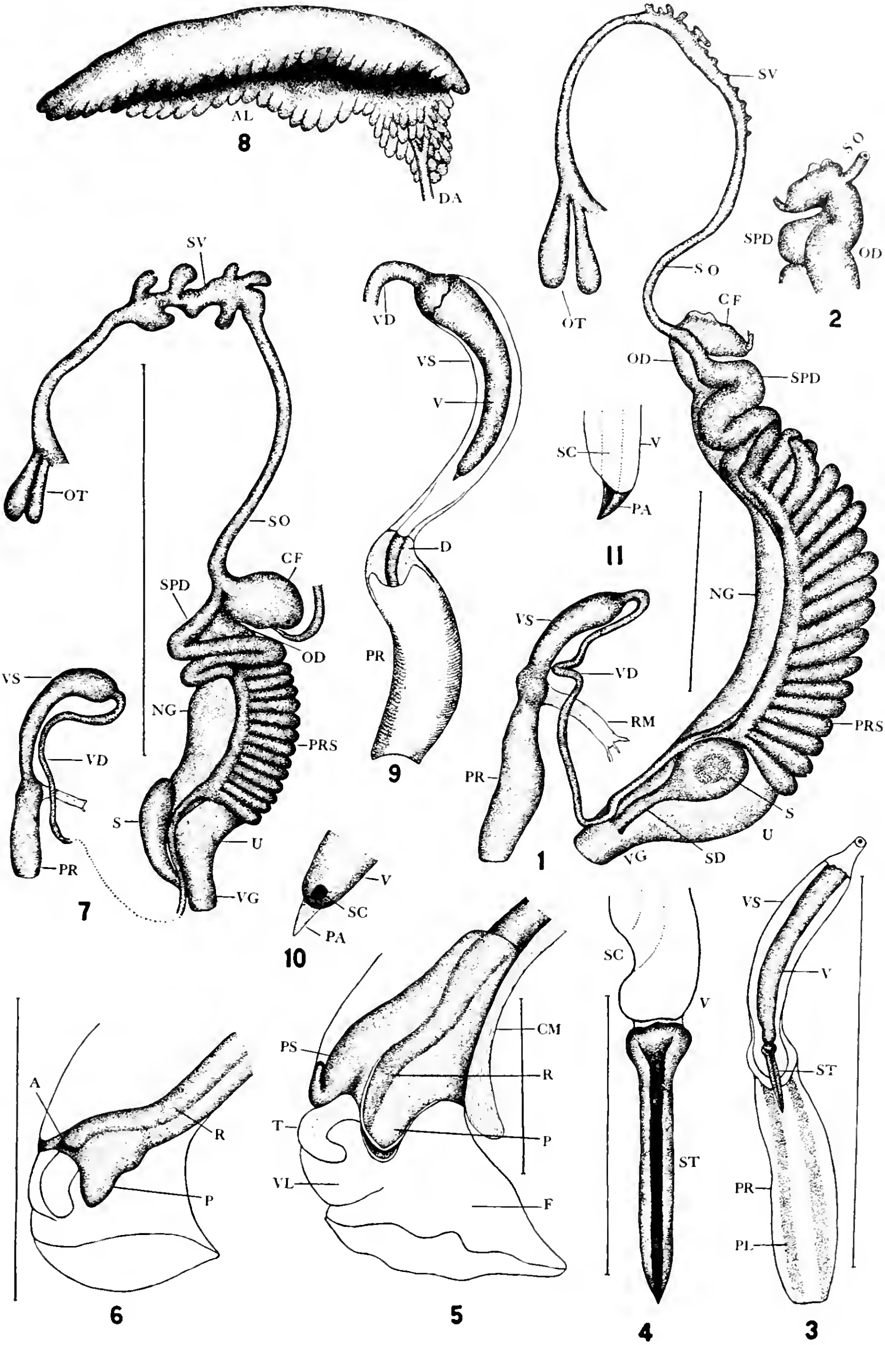
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PLATE 18

PLATE 19

Gyraulus

1–3. *Gyraulus convexiusculus* (Hutton). From Calcutta, India; from Dr. B. Prashad.
  1. Cross section of one diverticulum of prostate showing separate canals for prostate duct and sperm duct.
  2. Genitalia dissected and organs separated.
  3. Pseudobranch and pneumostome.

4–9. *Gyraulus latestomus* F. C. Baker. From Cedar Lake, Algonquin Park, Ontario, Canada; collected by A. LaRocque.
  4. Distal end of genitalia from left side.
  5. Albumen gland from below, showing loop of intestine.
  6. Penial complex.
  7. Cross section of one diverticulum of prostate.
  8. Anterior end of body showing pseudobranch and pneumostome.
  9. Genitalia dissected and the organs separated.

Line near figure indicates 1 mm. in length. Figures 1 and 7 are greatly enlarged.

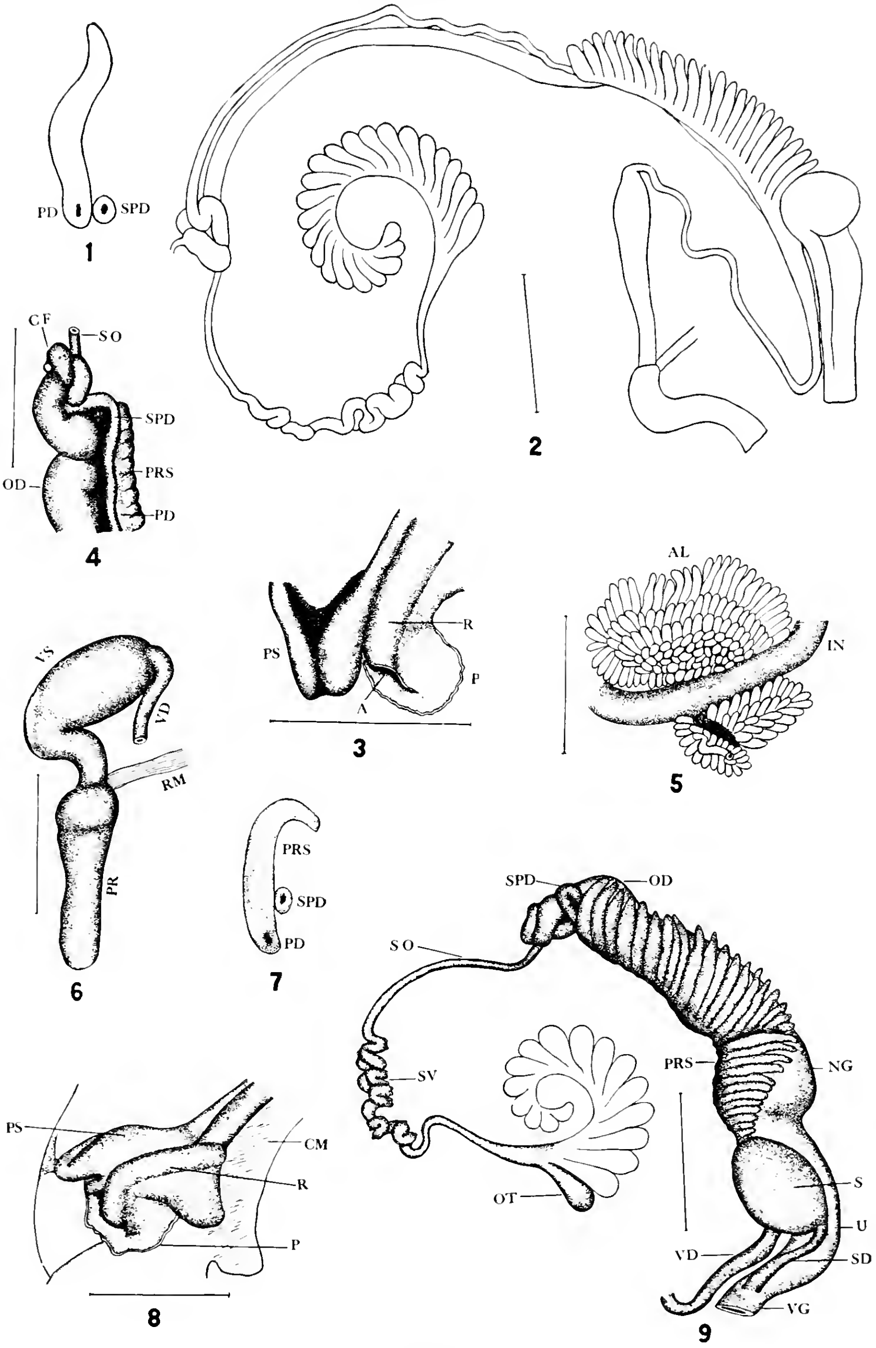
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PLATE 19

PLATE 20

Planorbarius corneus (Linn.).

From branch of Wista River at Morysinek, 5 km. south of Warsaw, Poland; collected by A. Jankowski.

1. Penial gland and appendages in extended position.
2. Section through appendage at C in fig. 1.
3. One diverticulum of ovotestis with ripe ovum (greatly enlarged).
4. Cross section through prostate, uterus, and nidamental gland.
5. Cross section of ovotestis in gravid specimen.
6. Vergic sac opened to show verge and canal in gland.
7. Retractor muscles in typical specimen.
8. End of verge showing penial appendage.
9. Albumen gland.
10. Portion of head showing pseudobranch, pneumostome, and rectum with ridge.
11. Penial complex opened to show position of penial gland, verge, pilasters, etc. Penial appendage is retracted.
12. Penial complex from outside showing muscles.
13. Genitalia dissected and organs separated, showing particularly the form of prostate and its junction with the vas deferens and sperm duct.

Line near figure indicates 1 mm. in length. Line at right of fig. 1 is also for fig. 2. Line at left of fig. 6 represents 0.5 mm. in length.

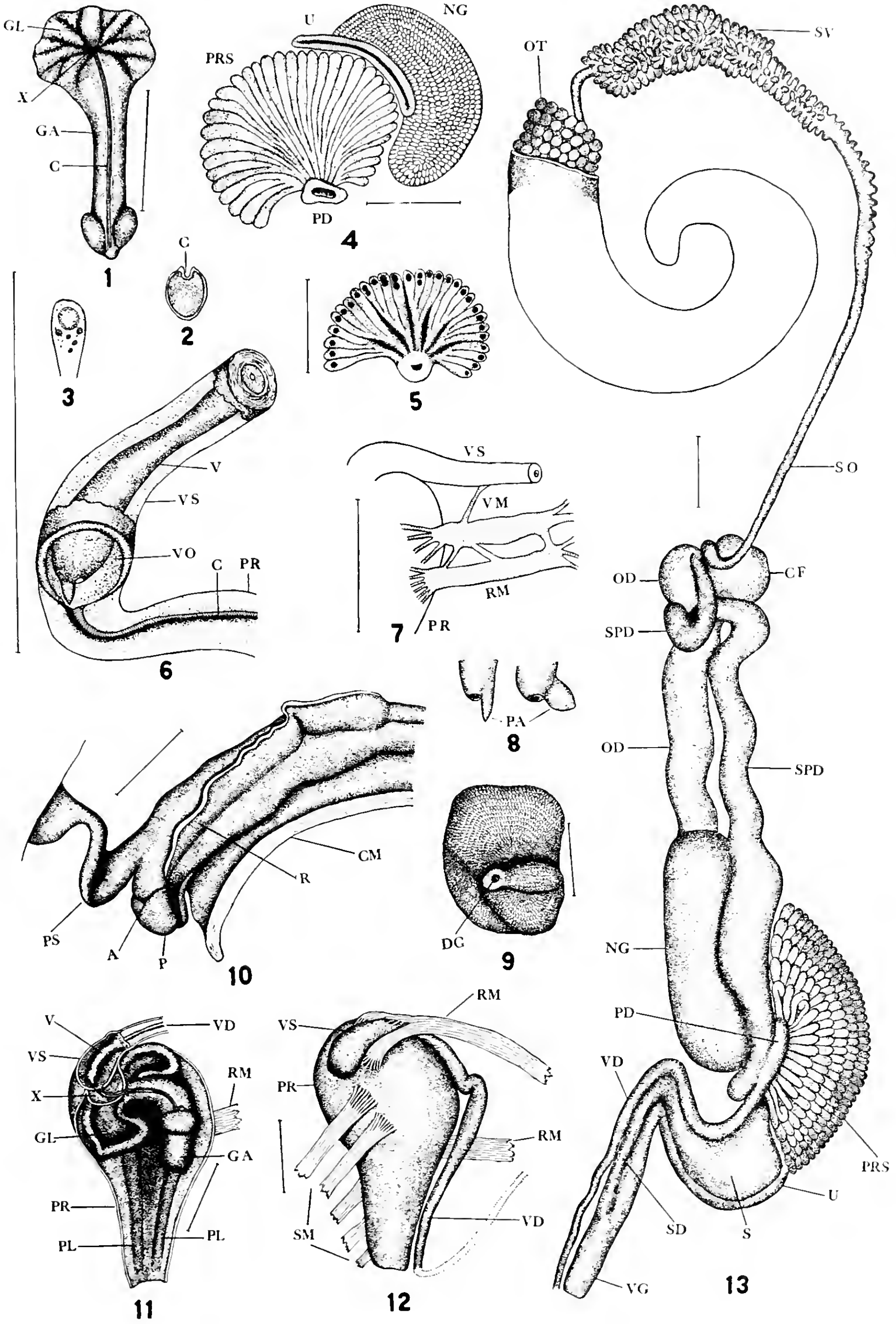
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PLATE 20

PLATE 21

Indoplanorbis exustus (Deshayes)

From Hsipaw, North Shan State, Burma, India; collected by Dr. B. N. Chopra and Dr. H. S. Rao; contributed by Dr. B. Prashad.

1. Penial complex in natural position.
2. Fore part of animal showing pseudobranch and pneumostome, with preputium protruded from male opening and lying on the neck of the animal.
3. Genitalia dissected and organs separated.
4. Pleated pseudobranch and pneumostome.
5. Under side of preputium everted through male opening in the neck of the animal.
6. Pseudobranch from side showing branched or pleated condition.
7. Cross section of ovotestis showing several gravid diverticula.
8. Cross section of prostate.
9. Two diverticula of prostate.
10. Portion of prostate showing relationship of vas deferens, sperm duct, and diverticula of gland.

Line near figure indicates 1 mm. in length. Figures 9 and 10 are greatly magnified. Figures 1, 2, 3, and 10 were published in Jour. Morph., LV, plates 1 and 2.

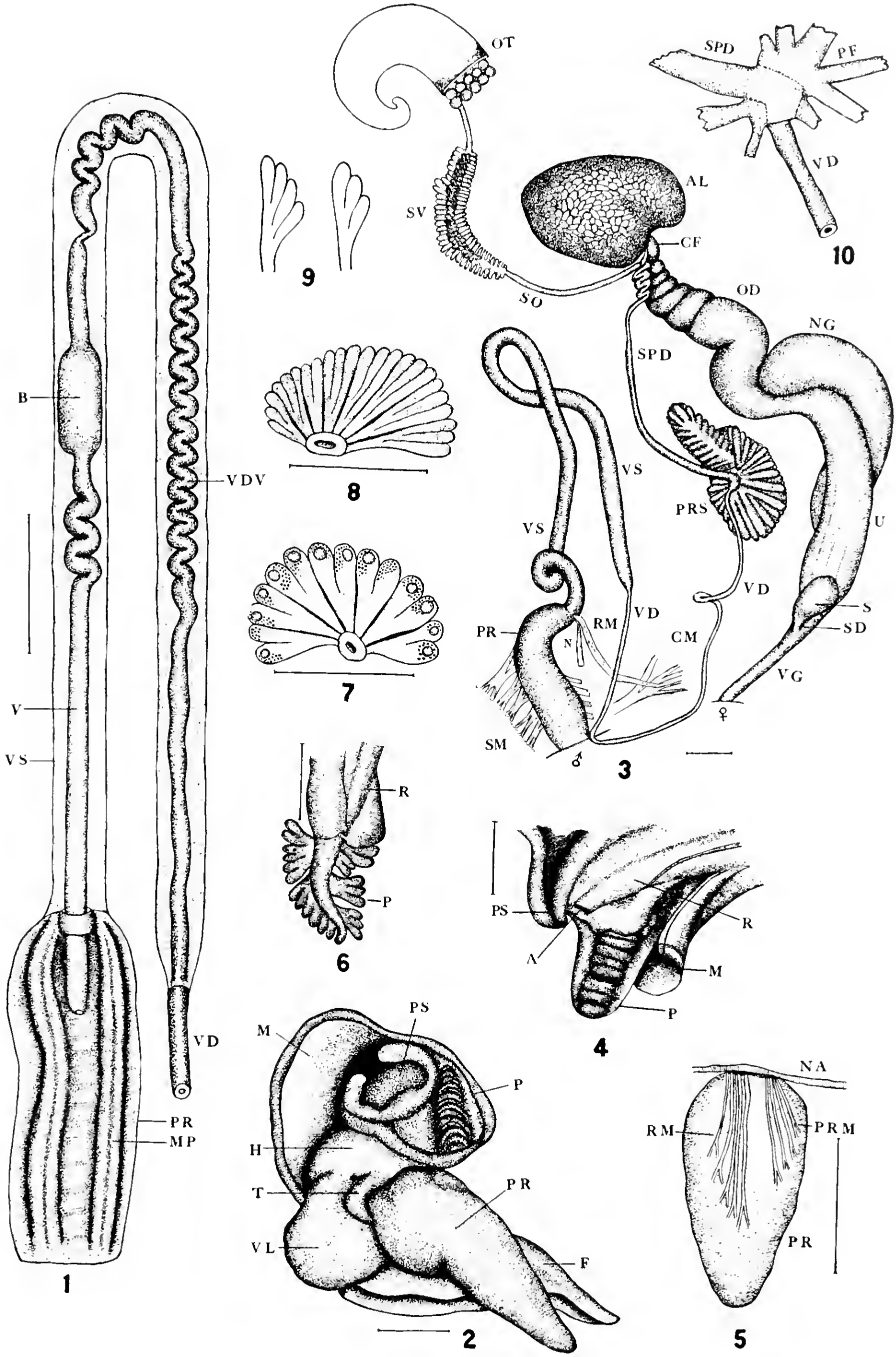
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PLATE 21

PLATE 22

Indoplanorbis and *Helisoma*

5–9. *Indoplanorbis exustus* (Deshayes). Continued from plate 21.
- 5. Retractor muscle of verge showing branching to vergic sac. Also nerve connection.
- 6. Cross section of preputium in extended condition as shown in fig. 7.
- 7. Penial complex of specimen in breeding condition with preputium extended from male opening in neck. Compare with fig. 1 on plate 21.
- 8. Section of vergic sac through bulbous termination of verge.
- 9. Section of vergic sac through verge.

Line near figure indicates 1 mm. in length. Figure 5 is enlarged. Figure 6 has same magnification as fig. 7. These figures were published in Jour. Morph.

1. *Helisoma anceps latchfordi* (Pilsbry).
- 1. Verge. Also enlarged portion of vas deferens (epiphallus).

2–4, 11. *Helisoma anceps percarinatum* (Walker).
- 2–4. Variation in form of muscles and in position of verge in preputium. Greatly enlarged.
- 11. Penial gland with cup turned back to show folds in inner cup.

10, 12. *Helisoma anceps* (Menke).
- 10. End of verge showing papilla and sperm canal outlet.
- 12. Prostate showing attachment of prostate duct to sperm duct.

Line near figure indicates 1 mm. in length

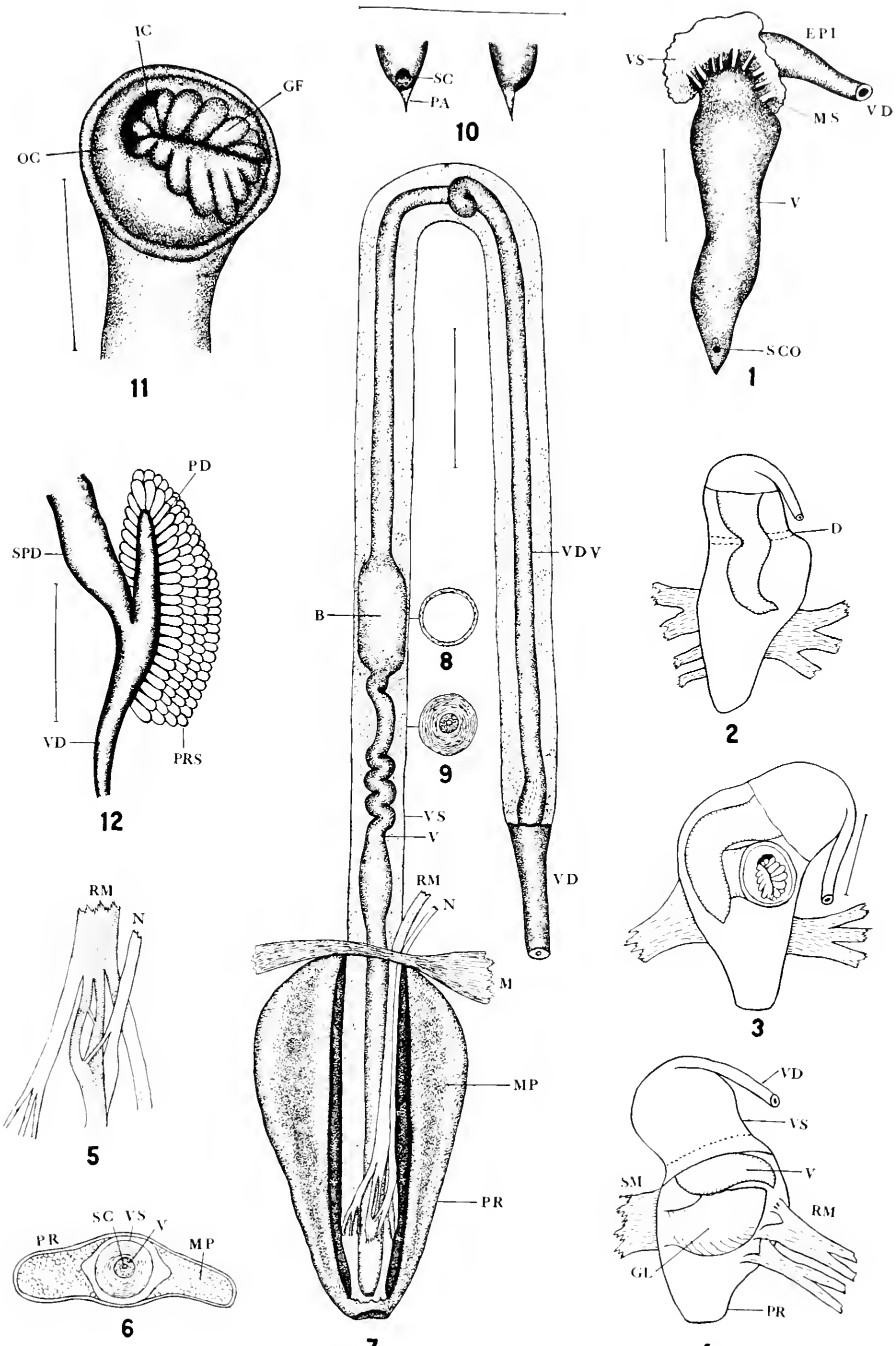
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PLATE 22

PLATE 23

Helisoma anceps (Menke)

1–4, 7–11. *Helisoma anceps* (Menke). From Gillespies Pond, Collinsville, Connecticut; collected by F. C. Baker and Leslie Brewer.

1. Cross section of penial gland showing cup, folds, and duct.
2. Section of penial complex to show position of gland in preputium.
3. Exterior view of penial complex showing short duct on outside of preputium.
4. Region of the neck showing pseudobranch, pneumostome, and rectum.
7. Albumen gland from below.
8. Penial complex of specimen in which gland in preputium has been pushed upward.
9. Cross section of prostate showing multiple form of diverticula.
10. Cross section of ovotestis.
11. Genitalia dissected and organs separated.

5, 6. *Helisoma anceps latchfordi* (Pilsbry). From Meach Lake, Quebec, Canada; collected by A. LaRocque.

5. Diaphragm in preputial sac view from below.
6. Section through diaphragm showing entrance of gland duct into vergic sac cavity just above diaphragm.

Line near figure indicates 1 mm. in length

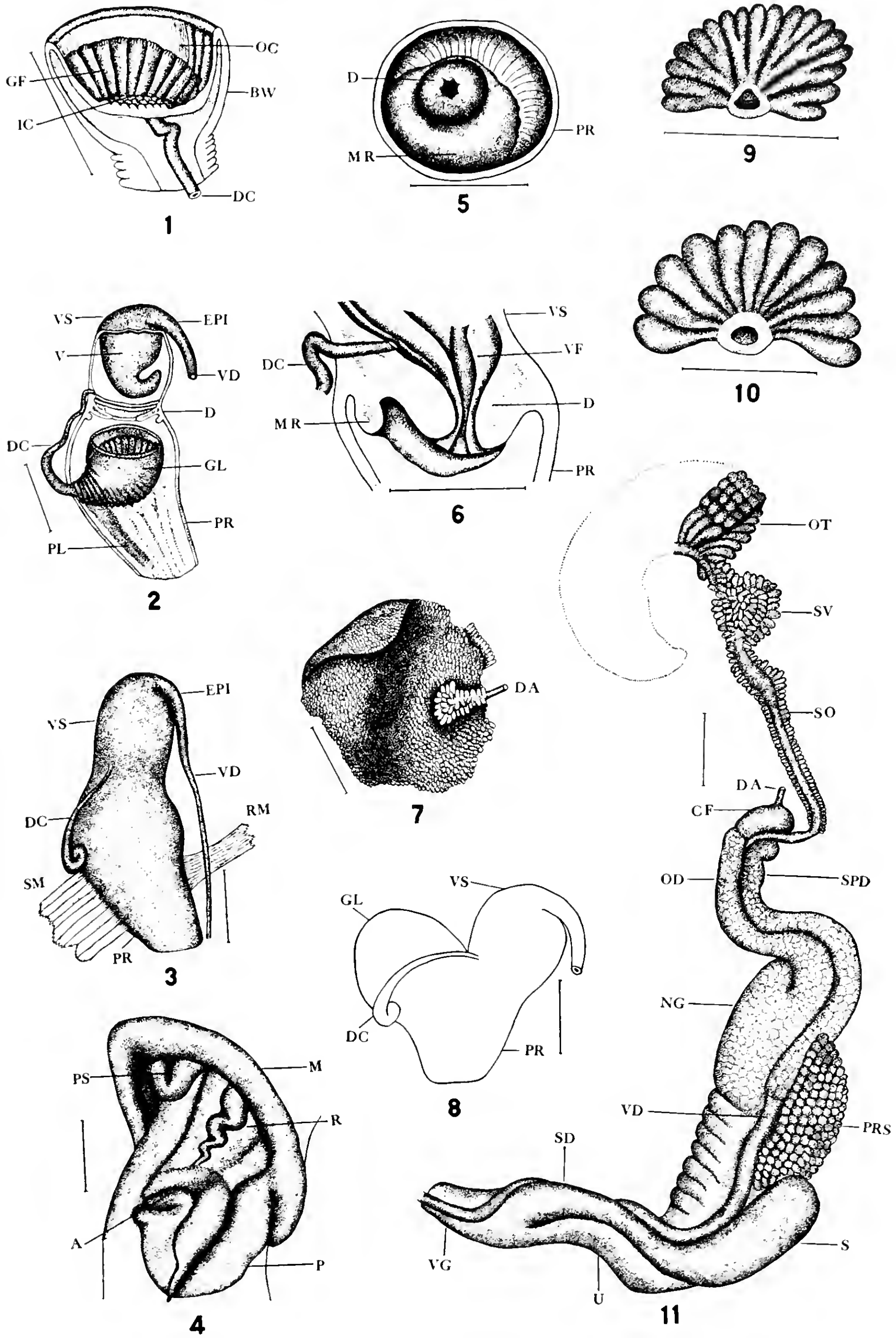
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PLATE 23

PLATE 24

Helisoma trivolvis (Say)

Collected from Oneida Lake, New York, by F. C. Baker,
except where otherwise stated.

1. Penial complex. Specimen with portion of preputium containing gland pushed upward. Pool near Green Lake, Wisconsin.
2. Penial complex in vertical section. Specimen with preputium pushed upward. Illinois River, near Peoria, Illinois.
3. Penial complex. Young specimen with 3½ whorls. Devils Lake, Wisconsin.
4. Section through penial gland showing folds in cup.
5. Penial complex in immature specimen. Pond near Sturgeon Bay, Wisconsin.
6. Side view of albumen gland.
7. Albumen gland from below.
8. Section through penial gland in specimen in normal, non-breeding condition.
9. Section through ovotestis near anterior end.
10. Section through penial complex in region of diaphragm.
11. External view of penial complex showing duct uncoiled and stretched out, indicating great length.
12. Region of neck showing pseudobranch, pneumostome, rectum, etc.
13. Section through prostate and uterus near middle of gland.
14. Penial gland somewhat contracted at cup end.
15. Genitalia dissected and organs separated.

Line near figure indicates 1 mm. in length

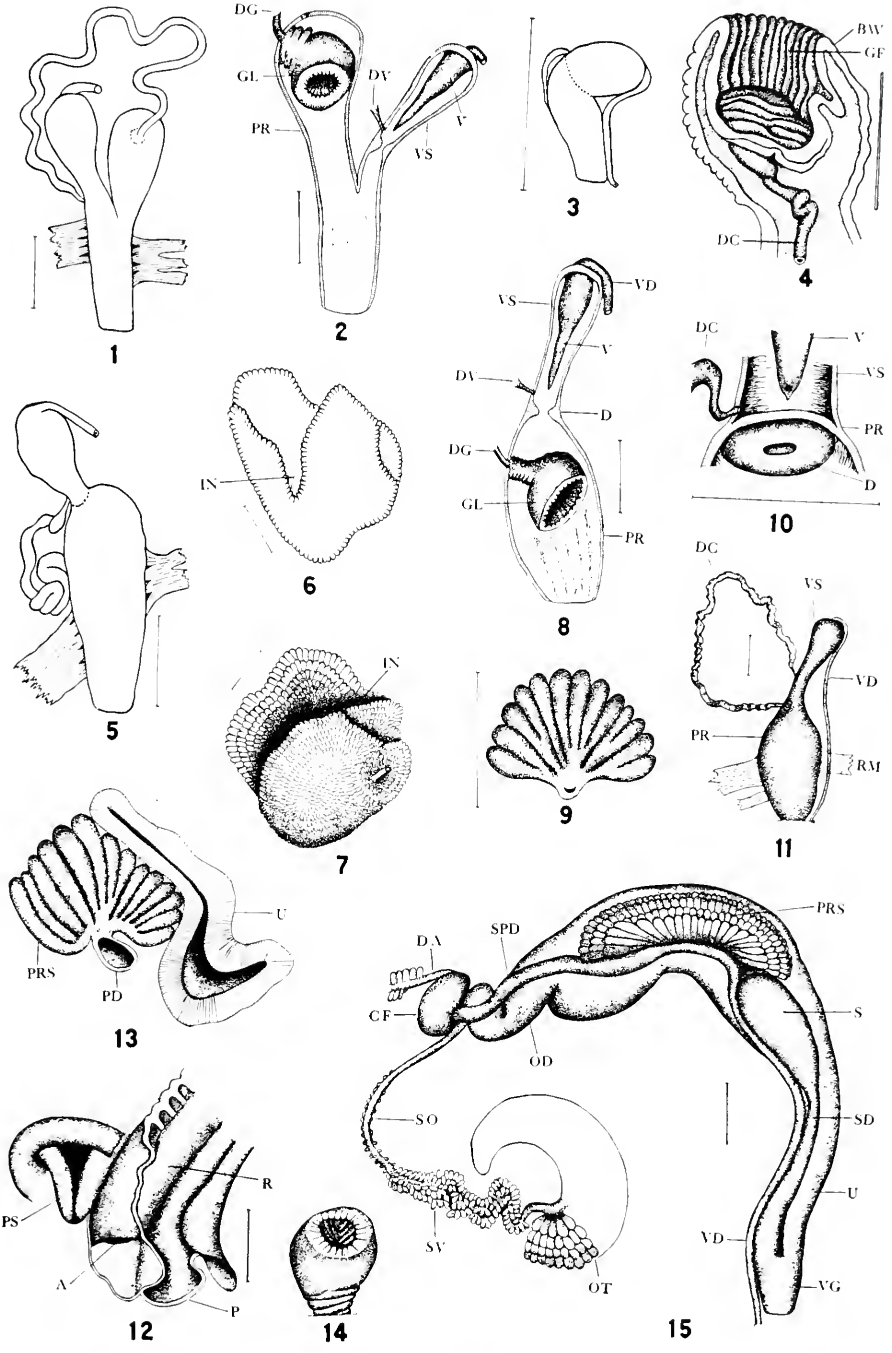
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PLATE 24

PLATE 25

Helisoma pilsbryi (F. C. Baker)

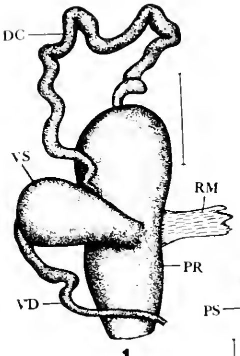
1–7. *Helisoma pilsbryi* (F. C. Baker). From Chetek Lake, Barron County, Wisconsin; collected by F. C. Baker.

1. Penial complex with vergic sac drawn to side of preputium.
2. Cross section of penial gland.
3. Pseudobranch and pneumostome.
4. Outline of genitalia with organs separated.
5. Penial complex from outside, in normal position.
6. Penial complex of specimen with preputium pushed upward.
7. Penial complex showing great length of penial gland duct.

8–13. *Helisoma pilsbryi infracarinatum* F. C. Baker. Unless otherwise stated specimens are from Basswood River Rapids, Ontario, Canada; collected by A. R. Cahn.

8. Penial complex of specimen with large preputium. From Rideau River Rapids, Ottawa, Canada; collected by A. LaRocque.
9. Penial complex with preputium pushed upward, showing length of penial gland duct.
10. Penial complex of immature specimen. From Bamiji Lake, Ontario, Canada; collected by Dr. A. R. Cahn.
11. Pseudobranch and adjacent organs.
12. Section through prostate and uterus.
13. Outline of genitalia dissected and organs separated.

Line near figure indicates 1 mm. in length



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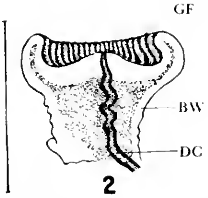

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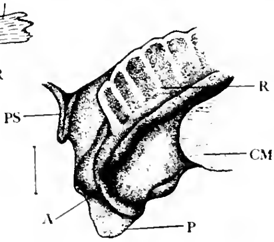

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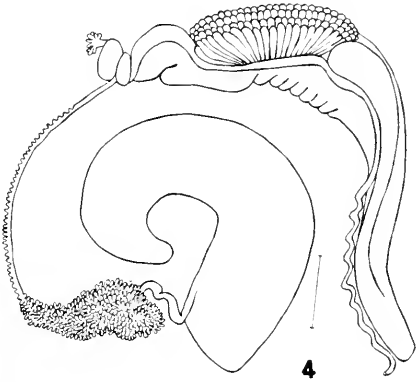

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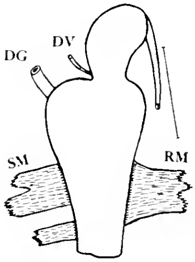

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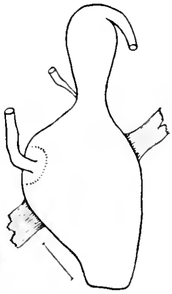

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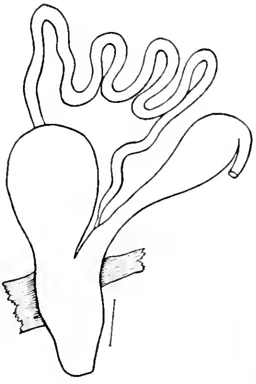

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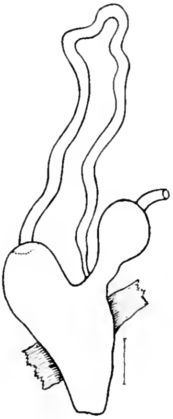

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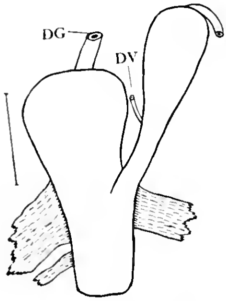

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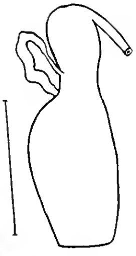

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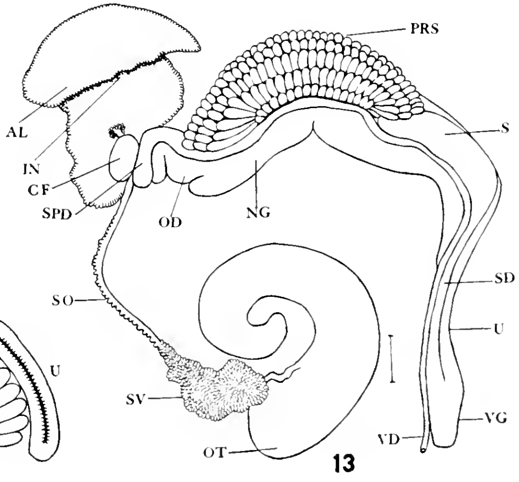

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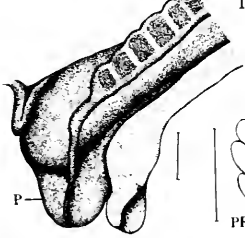

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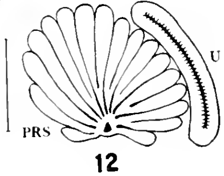

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PLATE 25

PLATE 26

Helisoma

1-5. *Helisoma horni* (Tryon). From Paul Lake, British Columbia; collected by Prof. D. S. Rawson.

1. Penial complex in breeding condition, the preputium pushed upward.
2. Outline of penial gland.
3. Outline of genitalia dissected and organs separated.
4. Cross section through oviduct, sperm duct, and nidamental gland.
5. Cross section through prostate and oviduct, near middle of gland.

6-13. *Helisoma truncatum* (Miles). From Winnebago Lake, near Oshkosh, Wisconsin; collected by F. C. Baker.

6. Penial complex with penial gland duct in normal position coiled on surface of preputium.
7. Penial complex with penial gland duct pulled out to show great length.
8. Cross section of ovotestis near anterior end.
9. Cross section of penial gland.
10. Cross section of prostate and oviduct near anterior end.
11. Head showing position of pseudobranch, pneumostome, and rectum.
12. Penial complex with penial gland duct spread out. Preputium is partly pushed upward.
13. Genitalia dissected and organs separated.

Line near figure indicates 1 mm. in length

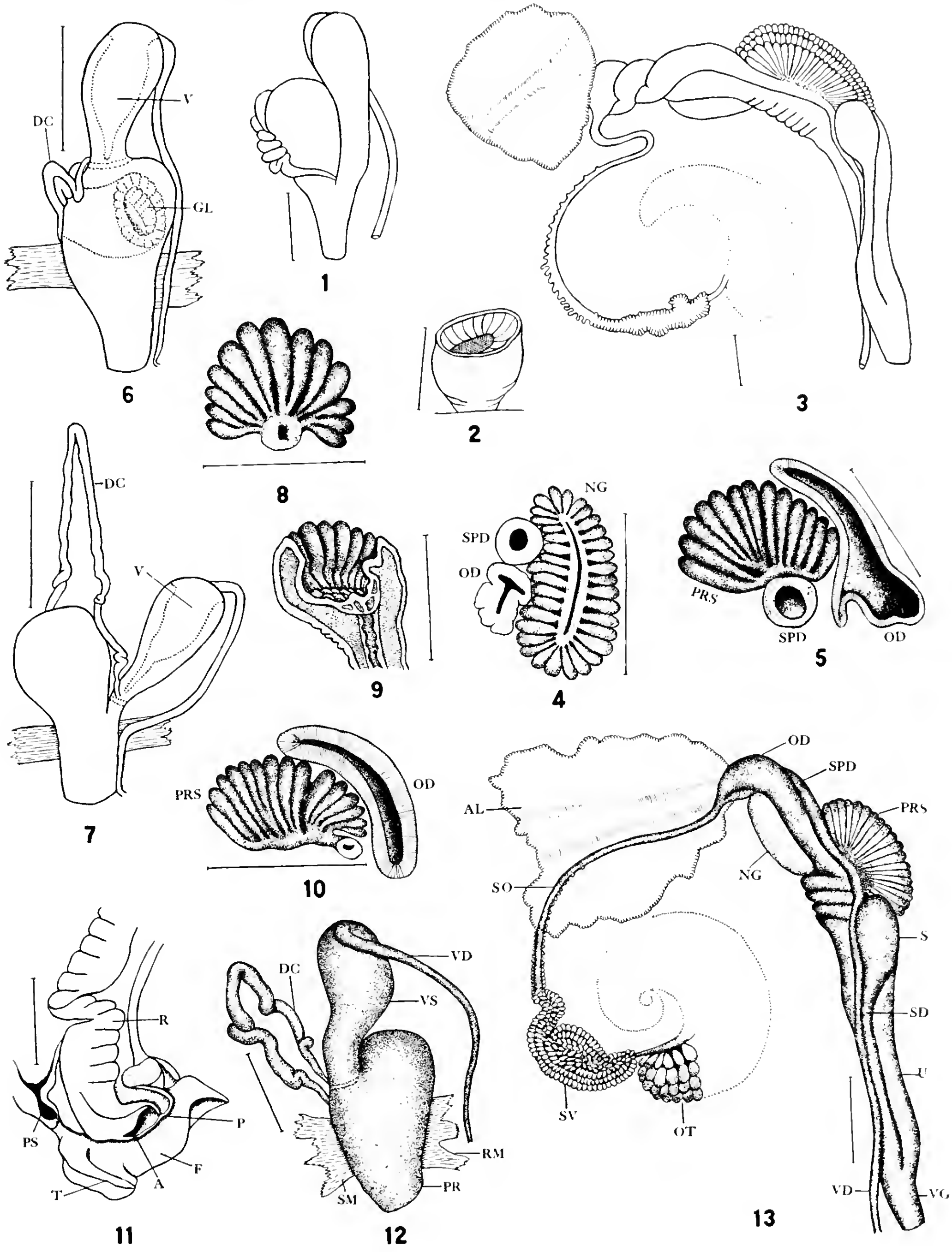
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PLATE 26

PLATE 27

Helisoma campanulatum (Say)

From Oneida Lake, New York, near Brewerton; collected by F. C. Baker.

1. Section through penial gland.
2. Albumen gland from below.
3. Section through diaphragm showing relationship of penial gland duct to vergic sac.
4. Section through ovotestis near anterior end.
5–7. Penial complex of *Helisoma campanulatum smithi* (F. C. Baker), from Douglas Lake, Michigan, showing variation in form, especially the preputium.

8–14. *Helisoma campanulatum canadense* F. C. Baker. From Sturgeon Lake, Ontario, Canada; collected by Dr. A. R. Cahn.

8. Penial complex.
9. Penial complex showing penial gland duct coiled between preputium and vergic sac. Also variation in muscles.
10. Section of penial complex showing relationship of penial gland to verge.
11. Penial complex with penial gland duct uncoiled to show length.
12. Section through prostate near middle of gland.
13. Pseudobranch, pneumostome, and rectum.
14. Genitalia dissected and organs separated.

Line near figure indicates 1 mm. in length

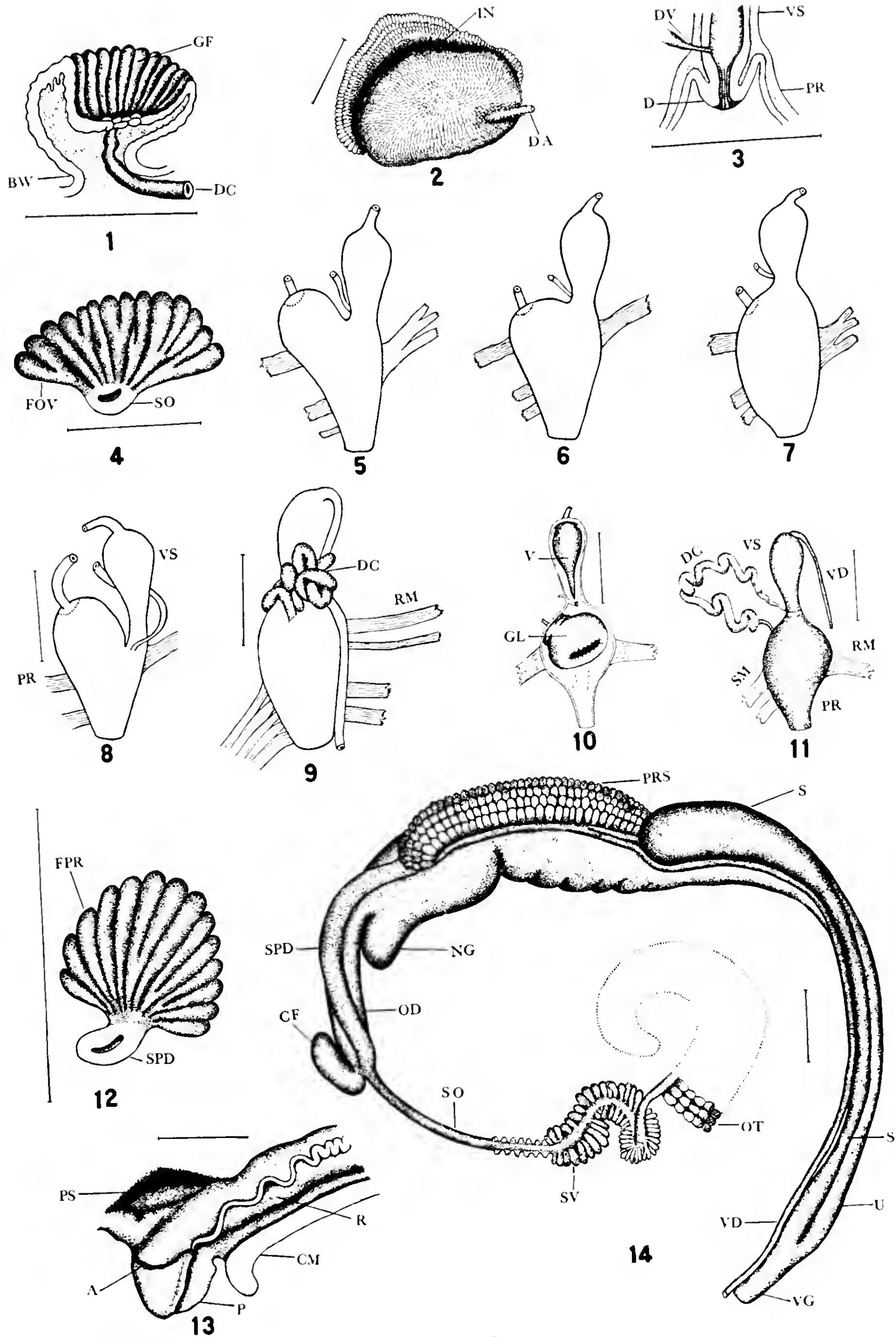
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PLATE 27

PLATE 28

Helisoma

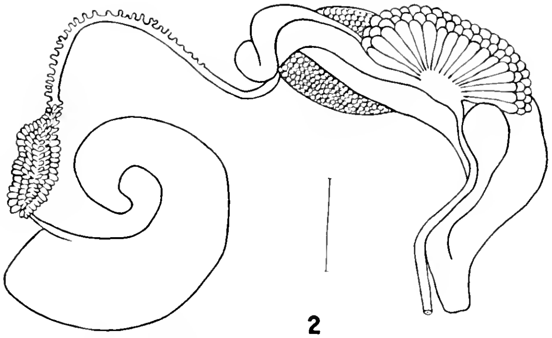
1–5. *Helisoma oregonense* (Tryon). From Tooele Co., Utah; collected by J. Henderson.

1. Penial complex showing long penial gland duct.
2. Genitalia dissected and organs separated.
3. Cross section of prostate near middle of gland.
4. Penial gland viewed from above.
5. Section through penial gland.

6–14. *Helisoma scalare* (Jay). From Lake Butler, Florida; received from Dr. E. A. Andrews.

6. Entrance of penial gland duct into vergic sac.
7. Section through penial gland.
8. Pseudobranch and pneumostome.
9. Penial complex with preputium pushed upward.
10. Penial complex in normal position, the penial gland duct extended.
11. Penial complex in section to show relationship of organs.
12. Section through prostate near middle.
13. Section through ovotestis near anterior end.
14. Genitalia dissected and organs separated.

Line near figure indicates 1 mm. in length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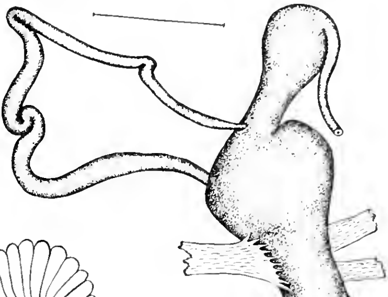
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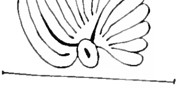
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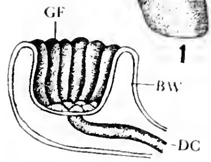

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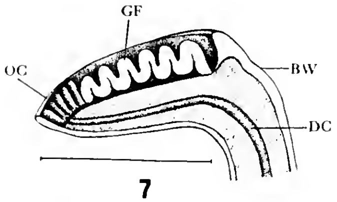

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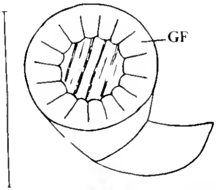

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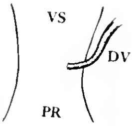

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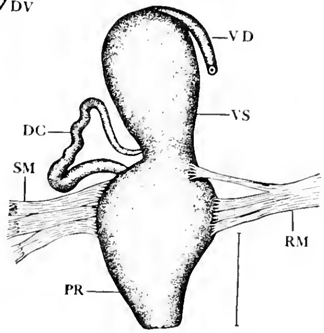

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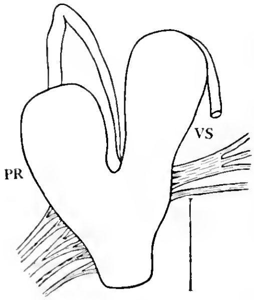

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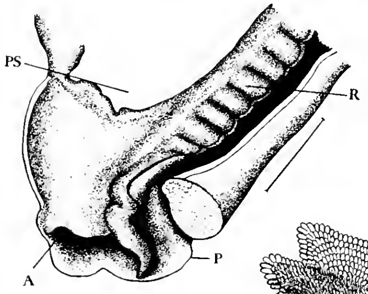

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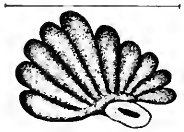
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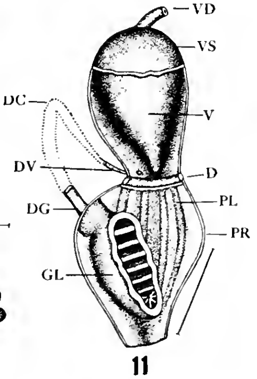

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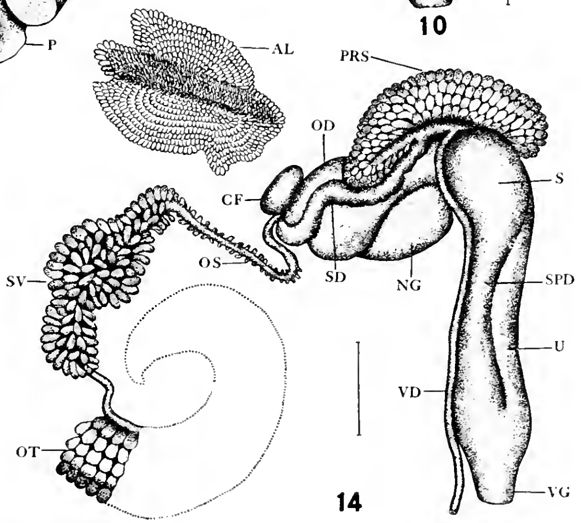

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PLATE 28

PLATE 29

Helisoma

1–6. *Helisoma trivolvis pseudotrivolvis* (F. C. Baker) = *lentum* Say. From St. Joseph, Champaign Co., Illinois; collected by F. C. Baker.
- 1. Penial complex with penial gland duct spread out to show length.
- 2. Penial complex in section showing penial gland in natural position in preputium.
- 3. Penial complex with penial gland duct coiled on preputium.
- 4. Penial gland in section.
- 5. Penial complex in section showing preputium pushed upward and penial gland duct uncoiled. From Illinois River, Peoria, Illinois.
- 6. Neck of animal showing penial gland everted. From Reelfoot Lake, Tennessee.

7–13. *Helisoma trivolvis lentum* (Say). From New Orleans, Louisiana; collected by E. C. Faust.
- 7. Penial complex with penial gland everted.
- 8. Penial complex with penial gland duct uncoiled.
- 9. Verge fully extended with sections in two places as indicated.
- 10. End of verge showing exit of sperm canal with small, lip-like processes surrounding the opening.
- 11. Head and neck of animal showing penial gland and verge everted.
- 12. Penial complex with penial gland and verge everted.
- 13. Verge in fig. 12 removed from penial complex.

14–16. *Helisoma trivolvis macrostomum* (Whiteaves).
- 14. Penial complex. From Bayfield, Wisconsin; collected by F. C. Baker.
- 15. Penial complex with preputium pushed upward. Same locality as fig. 14.
- 16. Penial complex with penial gland duct uncoiled. From Lake Gauvreau, Canada; collected by A. LaRocque.

17, 18. *Helisoma trivolvis fallax* (Haldeman). From Cambridge, Massachusetts; collected by W. J. Clench.
- 17. Penial complex showing large size of preputium.
- 18. Exterior view of penial gland.

19–22. *Helisoma chautauquense* F. C. Baker. From Chautauqua Lake, New York; collected by F. C. Baker.
- 19. Penial complex of immature specimen.
- 20. Exterior view of penial gland.
- 21. Verge much retracted.
- 22. Penial complex of adult specimen in normal condition.

Line near figure indicates 1 mm. in length. In fig. 10 line equals 0.5 mm.

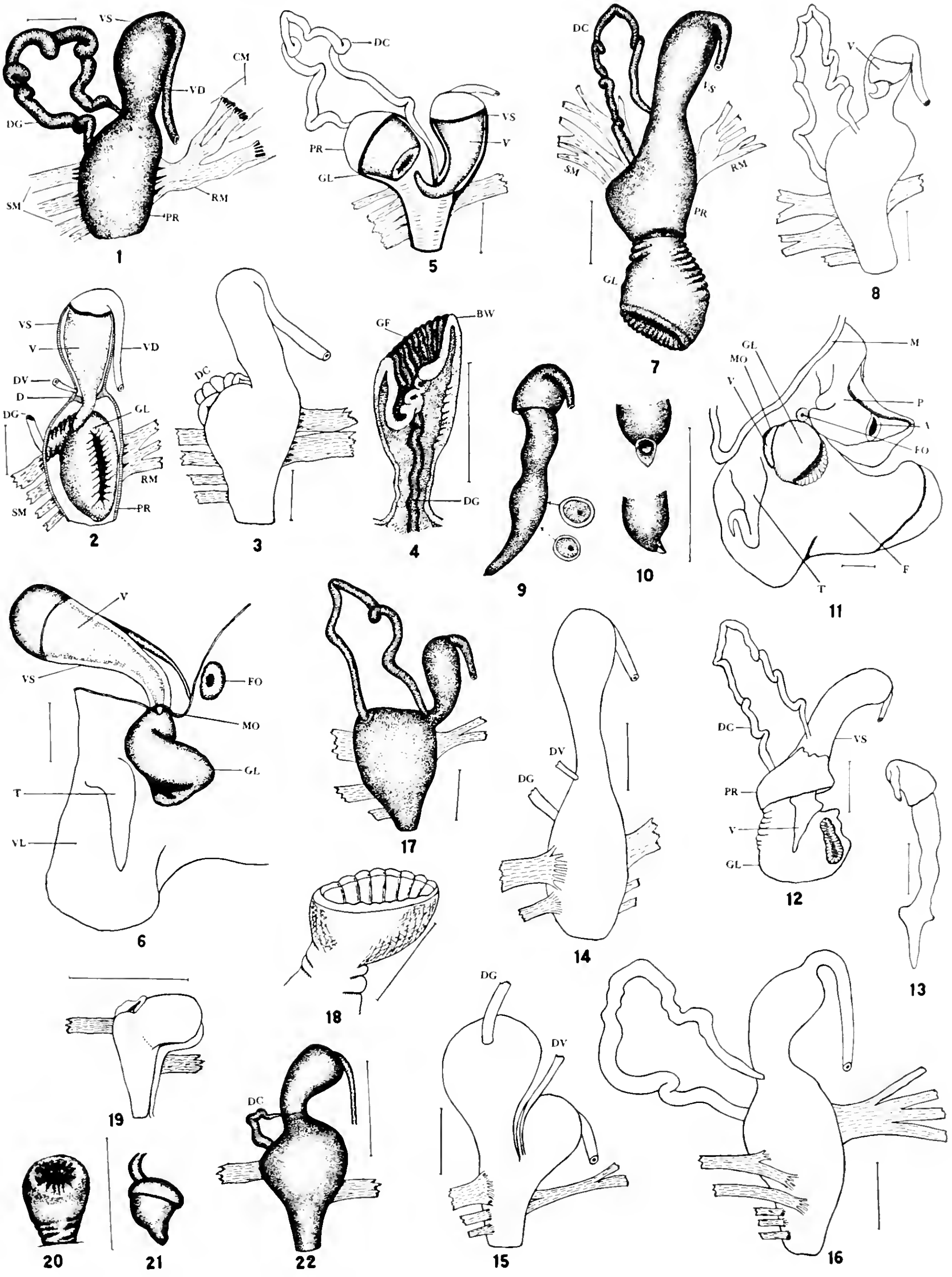
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PLATE 29

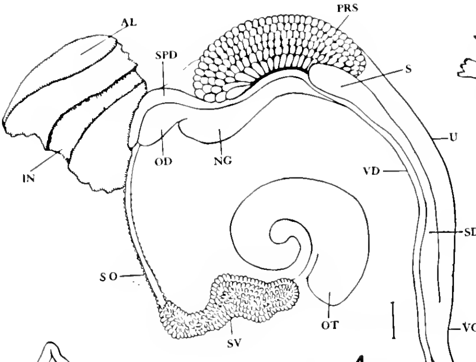
PLATE 30

Helisoma

1–9. *Helisoma plexatum* (Ingersoll). Collected by J. Henderson.
  1. Penial complex with penial gland duct uncoiled. From Columbine Lake, Colorado.
  2. Penial complex with vergic sac cut open to show form of verge.
  3. Penial complex in section to show form of gland. From Columbine Lake, Colorado.
  4. Genitalia dissected and organs separated. From Smartweed Lake, Colorado.
  5. Cross section of penial gland. From Lower Los Lagos, near Smartweed Lake.
  6–8. Section of vergic sac showing form of verge in different individuals. From Teton River, north of Rexburg, Idaho.
  9. Form of verge in a specimen from Smartweed Lake, Colorado.

10–19. *Helisoma subcrenatum* (P. P. Carpenter). From one mile west of Devon, Montana; collected by J. Henderson.
  10. Penial complex showing short penial gland duct in immature specimen.
  11. Section of penial gland.
  12. Cross section of prostate about midway of its length.
  13. Section through penial complex showing verge and penial gland.
  14. Albumen gland from below.
  15. Genitalia dissected and organs separated.
  16. Head showing pseudobranch, pneumostome, and rectum.
  17. Penial complex with penial gland duct uncoiled.
  18. Penial complex in section showing form of penial gland and verge.
  19. Penial complex with vergic sac cut open to show verge. Figures 17-19 are from specimens collected at Cottonwood Pass, near Gypsum, Colorado.

Line near figure indicates 1 mm. in length



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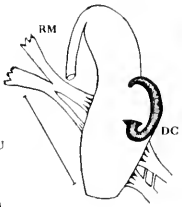

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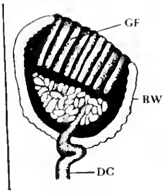

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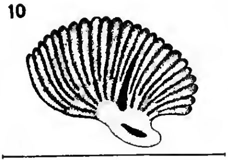

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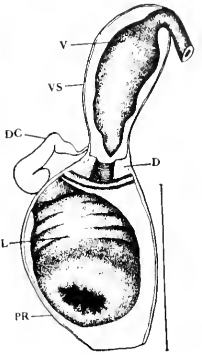

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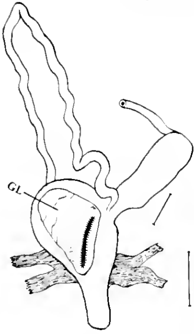

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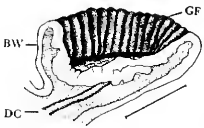

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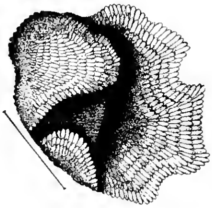

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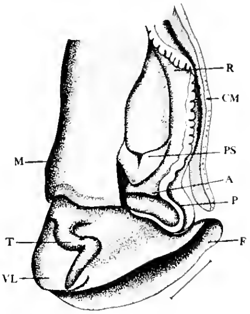

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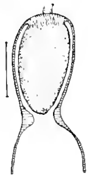

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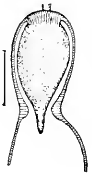

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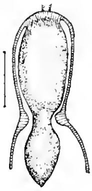

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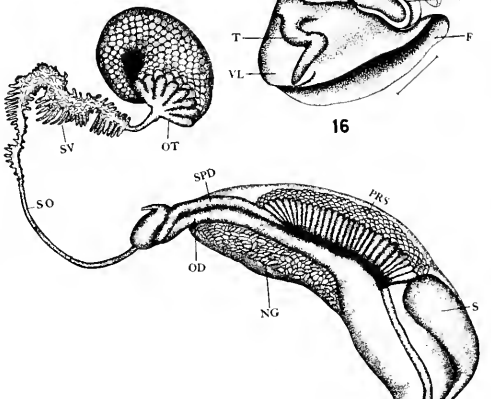

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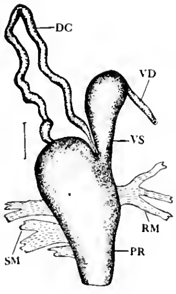

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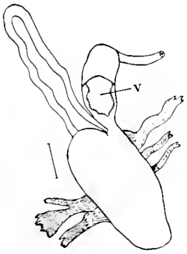

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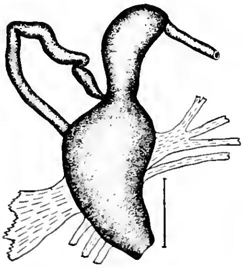

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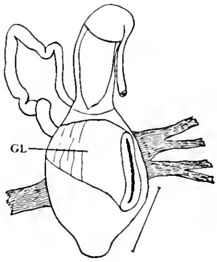

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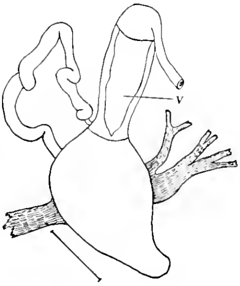

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PLATE 30

PLATE 31

Helisoma

1–7. *Helisoma corpulentum* (Say). From Knife Lake, Minnesota and Lake La Croix, Ontario; collected by Dr. A. R. Cahn.

- 1. Cross section of ovotestis. From Knife Lake.
- 2. Cross section of prostate and uterus at X in fig. 3. From Knife Lake.
- 3. Genitalia dissected and organs separated. From Knife Lake.
- 4. Penial complex with preputium pushed upward and penial gland duct uncoiled.
- 5. Penial complex and penial gland duct in natural position. From Knife Lake.
- 6. Penial complex of immature specimen, shell 12 mm. in diameter. From Lake La Croix.
- 7. Penial complex of specimen with shell 14 mm. in diameter. From Lake La Croix.

8–13. *Helisoma corpulentum multicostatum* F. C. Baker. From Kahnipiminanicock Lake, Ontario, Canada; collected by Dr. A. R. Cahn.

- 8. Cross section of penial gland. Duct not shown.
- 9. Penial complex of immature specimen, shell 5.5 mm. in diameter. Duct short.
- 10. Penial complex of half-grown animal, shell 14.5 mm. in diameter.
- 11. Penial complex of another half-grown specimen, shell 14.5 mm. in diameter.
- 12. Penial complex of specimen almost adult, shell 16 mm. in diameter.
- 13. Penial complex of adult animal, shell 23 mm. in diameter. Duct long, uncoiled.

14–18. *Helisoma corpulentum vermilionense* F. C. Baker. From Lake Vermilion, Minnesota; collected by F. C. Baker.

- 14. Penial complex showing preputium pushed upward. Duct uncoiled.
- 15. Section of penial gland showing cup and penial gland duct.
- 16. Penial complex, specimen about one-fourth grown.
- 17. Penial complex in specimen somewhat older than fig. 16.
- 18. Penial complex of animal about half-grown. Verge of different shape.

19. *Helisoma whiteavesi* F. C. Baker. From Mille Lacs, Ontario, Canada; collected by A. R. Cahn.

- 19. Penial complex with small vergic sac, the penial gland duct uncoiled.

20–22. *Helisoma magnificum* (Pilsbry). From Greenfield Pond, 1 mile south of Wilmington, North Carolina; collected by Dr. Paul Bartsch.

- 20. Penial complex with penial gland duct uncoiled.
- 21. Penial complex in section.
- 22. Penial gland in section.

Line near figure indicates 1 mm. in length

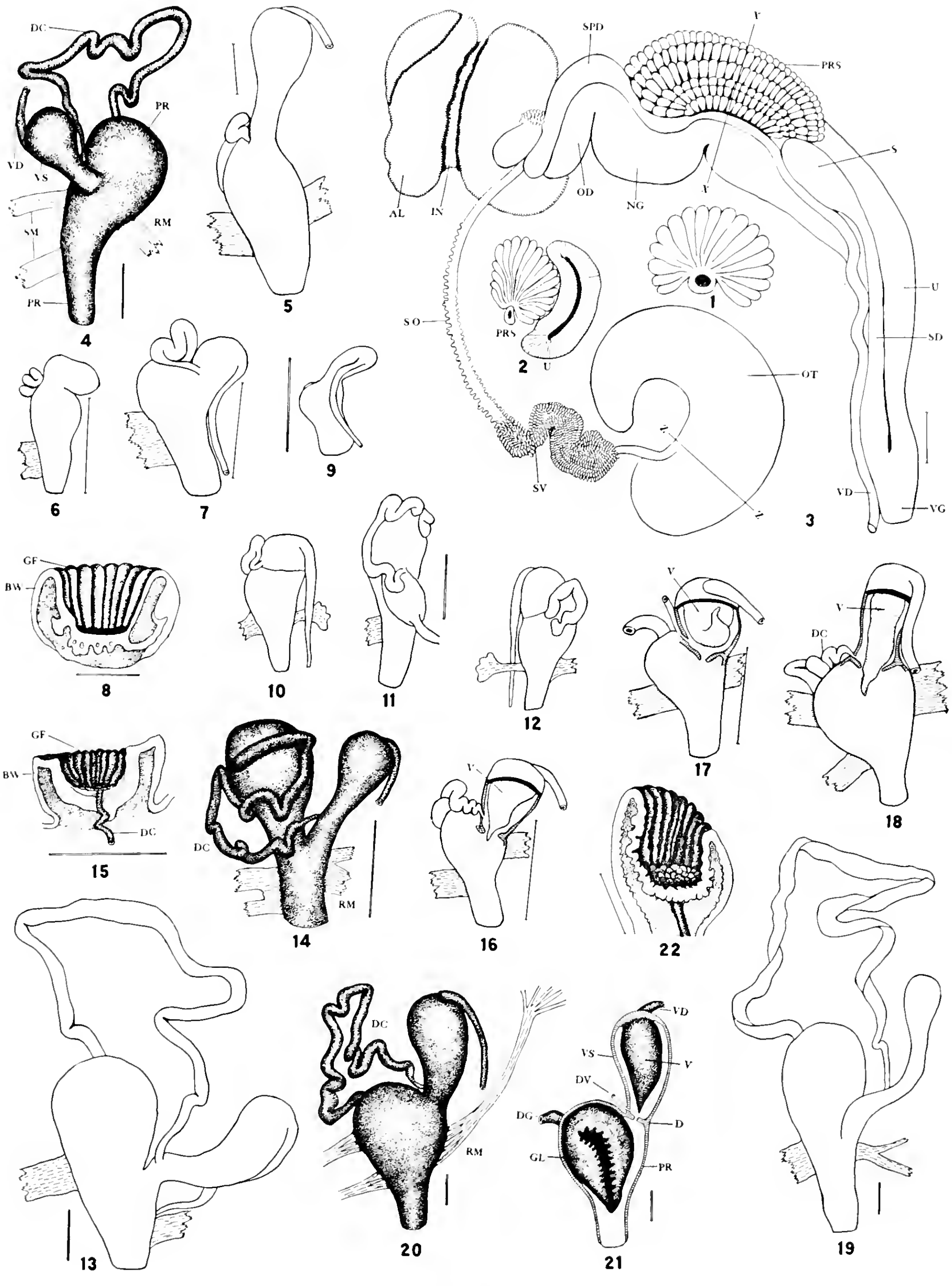
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PLATE 31

PLATE 32

Helisoma

1–7. *Helisoma tenue californiense* F. C. Baker. From pools from artesian wells, near Shandon, California; collected by Dr. G. D. Hanna.

1. Genitalia dissected and organs separated.
2. Penial complex cut open to show verge.
3. Penial complex with vergic sac at summit of preputium.
4. Pseudobranch, pneumostome, and rectum.
5. Penial gland viewed from the outside.
6. Section of prostate and uterus.
7. Penial complex with penial gland duct uncoiled. From Prospect Park, Redlands, California; collected by Dr. S. S. Berry.

8. *Helisoma subcrenatum* (P. P. Carpenter). Variety. From Pass Lake, Fidalgo Island, Puget Sound, Washington; collected by J. Henderson.

8. Penial complex with preputium pushed upward.

9, 10. *Helisoma occidentale* (Cooper). From Wacos Bay, Klamath Lake, Oregon; collected by J. Henderson.

9. Position of verge in vergic sac.
10. Penial complex with preputium pushed upward.

11–17. *Helisoma traskii* (Lea). From slough near Kern River, three miles northeast of Bakersfield, California; collected by L. G. Ingles.

11. Penial complex cut open to show form of penial gland.
12. Cross section through prostate, uterus, and nidamental gland.
13. Section through penial gland.
14. Penial complex in normal position with penial gland duct uncoiled.
15. Pseudobranch, pneumostome, and rectum.
16. Bifid tentacle.
17. Genitalia dissected and organs separated.

Line near figure indicates 1 mm. in length

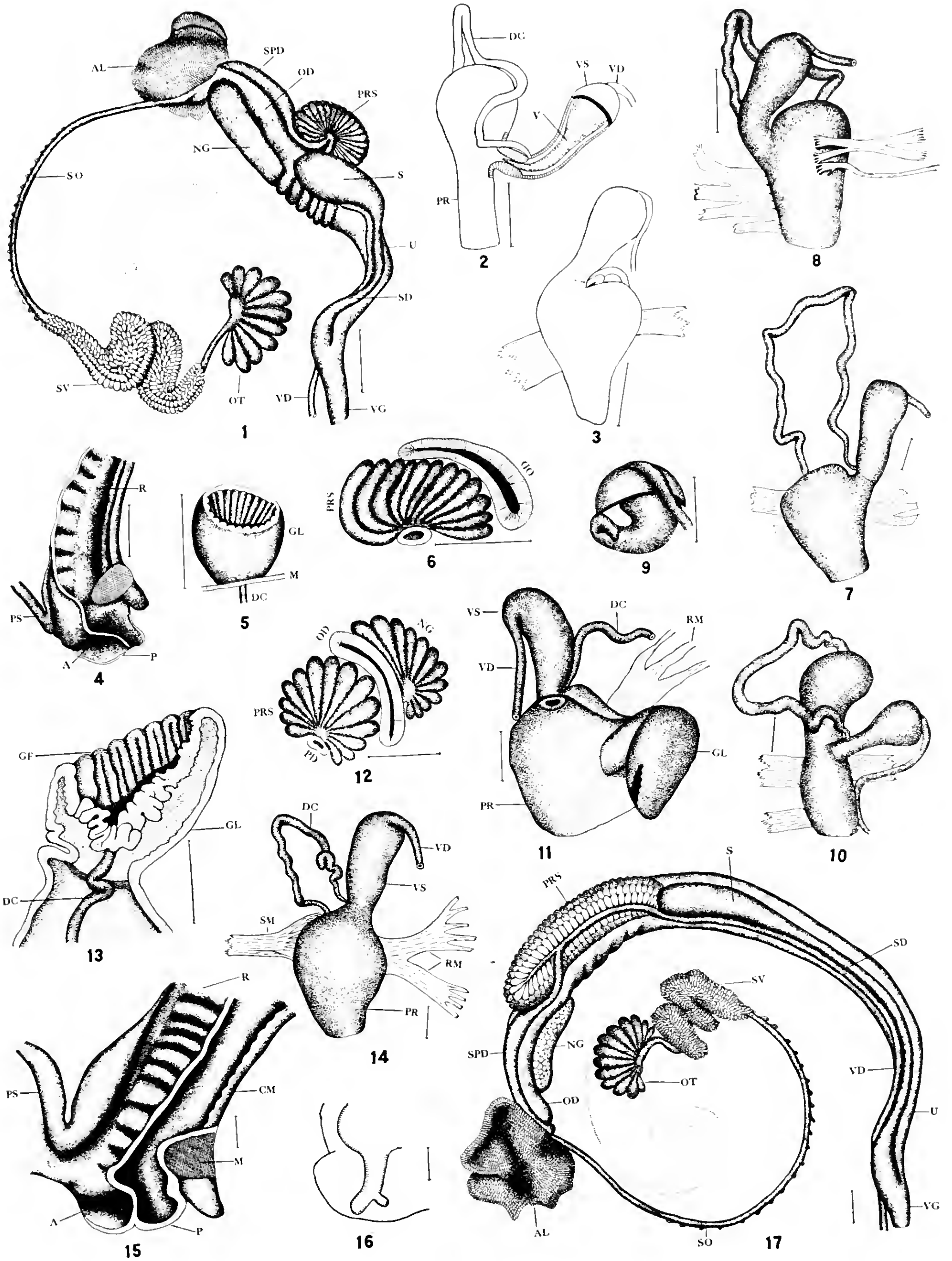
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PLATE 32

PLATE 33

Helisoma

1–7. *Helisoma duryi eudiscus* Pilsbry. From Silver Springs, Florida; collected by T. Van Hyning.

1. Penial complex showing swollen duct of penial gland and position of verge in vergic sac.
2. Penial complex from exterior with penial gland duct uncoiled.
3. Penial gland in section showing the long, shallow cup.
4. Exterior view of penial gland.
5. Penial complex with preputium pushed upward.
6. Penial complex of immature specimen, shell 6.5 mm. in diameter.
7. A very wide example of penial complex.

8–10, 12, 16–19. *Helisoma duryi normale* Pilsbry.

8. Penial complex. From near Paines Prairie, Gainesville, Florida; collected by T. Van Hyning.
9. Penial complex with swollen preputium. From Santa Fe River, High Springs, Alachua Co., Florida; collected by T. Van Hyning.
10. Penial gland in section. Same locality as fig. 9.
12. Penial complex. Variation in form. From Tamiami Trail, 40 miles west of Miami, Florida; collected by W. F. Shay.
16. Head and neck with penial gland protruding from male opening. Same locality as fig. 12.
17. Penial complex. A normal form showing short penial gland duct. Same locality as fig. 12.
18. Penial complex. A very wide example. Same locality as fig. 12.
19. Penial gland of half-grown specimen. From near Gainesville, Florida.

11, 13, 14. *Helisoma duryi* (Wetherby), near typical form. Same locality as fig. 12.

11. Penial gland, partly contracted.
13. Penial complex with penial gland protruding from male opening.
14. Penial complex of normal specimen

15. *Helisoma duryi normale* Pilsbry, varying toward *intercalare* (Pilsbry).

15. Genitalia dissected and organs separated. From canal at Boynton, Florida; collected by W. F. Shay.

Line near figure indicates 1 mm. in length

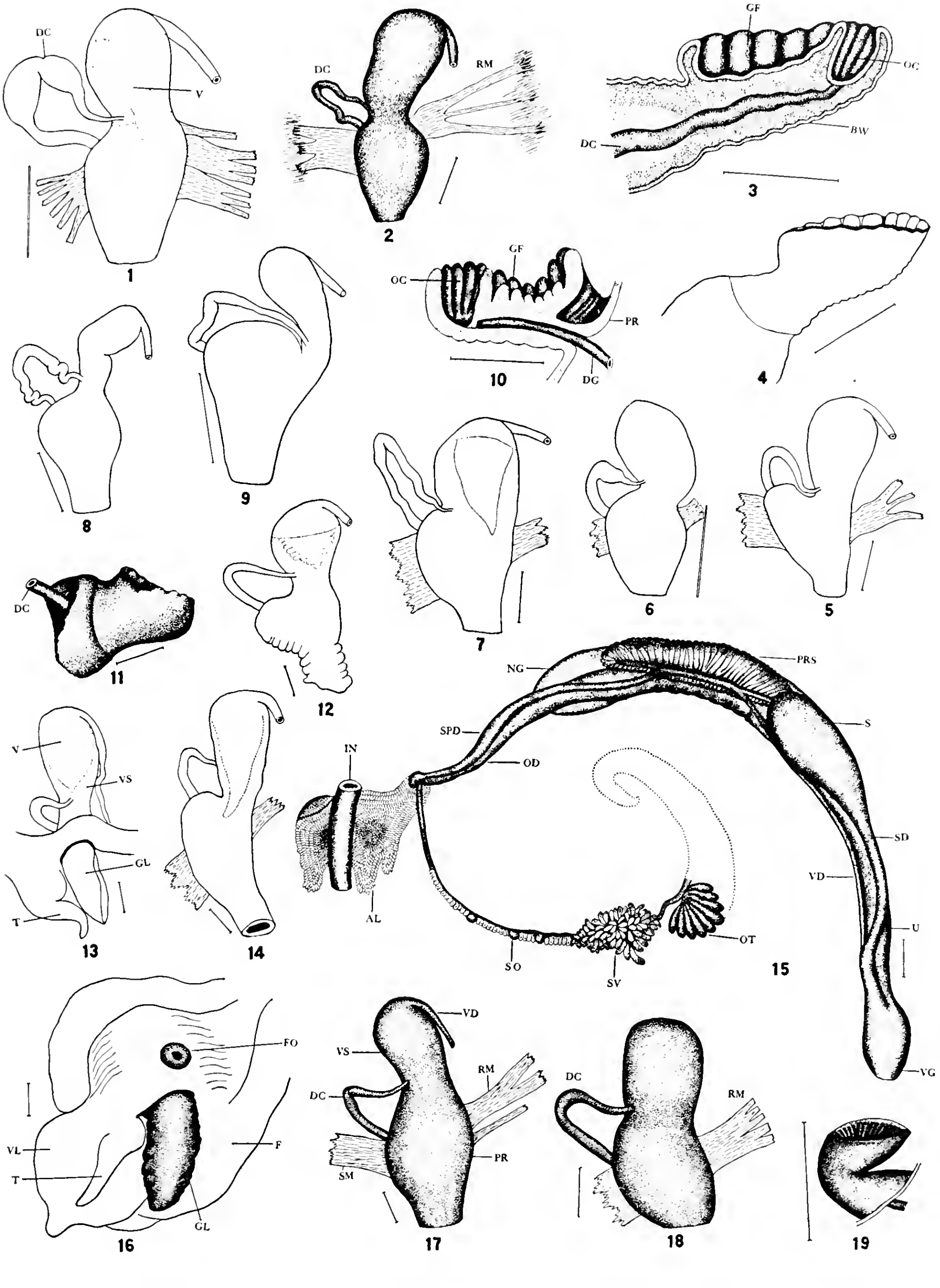
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PLATE 33

PLATE 34

Carinifex ponsonbyi E. A. Smith

From Upper Klamath Lake, Oregon; collected by J. Henderson.

1. Head and foot showing pseudobranch and pneumostome.
2. Penial complex showing muscle system and short penial gland duct.
3. Penial complex cut open to show verge and penial gland.
4. Genitalia dissected and organs separated. Shows unusual position of spermatheca.
5. Albumen gland from below.
6. Portion of genitalia showing relationship of oviduct, sperm duct, ovisperm duct, and duct to albumen gland.
7. Cross section of prostate and uterus.
8. Cross section of prostate near distal end.
9. Cross section of ovotestis near proximal end.
10. Section through penial gland to show duct and folds.
11. Vagina and spermatheca of different form.
12. Cross section of preputial sac to show vertical ridges or pilasters.

Line near figure indicates 1 mm. in length. Figure 12 has same magnification as fig. 2.

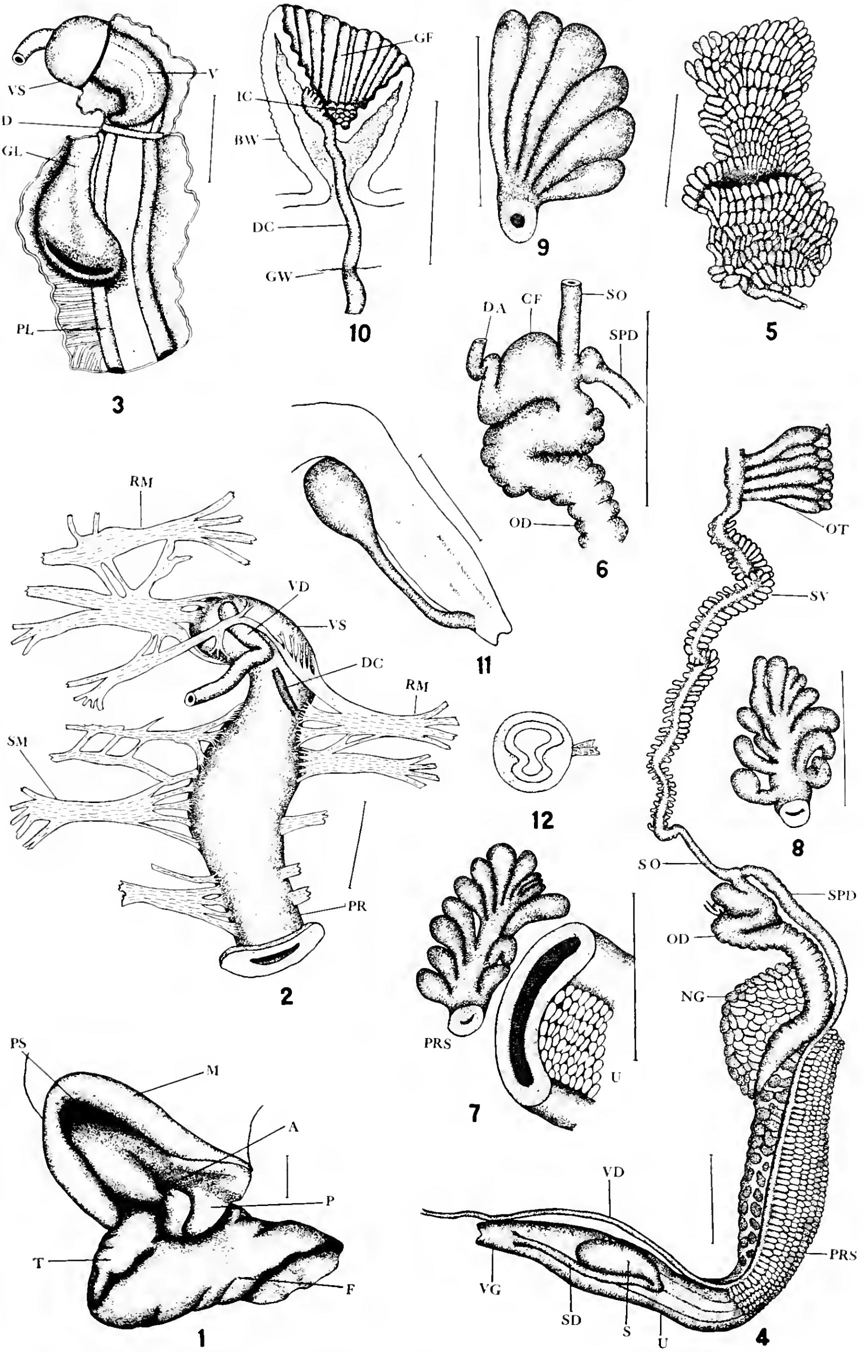
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PLATE 34

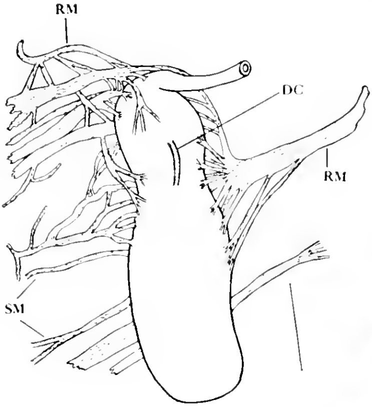
PLATE 35

Carinifex

1. *Carinifex ponsonbyi* E. A. Smith. From Upper Klamath Lake, Oregon.
    1. Penial complex showing variation in muscle system.

2–9. *Carinifex jacksonensis* J. Henderson. From Jackson Lake, Wyoming; collected by J. Henderson.
    2. Summit of verge showing attachment of retractor muscles.
    3. Penial complex showing multiplication of retractor muscles and short penial gland duct.
    4. Pseudobranch and pneumostome.
    5. Genitalia dissected and organs separated.
    6. Portion of genitalia showing relationship of oviduct, sperm duct, ovisperm duct, etc.
    7. Same organs as in fig. 6, from above.
    8. Albumen gland.
    9. Another form of spermatheca.

Line near figure indicates 1 mm. in length



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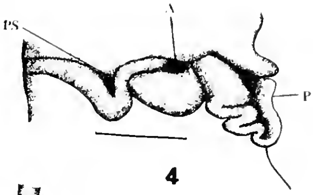

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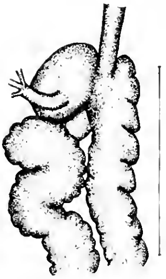

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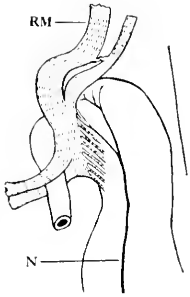

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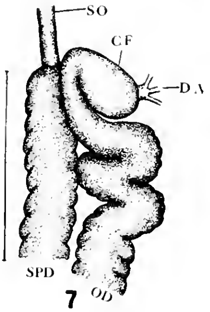

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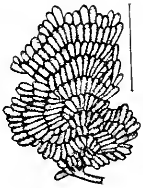

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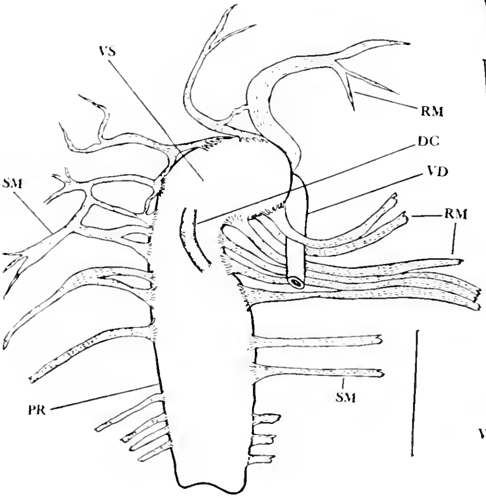

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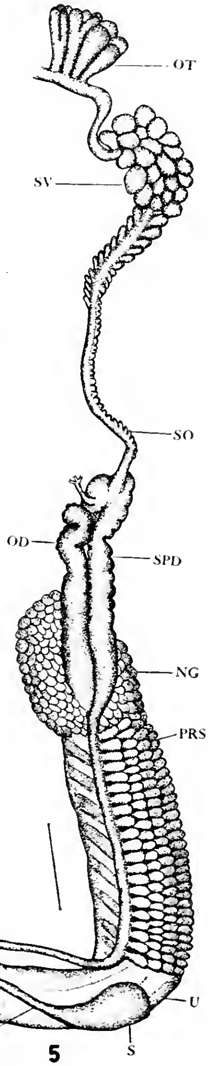

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PLATE 35

PLATE 36

Parapholyx

1–9, 11, 12. *Parapholyx effusa klamathensis* F. C. Baker. From Upper Klamath Lake, Oregon; collected by J. Henderson.

1. Whole animal removed from shell.
2. Pseudobranch and related organs.
3. Genitalia dissected and organs separated.
4. Cross section of prostate, uterus, and nidamental gland.
5. Cross section of ovotestis about midway of its length.
6. Cross section of ovotestis toward posterior end.
7. Penial complex showing retractor muscles and short penial gland duct.
8. Penial complex showing nerve and blood vessels.
9. Penial complex cut open to show verge and penial gland with its short duct. At X gland is cut open to show canal.
11. Section of penial gland showing pipe-like cup and canal.
12. Verge showing central position of exit for the sperm canal.

10. *Parapholyx effusa diagonalis* J. Henderson. From Crater Lake, Oregon; collected by J. Henderson.

10. Vergic sac and upper part of preputium showing verge, muscular ring or diaphragm, and entrance of penial gland duct into diaphragm.

Line near figure indicates 1 mm. in length

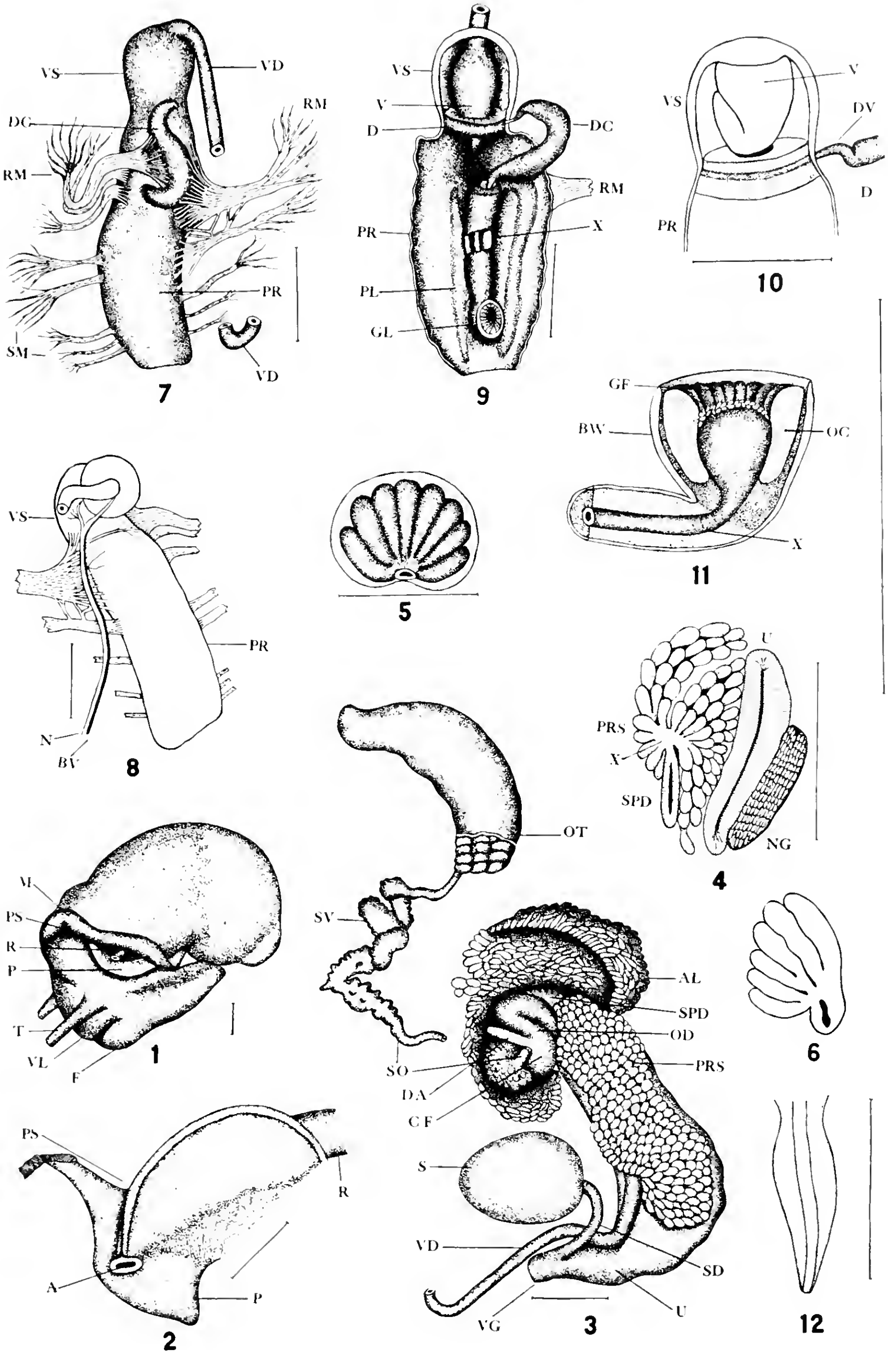
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PLATE 36

PLATE 37

Planorbula armigera (Say)

From Murphy Creek swamp, near Madison, Wisconsin;
collected by J. E. Morrison.

1. Section of prostate near middle of gland.
2. Section of prostate near middle.
3. Portion of genitalia showing relationship of oviduct, sperm duct, ovisperm duct, and carrefour.
4. Genitalia dissected and organs separated, with albumen gland in natural position.
5. Head and foot showing pseudobranch and pneumostome.
6. Section of penial gland.
7. Section of ovotestis to show paired condition of diverticula, which are extended laterally, appearing as though digitate.
8. End of verge to show outlet of sperm canal.
9. Penial complex showing muscles and general form of vergic sac and preputium.
10. Penial complex of small, immature specimen showing wide form of preputium.
11. Section of penial complex showing penial gland spread out and opened, with a short, internal duct.
12. Verge in vergic sac.

Line near figure indicates 1 mm. in length. Long line at left of plate is for figs. 6, 7, and 8. Long line at right of plate is for figs. 1 and 2.

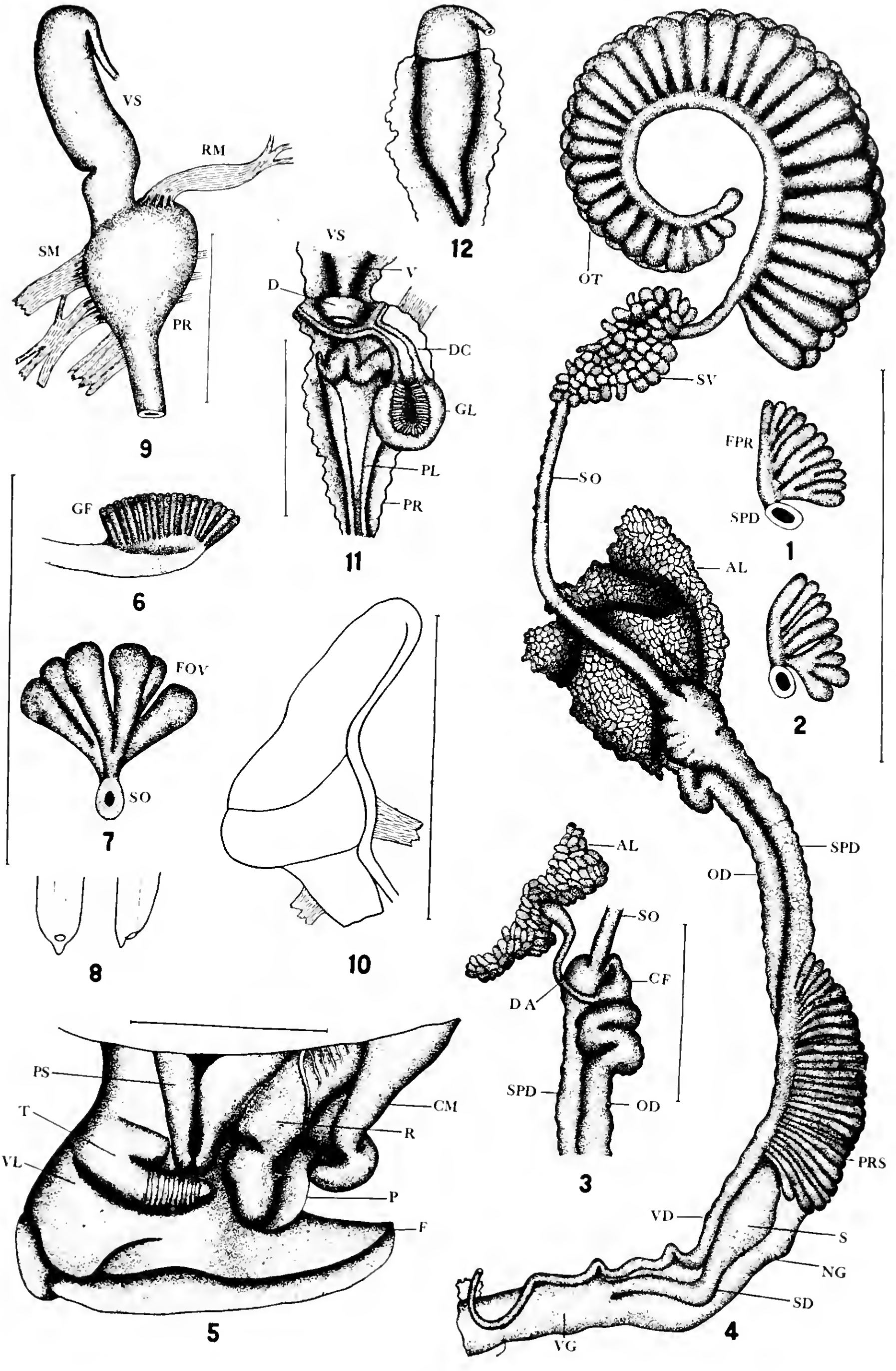
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PLATE 37

PLATE 38

Menetus

1, 2, 4–10. *Menetus opercularis* (Gould). From Mountain Lake, San Francisco, California; collected by H. Walton Clark.

1. Genitalia dissected and organs separated.
2. Section of prostate near distal end.
4. Head showing position of pseudobranch.
5. Section of ovotestis.
6. Penial gland with cup expanded.
7. Albumen gland.
8. Section through penial complex showing natural position of penial gland.
9. Albumen gland in natural position overlying stomach.
10. Exterior view of penial complex.

3, 11–15. *Menetus cooperi callioglyptus* (Vanatta). From Crescent City, California; received from Dr. G. D. Hanna. Also from Quatsino Sound, British Columbia; collected by A. Peake.

3. Section of prostate about midway of its length. California specimen.
11. Penial complex from the outside. California specimen.
12. Penial complex. British Columbia specimen.
13. Entire prostate. British Columbia specimen.
14. Cross section of prostate and uterus near front end. British Columbia specimen.
15. End of verge showing central outlet of sperm canal. British Columbia specimen.

Line near figure indicates 1 mm. in length. Line at left of fig. 10 is also for figs. 7 and 8. Line at left of fig. 14 is also for figs. 2, 3, 5, 6, 14, and 15.

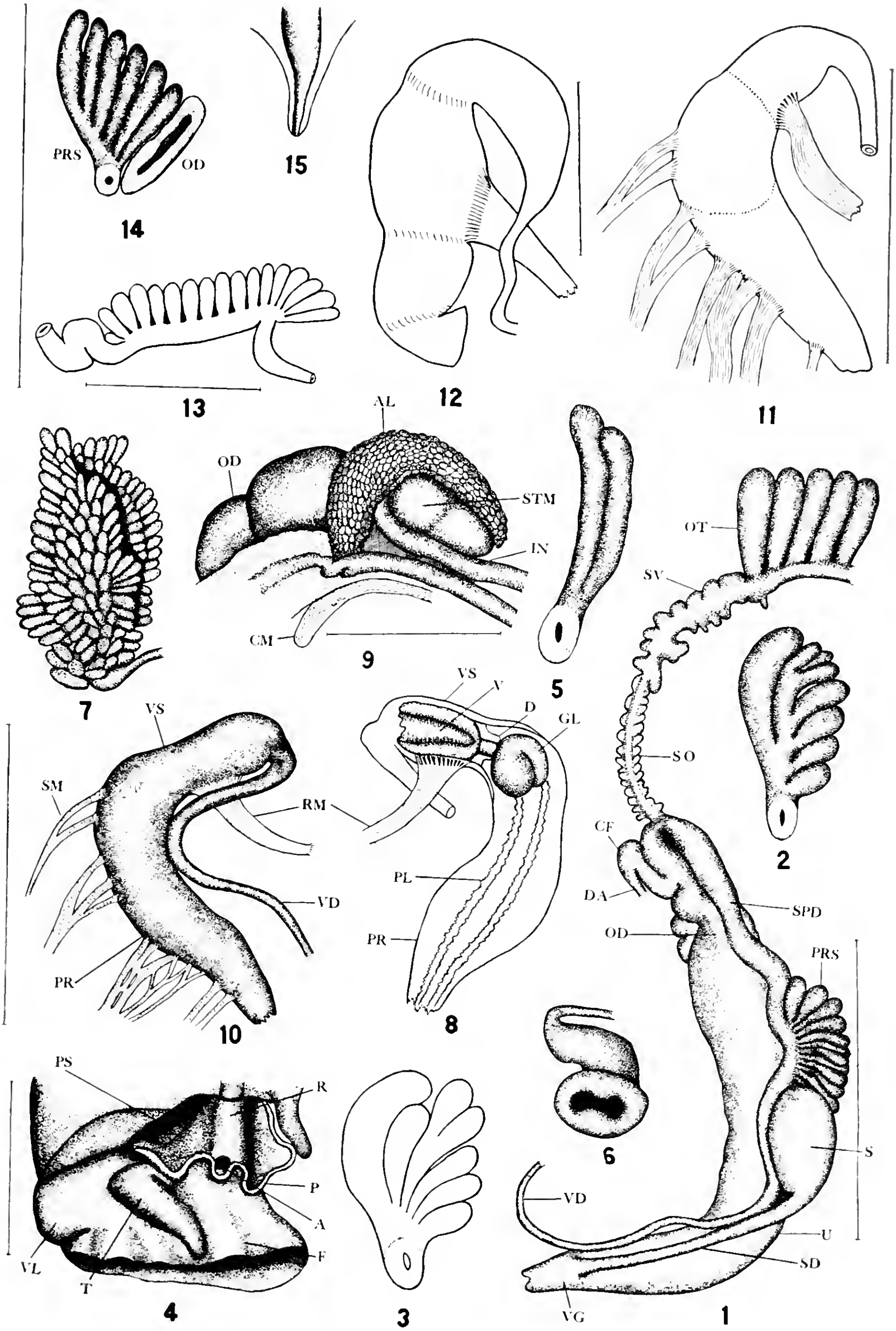
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PLATE 38

PLATE 39

Menetus

1–6, 9, 10. *Menetus cooperi callioglyptus* (Vanatta). From Quatsino Sound, Vancouver Island, British Columbia; collected by Arthur Peake. Also from Crescent City, California. See plate 38.

1. Genitalia dissected and organs separated. California specimen.
2. Head showing form of pseudobranch. California specimen.
3. Penial complex in natural position under female complex. British Columbia specimen.
4. Head showing pseudobranch. California specimen.
5. Penial gland attached to wall of preputium. California specimen.
6. Seminal vesicle and ovisperm duct. California specimen.
9. Penial complex showing enlargement of vas deferens as it enters the vergic sac to form an epiphallus. Also form of penial gland in preputium.
10. Penial complex of specimen badly infested with Trematode worms (flukes). Note peculiar form. British Columbia specimen.

7, 8. *Menetus cooperi* F. C. Baker (= *planulatus* Cooper, preoccupied). From Orcas Island, Puget Sound, Washington; collected by Dr. T. Dale Foster.

7. Penial complex cut open to show verge, penial gland with its short, internal duct, enlargement of vas deferens (epiphallus), and position of retractor muscle.
8. Penial gland in section.

Line near figure indicates 1 mm. in length. Line above fig. 6 is also for figs. 5 and 8. Line near fig. 9 is also for fig. 7.

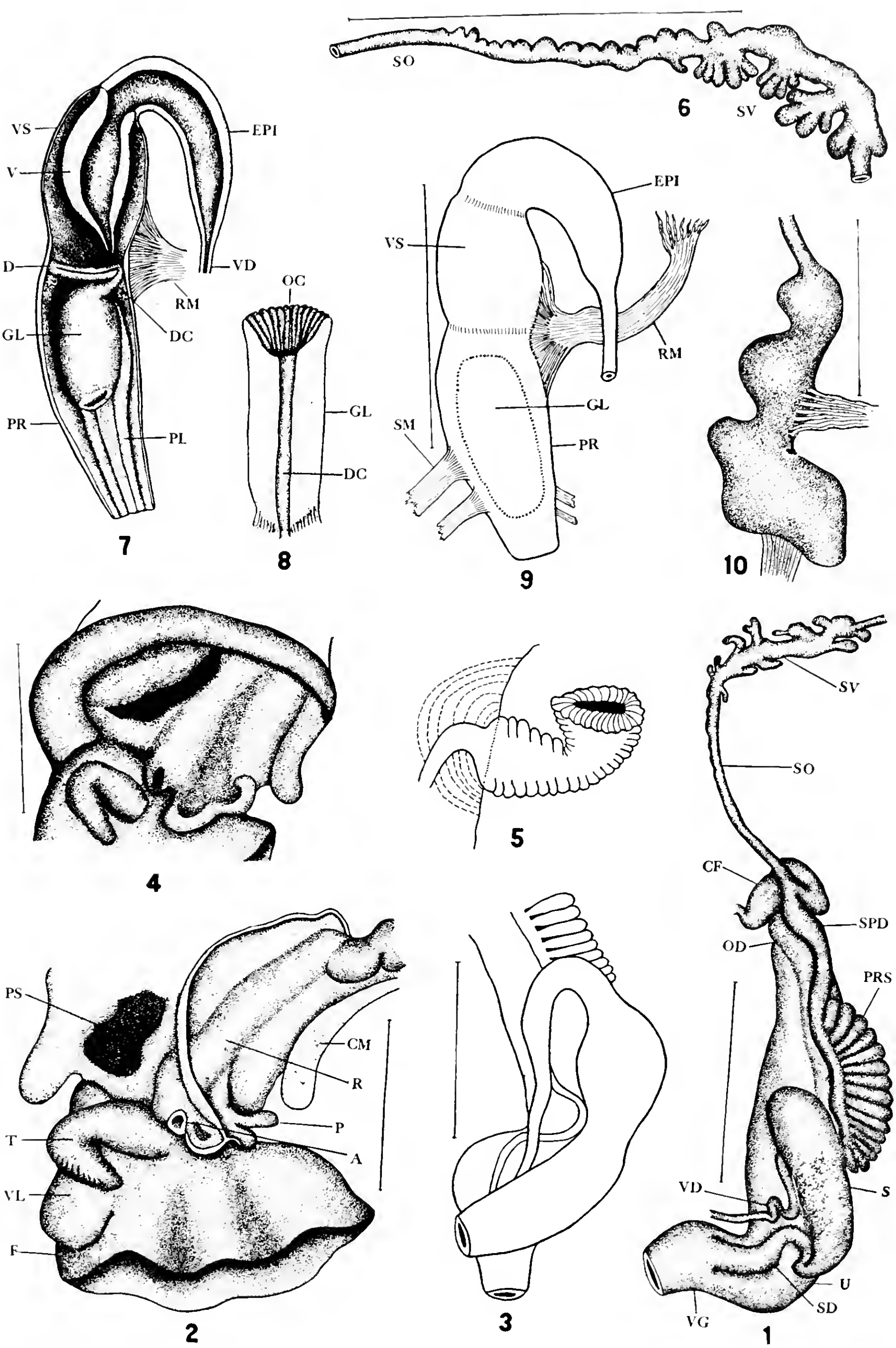
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PLATE 39

PLATE 40

Menetus

3–5, 7, 9, 12. *Menetus dilatatus* (Gould). From pond in field near Unionville, Connecticut; collected by F. C. Baker and Leslie Brewer. Also from Hyannis, Massachusetts; collected by F. C. Baker.

3. Penial complex with preputium pushed upward.
4. Penial complex in natural position, the preputium inflated.
5. Penial complex shown in fig. 4 cut open to show position of verge and penial gland.
7. Pseudobranch of specimen from Hyannis, Massachusetts. A broad form.
9. Pseudobranch of specimen from Unionville.
12. Genitalia dissected and organs separated. Small specimen shows reverse side of prostate and vas deferens.

1, 2, 6, 8, 10, 11. *Menetus sampsoni* (Ancey). From six miles northeast of Dallas, Texas; collected by Dr. E. P. Cheatum. Also from Meremac River, near Stanton, Missouri; collected by Leslie Hubricht.

1. Ovisperm duct and seminal vesicle. Missouri specimen.
2. Penial gland. Texas specimen.
6. Diverticulum of ovotestis with ova in upper part. Texas specimen.
8. Pseudobranch in cylindrical form. Texas specimen.
10. Penial complex cut open to show verge and form of penial gland. Texas specimen.
11. External view of penial complex. Texas form.

Line at left of fig. 12 equals 1 mm. in length. Line at right of fig. 10 equals 0.5 mm. in length. All figures are greatly enlarged.

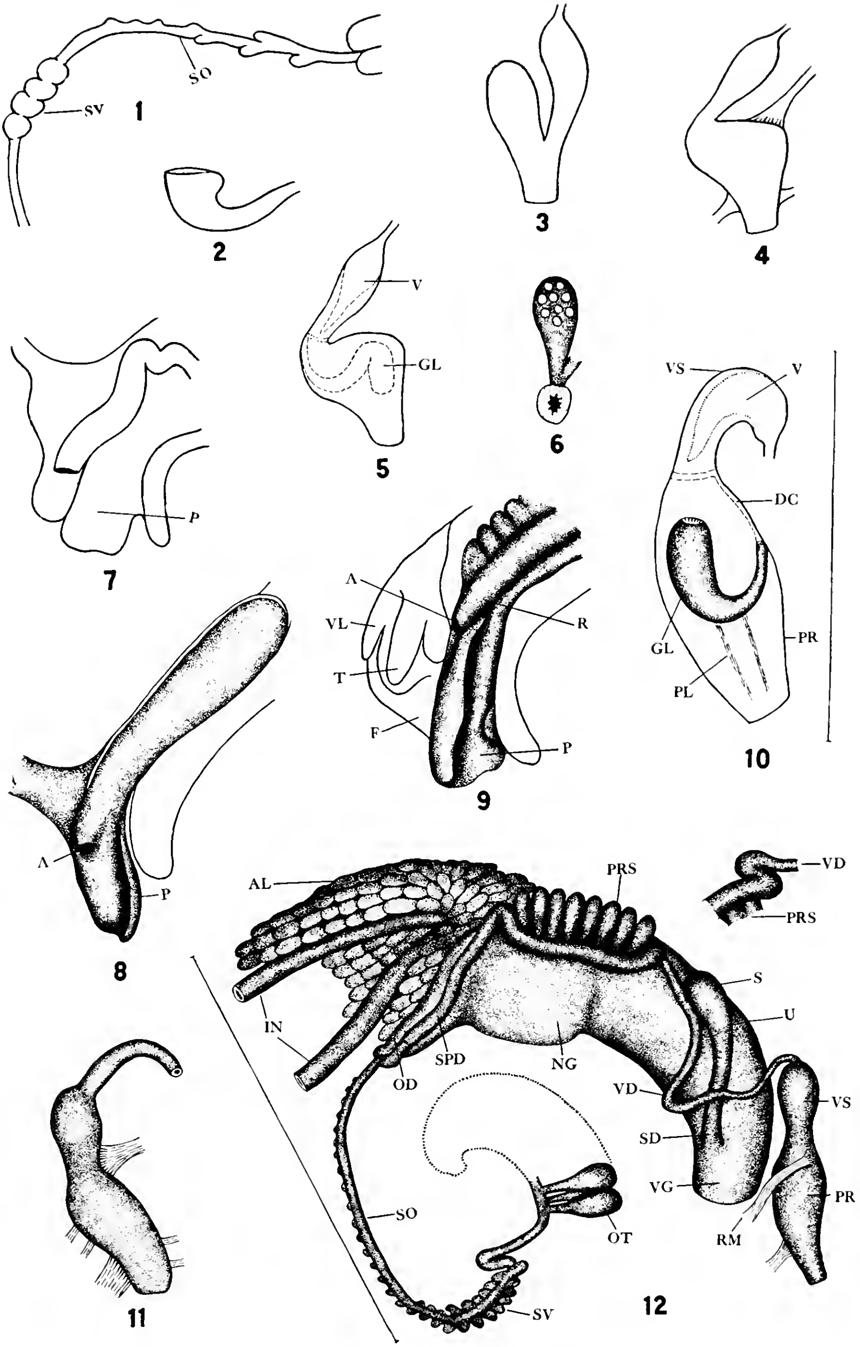
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PLATE 40

PLATE 41

Promenetus exacuous (Say)

From Winnebago Lake, near Oshkosh, Wisconsin; collected by F. C. Baker.

1. Penial complex. Swollen gland causing bulge in preputium.
2. Penial complex, external view, showing a single retractor muscle.
3. Penial complex opened to show verge and penial gland.
4. Cross section of ovotestis about midway of its length.
5. Cross section of prostate near anterior end.
6. Ovotestis viewed from left side of animal, showing diverticula.
7. Albumen gland from the side.
8. Head and neck of animal showing pseudobranch.
9. Head of animal showing verge and penial gland projecting from the male genital opening.
10. Genitalia dissected and organs separated.

Line near figure indicates 1 mm. in length. Line at left of figs. 4 and 5 is for both of these figures. Figure 7 has the same magnification as fig. 10.

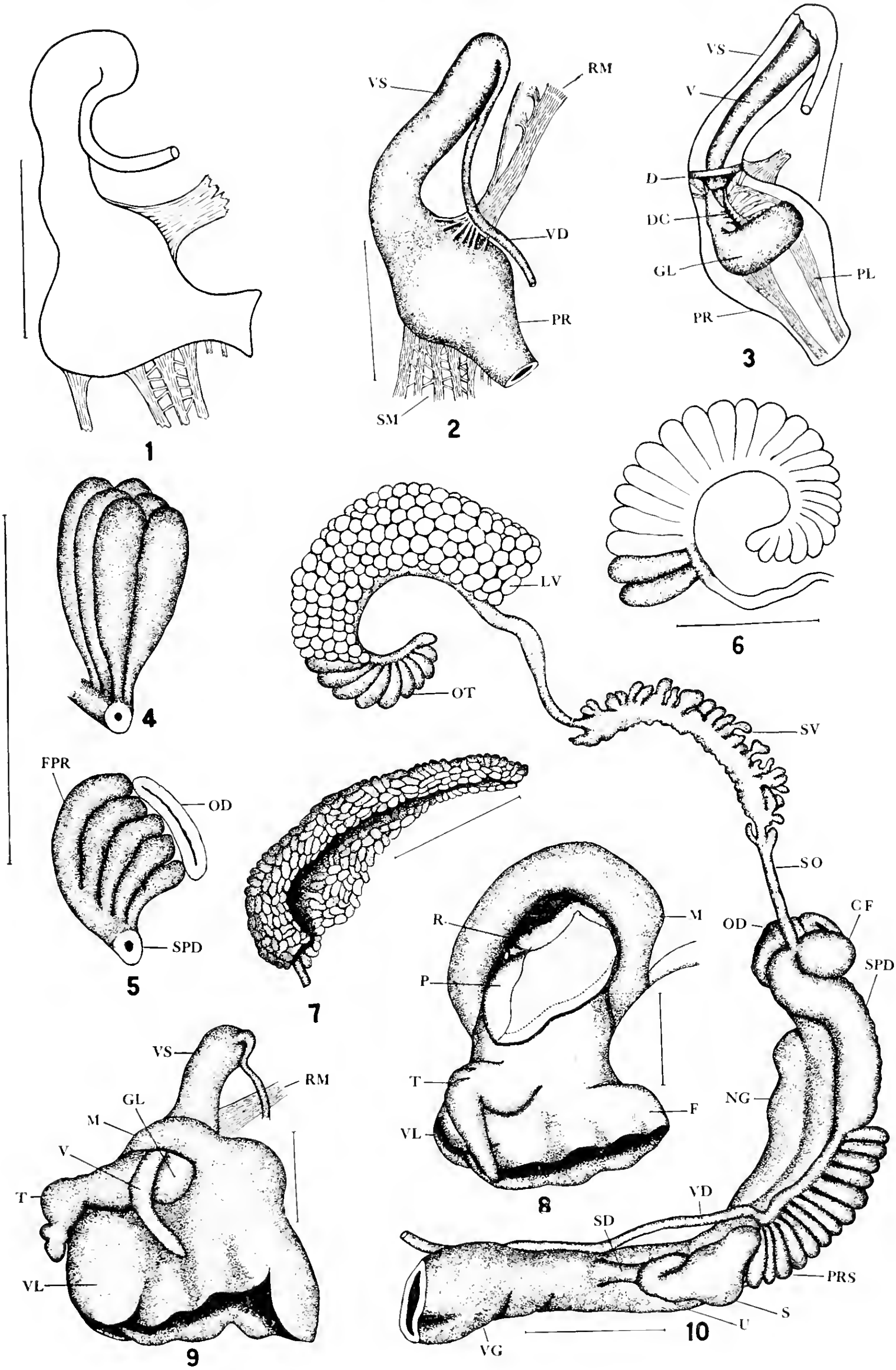
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PLATE 41

PLATE 42

Promenetus

1, 3, 7, 12. *Promenetus exacuous* (Say). From Mott Lake, Wainwright Park, Alberta; collected by Dr. Stiles. Received from Canadian National Museum.

1. Pseudobranch fully expanded.
3. Penial gland in preputium which has been cut open and the pilasters separated.
7. Section of penial gland.
12. Side view of preputium showing penial gland and end of verge passing through the diaphragm.

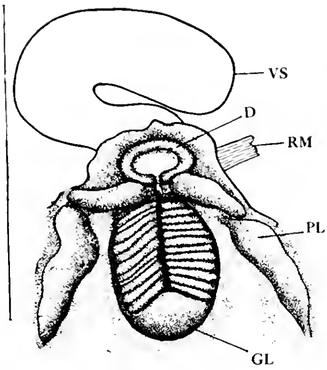
2, 4, 5, 8–11, 13. *Promenetus exacuous megas* (Dall). From Paul Lake, British Columbia; collected by Dr. D. S. Rawson.

2. Head of animal showing pseudobranch.
4. Penial gland from above showing trough-like duct leading to muscular ring or diaphragm at upper part of preputium.
5. Penial complex in natural position.
8. Cross section of ovotestis near middle.
9. Cross section of ovotestis near posterior end.
10. Portion of genitalia showing relationship of ducts.
11. Cross section of prostate. An unusual form with split diverticula.
13. Terminal end of verge showing central exit for sperm canal, small fleshy appendage, and peculiar ring near end.

6. *Promenetus umbilicatellus* (Cockerell). From Wainwright Park, Alberta; collected by Dr. Stiles. Received from Canadian National Museum.

6. Pseudobranch and pneumostome.

Line near figure indicates 1 mm. in length. Vertical line bordering figs. 8, 9, and 13 is also for figs. 7, 10, and 11.



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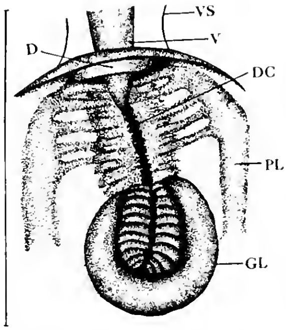

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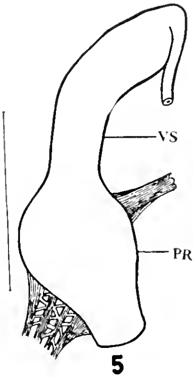

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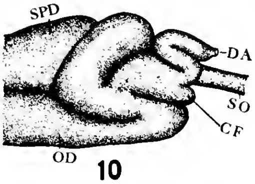

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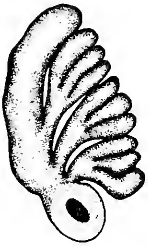

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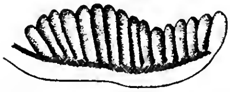

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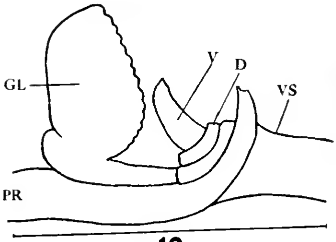

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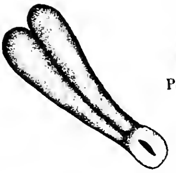

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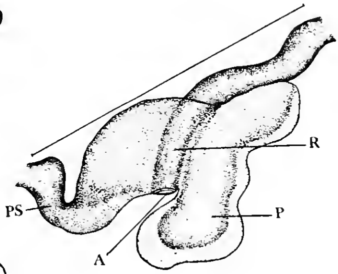

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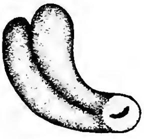

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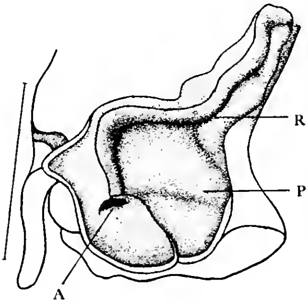

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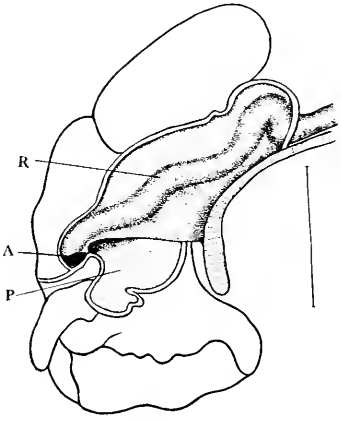

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PLATE 42

PLATE 43

Promenetus umbilicatellus (Cockerell)

From lake southwest of Mott Lake, Wainwright Park, Alberta; collected by Dr. Stiles. Received from the Canadian National Museum.

1. Genitalia dissected and organs separated.
2. Head showing pseudobranch and pneumostome.
3. Penial complex opened to show penial gland, verge, diaphragm, etc.
4. Penial complex in natural position.
5. Albumen gland from below.
6. Cross section of prostate and uterus about midway of length.
7. Portion of genitalia showing union of oviduct and sperm duct, also carrefour.
8. Cross section of ovotestis. Note developing ova.
9. Penial gland showing channel-like duct, viewed from above.
10. Penial gland viewed from the side showing how gland is folded and base attached to preputium at lower end.
11. Section of penial gland.
12. Termination of verge showing small fleshy appendage at end.

Line near figure indicates 1 mm. in length. Figures 5, 6, 7, and 8 have same measurements as fig. 1. Figures 9, 10, 11, and 12 have same measurements as fig. 3.

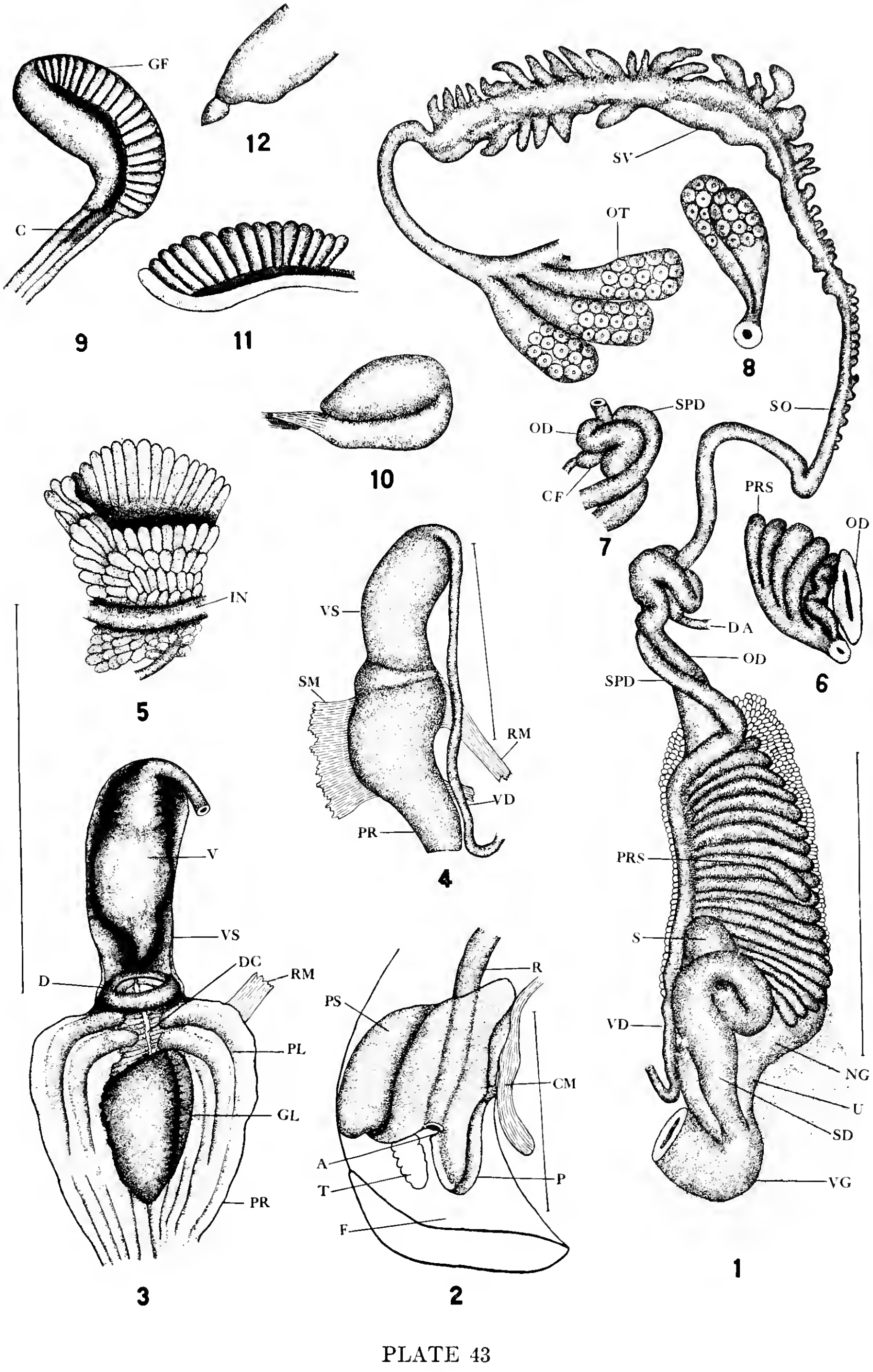
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PLATE 43

PLATE 44

Kidney of *Helisoma*

1. *H. anceps* (Menke). Gillespies Pond, Collinsville, Connecticut.
2. *H. trivolvis* (Say). Oneida Lake, New York.
3. *H. corpulentum* (Say). Lake of the Woods, Ontario, Canada.
4. *H. scalare* (Jay). Lake Butler, Florida.
5. *H. duryi normale* Pilsbry. Canal at Boynton, Florida.

Sections of kidneys

6. *H. oregonense* (Tryon). Tooele Co., Oregon. Near lower end of kidney.
7. *H. anceps* (Menke). Gillespies Pond, Collinsville, Connecticut. Above middle.
8. *H. a. latchfordi* (Pilsbry). Meach Lake, Quebec, Canada. Near middle.
9. *H. trivolvis* (Say). Oneida Lake, New York. About middle.
10. *H. t. macrostomum* (Whiteaves). Bayfield, Wisconsin. About middle.
11. *H. t. lentum* (Say). New Orleans, Louisiana. Lower end.
12. *H. pilsbryi* (F. C. Baker). Lake Chetek, Wisconsin. Near Middle.
13. *H. truncatum* (Miles). Winnebago Lake, Wisconsin. Near middle.
14. *H. magnificum* (Pilsbry). Near Wilmington, North Carolina. Near middle.
15. *H. corpulentum* (Say). Lake of the Woods, Ontario. Near middle.
16. *H. c. multicostatum* F. C. Baker. Crooked Pine Lake, Ontario. Lower end.
17. *H. p. infracarinatum* F. C. Baker. Basswood River Rapids, Ontario. At middle.
18. *H. occidentale* (Cooper). Klamath Lake, Oregon. Near middle.
19. *H. o. depressum* F. C. Baker. Klamath Lake, Oregon. Near middle.
20. *H. traskii* (Lea). Buena Vista Canal, California. Near middle.
21. *H. subcrenatum* (P. P. Carpenter). McMurray, Skagit Co., Washington. Near middle.
22. *H. plexatum* (Ingersoll). Columbine Lake, Colorado. Lower end.
23. *H. horni* (Tryon). Paul Lake, British Columbia. Near middle.
24. *H. tenue californiense* F. C. Baker. Shandon, California. Near middle.
25. *H. scalare* (Jay). Lake Butler, Florida. Near middle.
26. *H. duryi normale* Pilsbry. Canal at Boynton, Florida. Near middle.

Line near figure indicates 1 mm. in length. Arrow indicates point at which section was made.

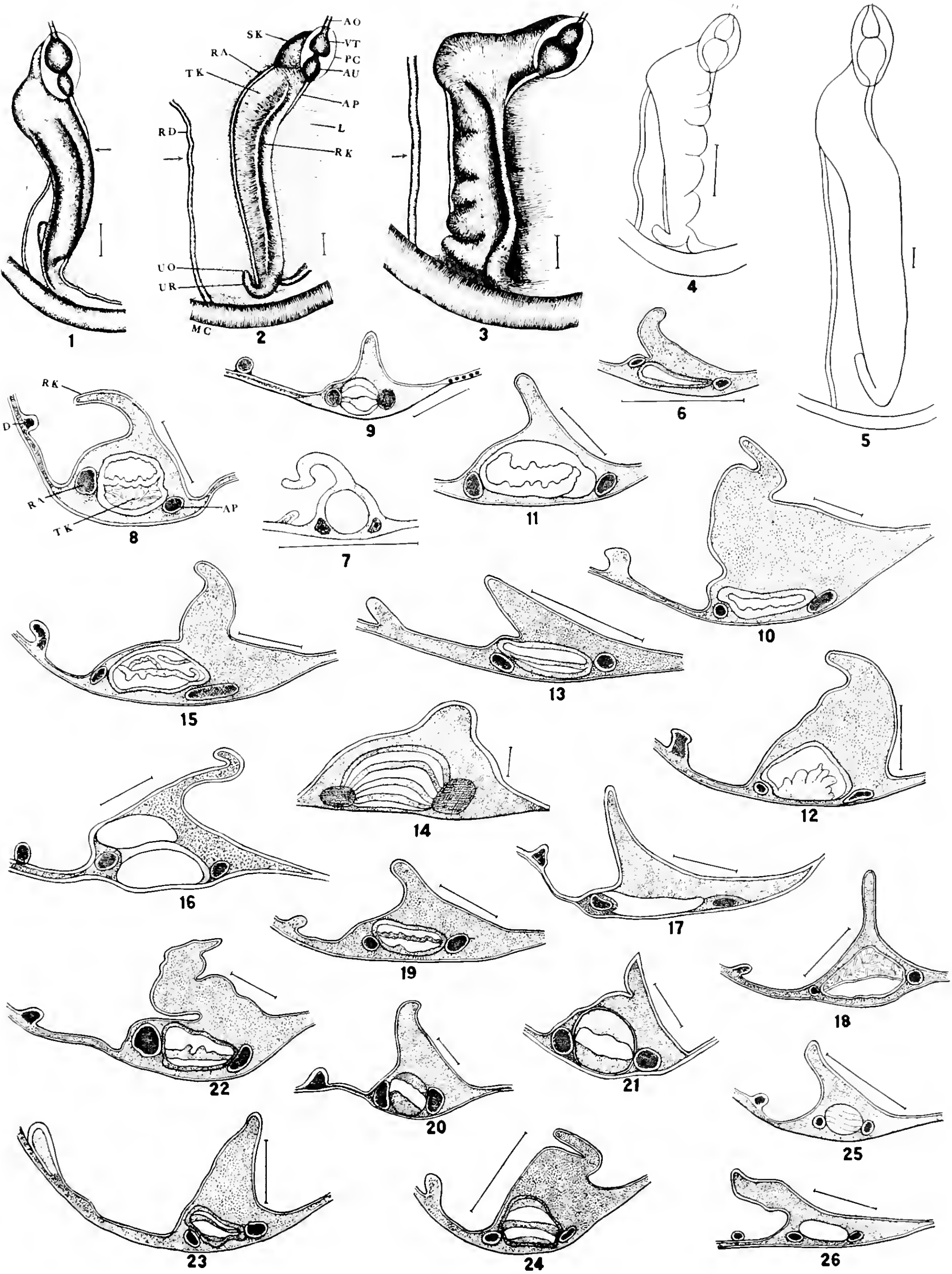
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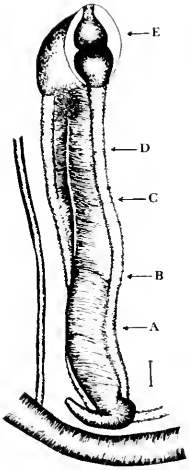
PLATE 44

PLATE 45

Kidneys of Planorbidae

1. *Australorbis glabratus* (Say). Puerto Rico.
2. *Carinifex ponsonbyi* E. A. Smith. Klamath Lake, Oregon.
3. *Planorbula armigera* (Say). Near Oshkosh, Wisconsin.
4. *H. tenue californiense* F. C. Baker. Near Redlands, California.
5. *H. tenue californiense* F. C. Baker. Section at B in fig. 4.
6. *H. tenue californiense* F. C. Baker. Section at A in fig. 4.
7. *Australorbis glabratus* (Say). Section at E in fig. 1.
8. *Australorbis glabratus* (Say). Section at D in fig. 1.
9. *Australorbis glabratus* (Say). Section at C in fig. 1.
10. *Australorbis glabratus* (Say). Section at B in fig. 1.
11. *Australorbis glabratus* (Say). Section at A in fig. 1.
12. *Carinifex ponsonbyi* E. A. Smith. Section near middle.
13. *Planorbula armigera* (Say). Section near middle.
14. Four spherical bodies from ridge of kidney. Greatly enlarged.
15. *Helisoma campanulatum wisconsinense* (Winslow). Section through upper part.
16. *H. campanulatum wisconsinense* (Winslow). Section through middle.
17. *H. campanulatum wisconsinense* (Winslow). Section through lower end.
18. *Planorbarius corneus* (Linn.). Section through lower end. From Poland.
19. *Indoplanorbis exustus* (Deshayes). Section near middle. From India.

Line near figure indicates 1 mm. in length. Letters A, B, C, D, E, etc., indicate points of kidney through which sections have been made and are figured.



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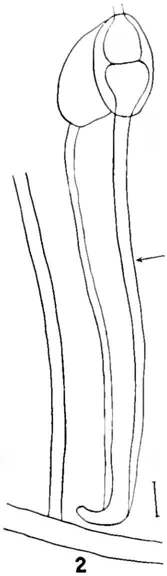

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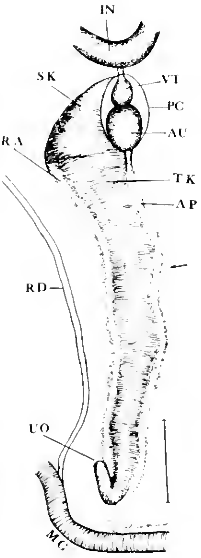

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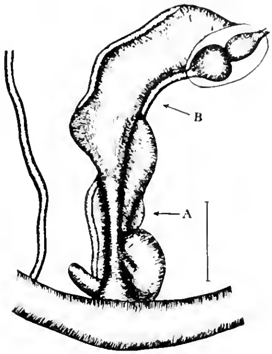

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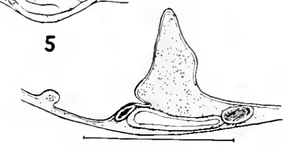

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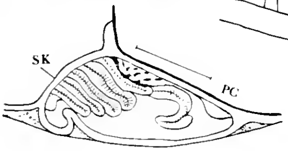

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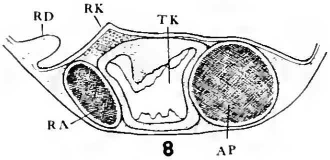

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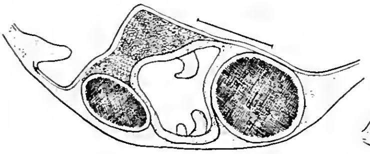

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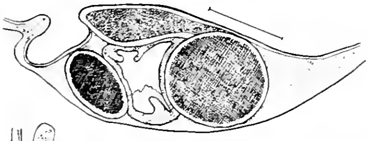

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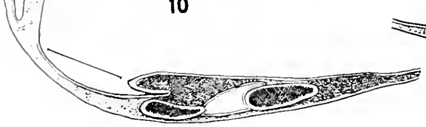

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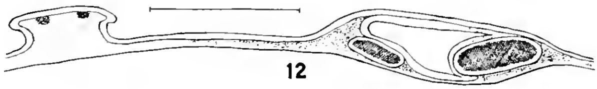

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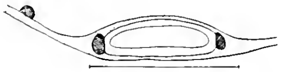

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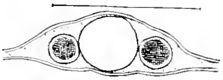

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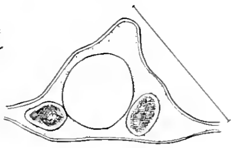

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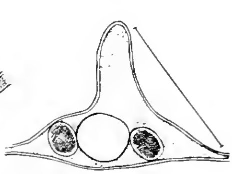

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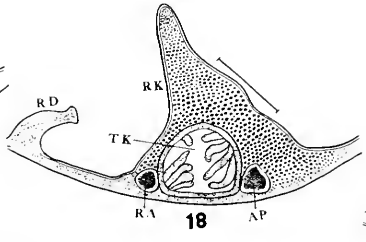

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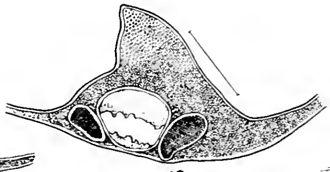

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PLATE 45

PLATE 46

Kidneys of Planorbidae

1. *Parapholyx effusa klamathensis* F. C. Baker. Klamath Lake, Oregon.
2. *P. effusa klamathensis* F. C. Baker. Section near middle.
3. *Promenetus exacuous* (Say). Winnebago Lake, near Oshkosh, Wisconsin.
4. *Promenetus exacuous* (Say). Section near middle. Line is 0.3 mm. long.
5. *Menetus dilatatus* (Gould). Unionville, Connecticut.
6. *Menetus dilatatus* (Gould). Section near middle. Line is 0.3 mm. long.
7. *Menetus cooperi callioglyptus* (Vanatta). Vancouver Island, British Columbia.
8. *M. cooperi callioglyptus* (Vanatta). Section near middle.
9. *Planorbis planorbis* (Linn.). Near Warsaw, Poland.
10. *Planorbis planorbis* (Linn.). Section near middle.
11. *Tropicorbis riisei* (Dunker). Puerto Rico.
12. *Tropicorbis riisei* (Dunker). Section near middle.
13. *Tropicorbis havanensis* (Pfeiffer). Section near middle.
14. *Drepanotrema hoffmani* F. C. Baker. Isabela, Puerto Rico.
15. *Drepanotrema hoffmani* F. C. Baker. Section at point indicated by arrow.
16. *Drepanotrema lucidum* (Pfeiffer). Section near middle.
17. *Hippeutis complanatus* (Linn.). Near Warsaw, Poland.
18. *Hippeutis complanatus* (Linn.). Section at point indicated by arrow. Line equals 0.5 mm. in length.
19. *Bathyomphalus contortus* (Linn.). Near Warsaw, Poland.
20. *Bathyomphalus contortus* (Linn.). Section at point indicated by arrow. Line equals 0.5 mm. in length.

Except where otherwise mentioned the line near the figure indicates 1 mm. in length.

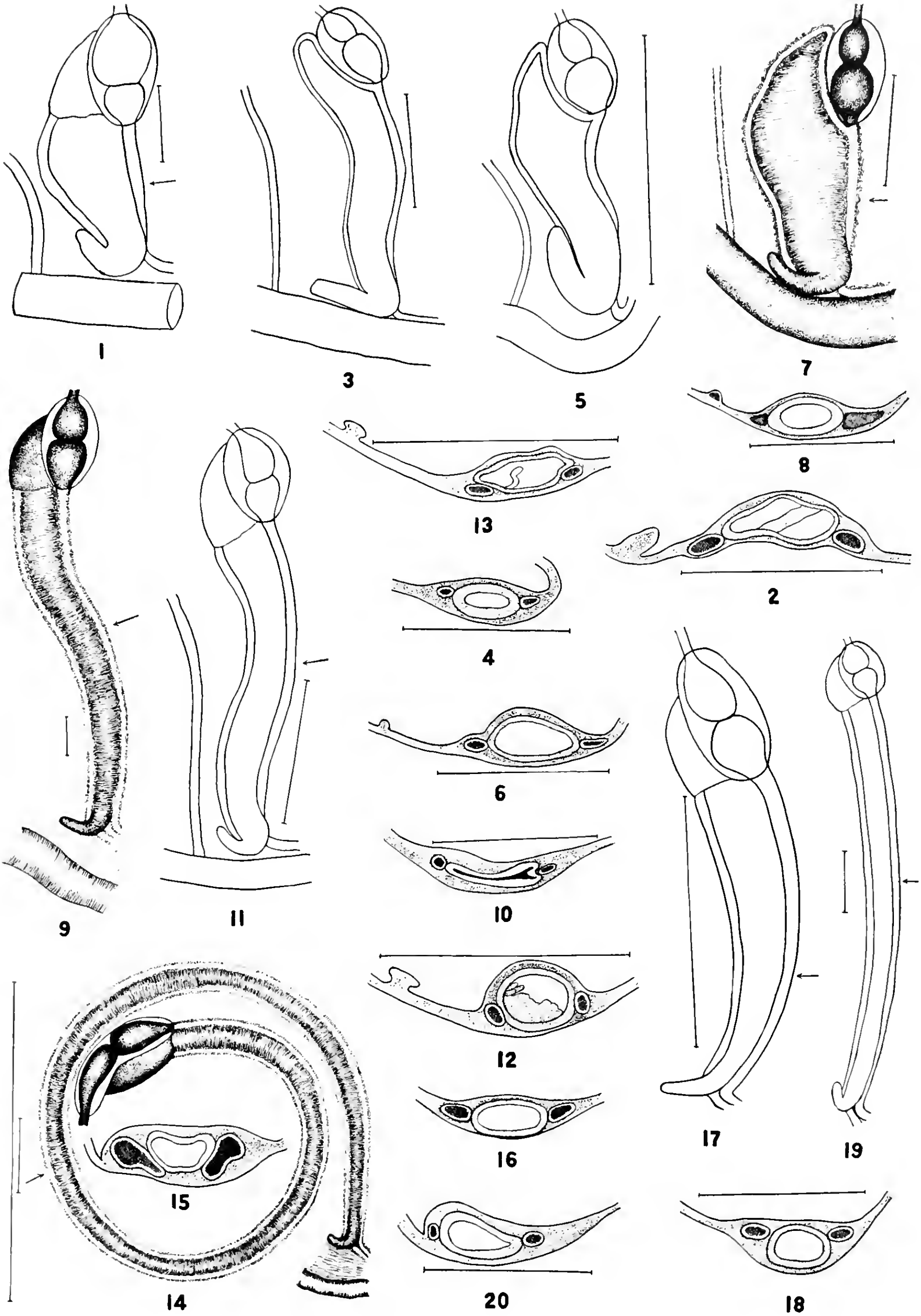

PLATE 46

PLATE 47

Kidneys of Planorbidae

1. *Gyraulus parvus* (Say). Winnebago Lake, Wisconsin.
2. *Gyraulus circumstriatus* (Tryon). Wainwright Park, Alberta.
3. *Gyraulus deflectus obliquus* (DeKay). Near Quebec, Canada.
4. *Gyraulus vermicularis* (Gould). Near San Francisco, California.
5. *Gyraulus parvus* (Say). Section near middle. Line equals 0.5 mm.
6. *Gyraulus circumstriatus* (Tryon). Section near middle. Line equals 0.5 mm.
7. *Gyraulus vermicularis* (Gould). Section near middle. Line equals 0.5 mm.
8. *Gyraulus convexiusculus* (Hutton). India. Section near middle.
9. *Gyraulus similaris* (F. C. Baker). Section near middle.
10. *Gyraulus deflectus obliquus* (DeKay). Section near middle.
11. *Gyraulus latestomus* F. C. Baker. Section below middle.

Figures 6 to 11 have same magnification as fig. 5.

12. *Anisus vortex* (Linn.). Near Warsaw, Poland.
13. *Anisus spirorbis* (Linn.). Near Warsaw, Poland.
14. *Anisus vortex* (Linn.). Section near middle. Line equals 0.5. mm.
15. *Anisus leucostomus* (Millet). Section near middle. Line equals 0.5 mm.
16. *Anisus spirorbis* (Linn.). Section near middle. Line equals 0.5 mm.
17. *Gyraulus convexiusculus* (Hutton). India.
18. *Gyraulus hirsutus* (Gould). Canada.
19. *Gyraulus hirsutus* (Gould). Section below middle.
20. *Armiger crista* (Linn.). Wisconsin.
21. *Armiger crista* (Linn.). Section near middle. Line equals 0.5 mm.
22. *Segmentina nitida* (Müller). Near Warsaw, Poland.
23. *Segmentina nitida* (Müller). Section below middle. Line equals 0.5 mm.
24. *Polypylis hemisphaerula* (Benson). Peiping, China.
25. *Polypylis hemisphaerula* (Benson). Section near middle. Line equals 0.5 mm.
26. *Intha capitis* Annandale. South Shan State, Burma.
27. *Intha capitis* Annandale. Section below middle. Line equals 0.25 mm.

Unless otherwise stated the line near the figure indicates 1 mm. in length.

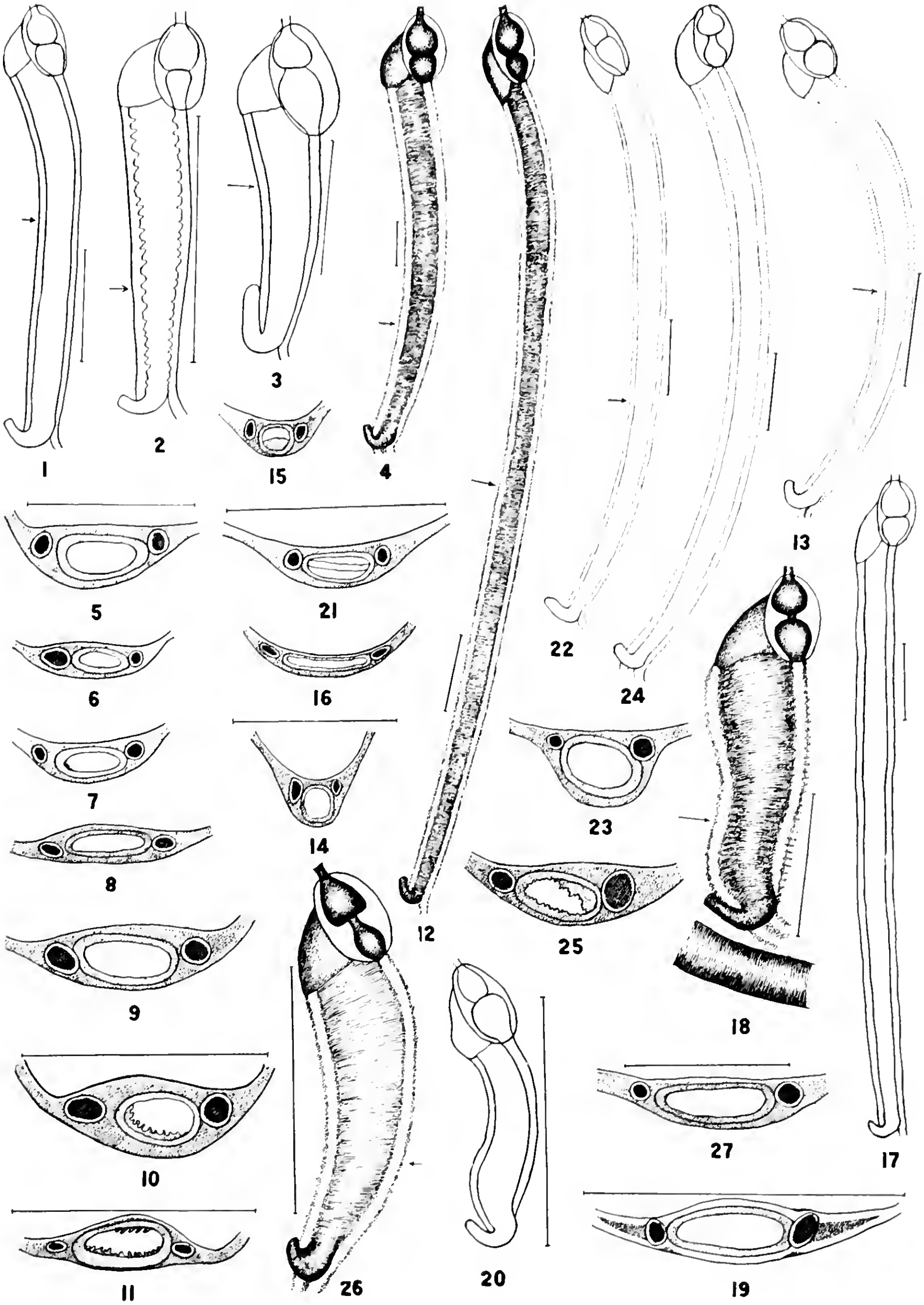

PLATE 47

PLATE 48

Digestive System of Planorbidae

1. *Helisoma trivolvis* (Say). Entire digestive system except liver. From above.
2. *Helisoma trivolvis* (Say). Region of the stomach from below.
3. *Carinifex ponsonbyi* E. A. Smith. Region of stomach from below.
4. *Promenetus exacuous* (Say). Region of stomach from above.
5. *Promenetus exacuous* (Say). Region of stomach from below.
6. *Planorbis planorbis* (Linn.). Region of stomach from above.
7. *Planorbis planorbis* (Linn.). Region of stomach from below.
8. *Bathyomphalus contortus* (Linn.). Portion of digestive system from above.
9. *Australorbis glabratus* (Say). Region of stomach from above.
10. *Australorbis glabratus* (Say). Region of stomach from below.
11. *Drepanotrema lucidum* (Pfeiffer). Region of stomach from above.
12. *Hippeutis complanatus* (Linn.). Region of stomach from above.
13. *Gyraulus albus* (Müller). Region of stomach from above.
14. *Gyraulus parvus* (Say). Region of stomach from above.
15. *Armiger crista* (Linn.). Region of stomach from above.
16. *Segmentina nitida* (Müller). Region of stomach from above.
17. *Helisoma anceps* (Menke). Nerves and blood vessels to penial complex. Nerve from left cerebral ganglion
18. Nerve ring of *Helisoma trivolvis* (Say), from above.

Line near figure indicates 1 mm. in length

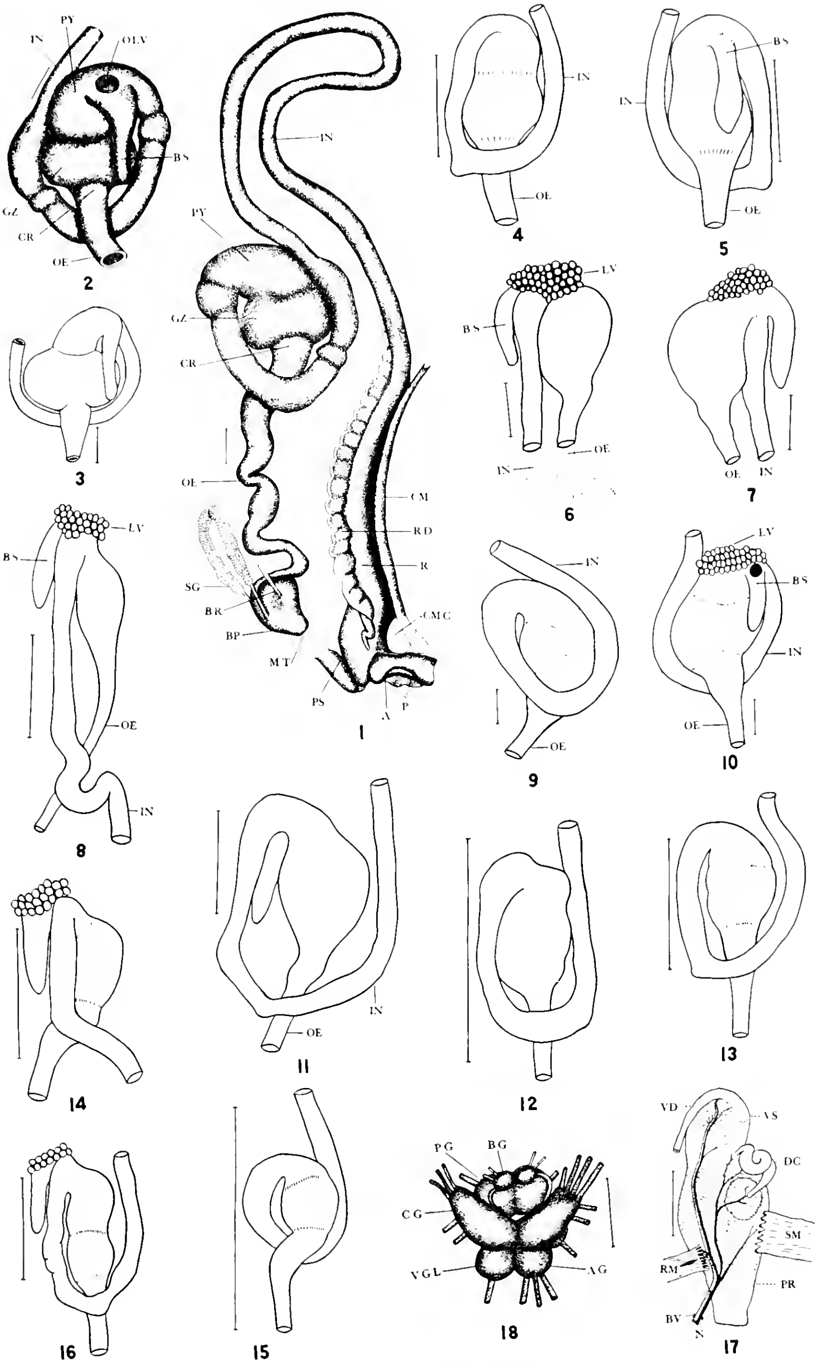
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PLATE 48

PLATE 49

Jaws of Planorbidae

1. *Helisoma anceps* (Menke). Chetek Lake, Wisconsin.
2. *Helisoma trivolvis* (Say). Devils Lake, Wisconsin. Small fig. indicates striation.
3. *Helisoma truncatum* (Miles). Oshkosh, Lake Winnebago, Wisconsin.
4. *Helisoma scalare* (Jay). Lake Butler, Florida.
5. *Helisoma pilsbryi* (F. C. Baker). Chetek Lake, Wisconsin.
6. *Helisoma oregonense* (Tryon). Tooele Co., Utah.
7. *Helisoma subcrenatum* (P. P. Carpenter). Gypsum, Colorado. Superior jaw.
8. *H. pilsbryi infracarinatum* F. C. Baker. Rideau River, Ontario. Superior jaw.
9. *Helisoma horni* (Tryon). Paul Lake, British Columbia.
10. *Helisoma plexatum* (Ingersoll). Grand Mesa, Colorado. Superior jaw.
11. *H. campanulatum smithi* (F. C. Baker). Douglas Lake, Michigan.
12. *Helisoma traskii* (Lea). Outlet of Kern Lake, California. Superior jaw.
13. *Helisoma occidentale* (Cooper). Klamath Lake, Oregon. Superior jaw.
14. *H. duryi normale* Pilsbry. Forty miles west of Miami, Florida. Superior jaw.
15. *Helisoma corpulentum* (Say). Bamiji Lake, Ontario, Canada.
16. *Helisoma magnificum* (Pilsbry). Near Wilmington, North Carolina.
17. *Carinifex jacksonensis* J. Henderson. Jackson Lake, Wyoming. Jaw and cartilage from the side.
18. *Carinifex jacksonensis* J. Henderson. Jaw from above.
19. *Carinifex ponsonbyi* E. A. Smith. Klamath Lake, Oregon. Jaw and cartilage from below.
20. *Helisoma campanulatum smithi* (F. C. Baker). Douglas Lake, Michigan. Vertical striation on jaw. Highly magnified.

Line at right of fig. 1 indicates 1 mm. in length. Line at lower extreme left is for figs. 18 and 19 and represents 0.5 mm. in length. Middle line is for fig. 6. Line at right is for figs. 2, 3, 4, 5, and 7 to 16. Figure 17 is diagrammatic.

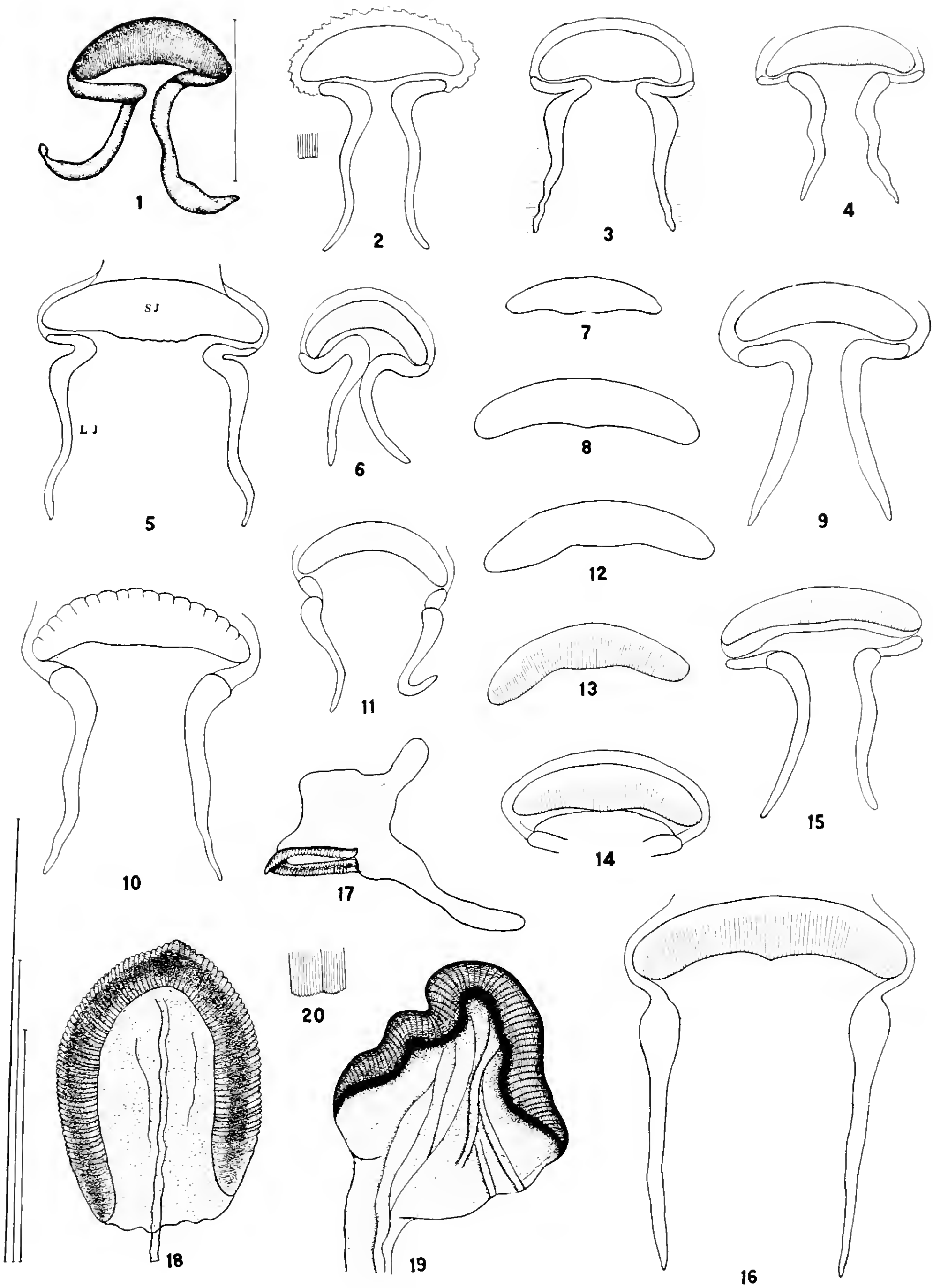

PLATE 49

PLATE 50

Jaws of Planorbidae

1. *Helisoma tenue californiense* F. C. Baker. Shandon, California.
2. *Planorbula armigera* (Say). Murphy Creek, near Madison, Wisconsin.
3. *Planorbula jenksii* (H. F. Carpenter). Unionville, Connecticut.
4. *Parapholyx effusa klamathensis* F. C. Baker. Klamath Lake, Oregon.
5. *Parapholyx effusa diagonalis* J. Henderson. Crater Lake, Oregon.
6. *Menetus sampsoni* (Ancey). Near Stanton, Missouri.
7. *Menetus cooperi callioglyptus* (Vanatta). Vancouver Island, British Columbia.
8. *Promenetus exacuous* (Say). Winnebago Lake, Wisconsin.
9. *Menetus dilatatus* (Gould). Unionville, Connecticut.
10. *Indoplanorbis exustus* (Deshayes). North Shan State, Burma.
11. *Tropicorbis obstructus* (Morelet). New Orleans, Louisiana. Superior jaw.
12. *Tropicorbis riisei* (Dunker). Puerto Rico.
13. *Australorbis glabratus* (Say). Puerto Rico.
14. *Planorbarius corneus* (Linn.). Near Warsaw, Poland.
15. *Promenetus umbilicatellus* (Cockerell). Wainwright Park, Alberta.
16. *Gyraulus parvus* (Say). Winnebago Lake, Wisconsin.
17. *Gyraulus hirsutus* (Gould). Lake Nipissing, Ontario, Canada.
18. *Gyraulus deflectus obliquus* (DeKay). Taylor Lake, Quebec, Canada.
19. *Gyraulus vermicularis* (Gould). Near San Francisco, California.
20. *Armiger crista* (Linn.). Wisconsin.
21. *Planorbis planorbis* (Linn.). Near Warsaw, Poland.
22. *Gyraulus circumstriatus* (Tryon). Wainwright Park, Alberta.
23. *Intha capitis* Annandale. Burma.
24. *Segmentina nitida* (Müller). Near Warsaw, Poland.
25. *Anisus spirorbis* (Linn.). Near Warsaw, Poland
26. *Drepanotrema hoffmani* F. C. Baker. Puerto Rico.
27. *Drepanotrema lucidum* (Pfeiffer). Cuba.
28. *Gyraulus albus* (Müller). Near Warsaw, Poland.

Figures are greatly enlarged. Sizes are disproportionate.

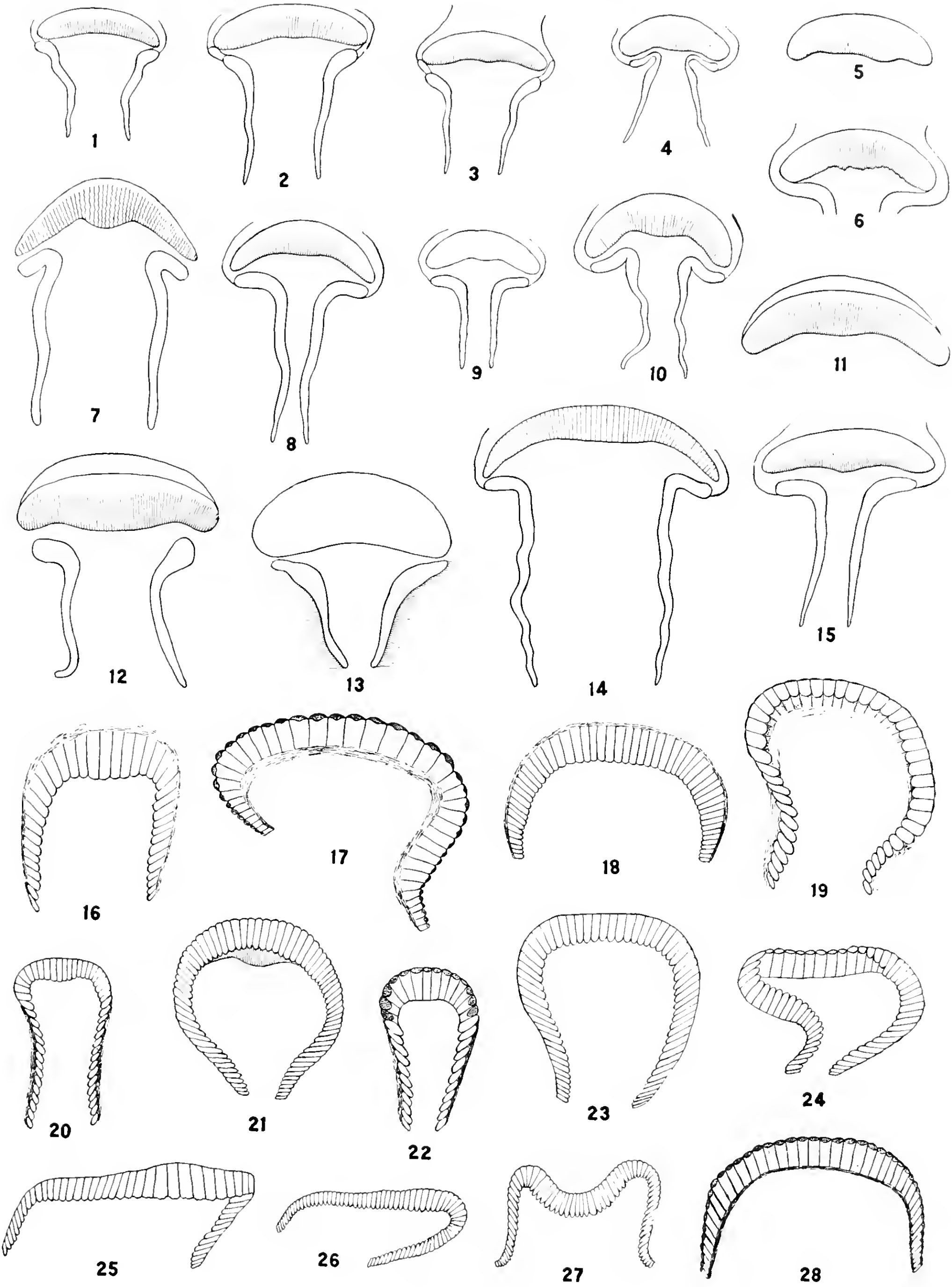

PLATE 50

PLATE 51

Development of *Helisoma scalare* (Jay)

1. Egg capsule containing 28 eggs, observed on March 1, 1932. Each egg is marked to correspond with the numbered figures below. Line near figure indicates 1 mm. in length.
2. The 24-cell stage of segmentation in egg No. 7. March 7.
3. Gastrula stage of segmentation in egg No. 7. March 8.
4. Post-trochophore stage in egg No. 11. March 4.
5. Post-trochophore stage in egg No. 11. March 5.
6. Veliger stage of embryo in egg No. 11. March 9.
7. Veliger stage of embryo in egg No. 8. Front view. March 9.
8. Veliger stage of embryo in egg No. 8. Side view. March 9.
9. Veliger stage of embryo in egg No. 8. Top view. March 10.
10. Embryo in egg No. 3. March 12.
11. Embryo in egg No. 1 showing heart and stomach. March 11.
12. Young snail in egg No. 3. March 14. A similar young snail was observed in egg No. 20 on March 14. Shell growth distinct.
13. Young snail just out of egg No. 1. March 15.
14. Young snail two days out of egg No. 1. March 16. Shell now shows both growth lines and spiral striae.

Line at lower left indicates 1 mm. in length

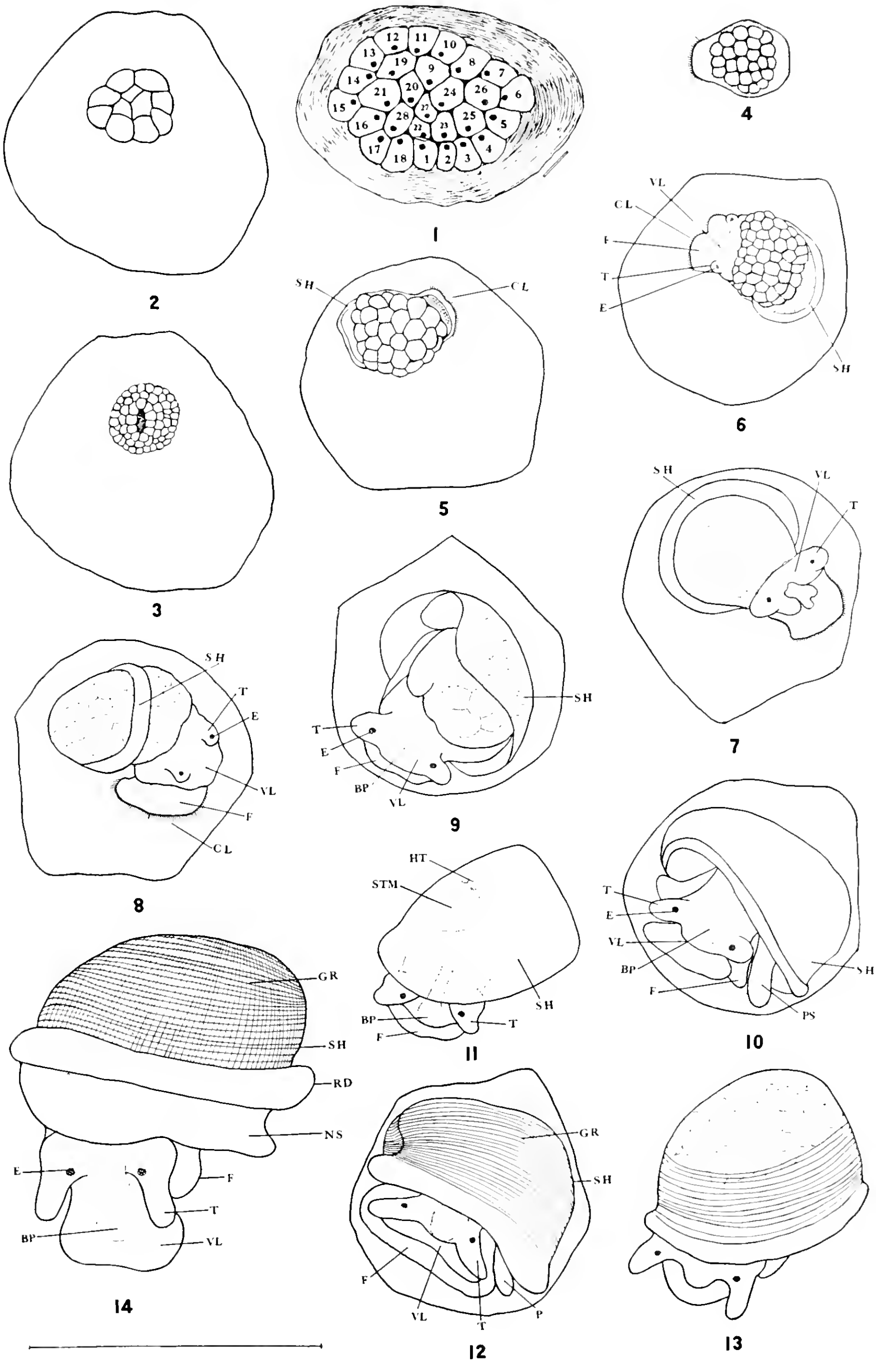
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PLATE 51

PLATE 52

Nidification in Planorbidae

1–3. *Helisoma scalare* (Jay). Lake Butler, Florida.
    1. Five eggs laid March 13, 1931.
    2. Fourteen eggs laid April 1, 1931.
    3. Ten eggs laid April 2, 1931.

4–5. *Helisoma trivolvis lentum* (Say). New Orleans, Louisiana.
    4. Twenty eggs laid June 5, 1933.
    5. Ten eggs laid May 27, 1933.

6–8. *Helisoma duryi normale* Pilsbry. Gainesville, Florida.
    6. Two eggs laid Dec. 25, 1931.
    7. Three eggs laid Dec. 26, 1931.
    8. Four eggs laid Jan. 17, 1932.

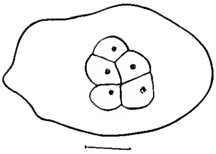
9–11. *Helisoma duryi eudiscus* Pilsbry. Silver Springs, Florida.
    9. Five eggs laid Dec. 13, 1931.
    10. Nine eggs laid Feb. 6, 1932.
    11. Twelve eggs laid Feb. 10, 1932.

12. *Helisoma duryi normale* Pilsbry. Tamiami Trail, 40 miles west of Miami, Florida.
    12. Sixteen eggs laid Jan. 17, 1932.

13. *Helisoma traskii* (Lea). Buena Vista Canal, outlet of Kern Lake, California.
    13. Alcoholic specimen with 50 eggs laid on adult shell.

14–16. *Gyraulus circumstriatus* (Tryon). Wainwright Park, Alberta.
    14. Nucleated ovum from ovotestis.
    15. Spermatozoa from ovotestis. Typical (eupyrene) spermatozoa as seen in active group.
    16. Eupyrene spermatozoa from the side and from above.

Line near figs. 1-13 indicates 1 mm. in length. Line near figs. 14-16 indicates 25 microns in length.



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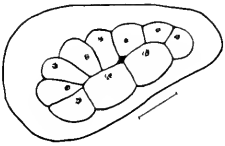

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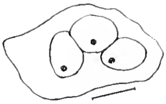

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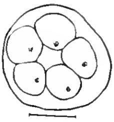

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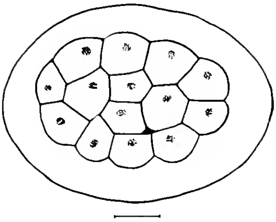

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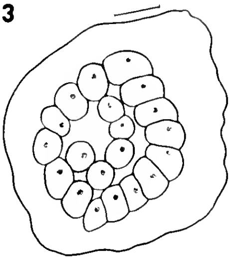

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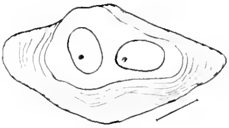

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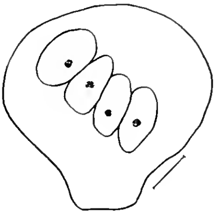

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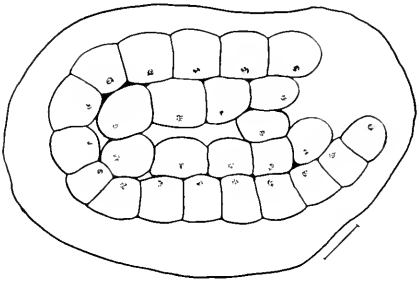

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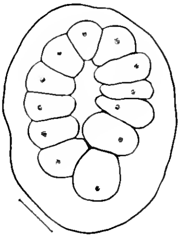

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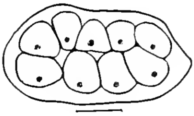

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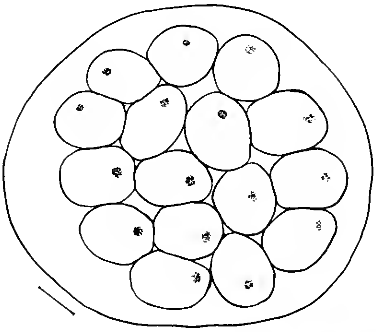

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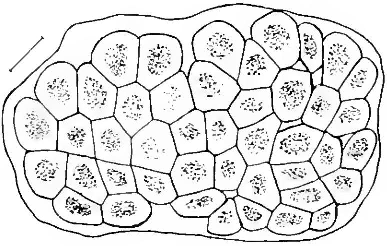

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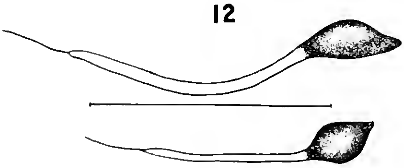

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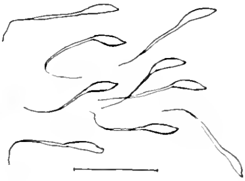

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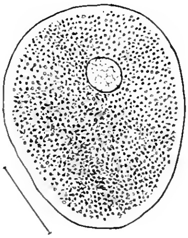


14

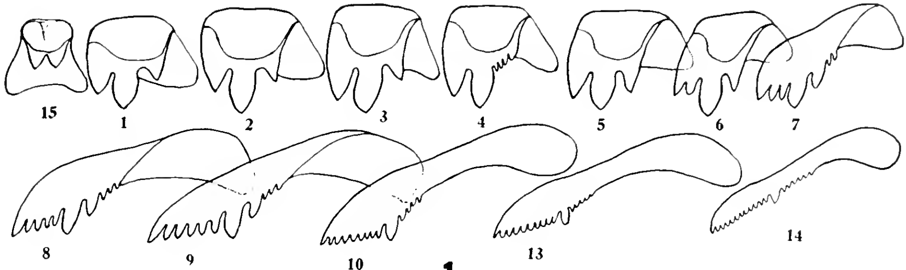
PLATE 52

PLATE 53

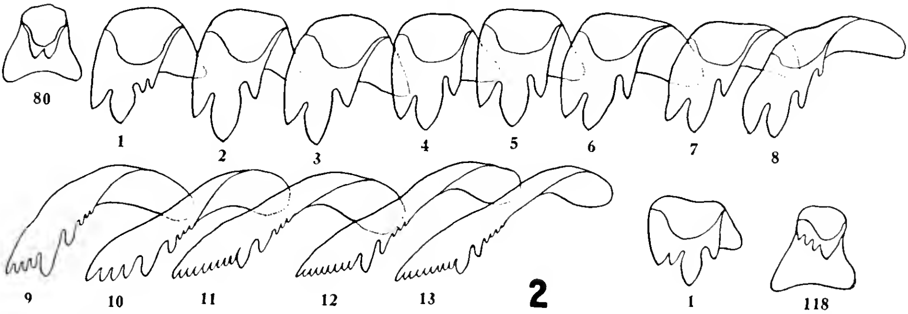
Radulae of *Helisoma*

In the plates of radulae, the number under the central tooth (as 15, 80, 98, 50, and 75 on this plate) indicates the number of the transverse row, counting from the front end of the radula. The numbers following indicate the number of the tooth in this row, counting from the central tooth, the first lateral tooth being number 1. The line at the lower part of the plate indicates 25 microns.

1. *Helisoma anceps* (Menke). Maple River, Michigan.
    15, center tooth; 1-5, lateral teeth; 6, 7, intermediate teeth; 8-14, marginal teeth.
2. *Helisoma anceps* (Menke). Chautauqua Lake, New York.
    80, center tooth; 1-5, lateral teeth; 6-8, intermediate teeth; 9-13, marginal teeth. 118, center tooth (of 118th row) with first left marginal beside it.
3. *Helisoma anceps* (Menke). Unionville, Connecticut.
    98, center tooth; 1, 2, lateral teeth; 6, 7, intermediate teeth; 8, 9, marginal teeth on right side; 11-16, marginal teeth on left side of row. 90, 90th row, center tooth; 5, lateral tooth with two ectocones; 8, intermediate tooth; 9, 10, marginal teeth.
4. *Helisoma anceps sayi* F. C. Baker. Bayfield, Wisconsin.
    50, center tooth in 50th row; 1-5, lateral teeth; 6, 7, intermediate teeth; 8-14, marginal teeth. 75, 75th row, pathologic center tooth; 1-5, pathologic lateral teeth.



1



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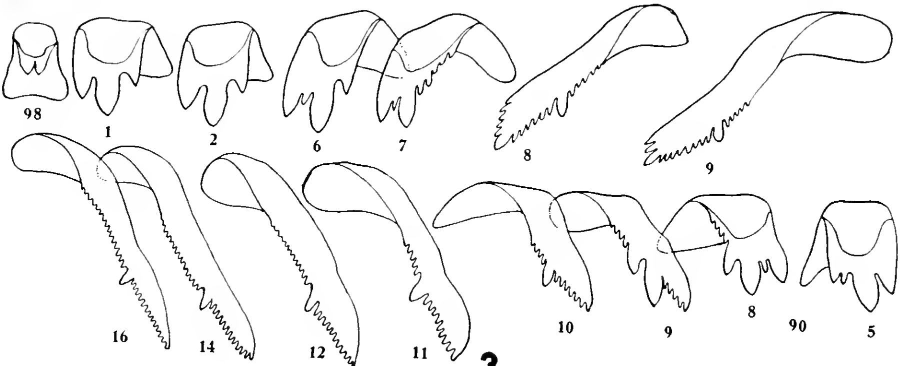

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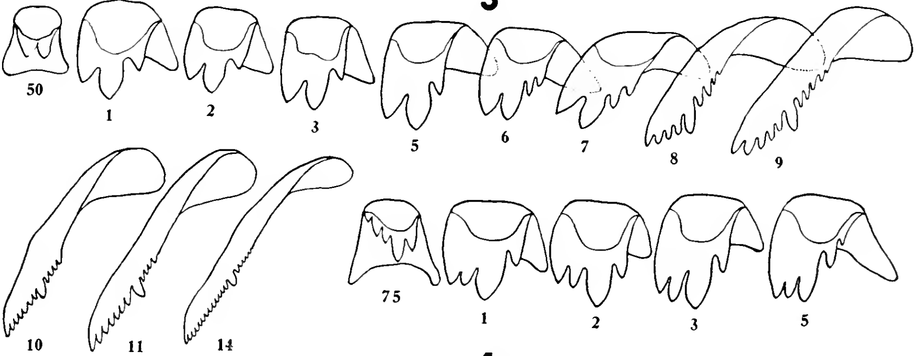

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PLATE 53

PLATE 54

Radulae of *Helisoma*

See remarks on plate 53. Line at bottom of plate indicates 25 microns in length.

1. *Helisoma anceps percarinatum* (Walker). Douglas Lake, Michigan.
   85, center tooth; 1-6, lateral teeth; 7-9, intermediate teeth; 10-23, marginal teeth. 100, 100th row, center tooth; 1-3, lateral teeth, pathologic (2 entocones); 9, intermediate tooth; 10, marginal tooth.

2. *Helisoma anceps royalense* (Walker). Bamiji Lake, Ontario, Canada.
   60, center tooth; 1-6, lateral teeth; 7-9, intermediate teeth; 10-19, marginal teeth.

3. *Helisoma anceps cahni* F. C. Baker. Big Muskallonge Lake, Wisconsin.
   60, center tooth; 1-6, lateral teeth; 7-9, intermediate teeth; 10-18, marginal teeth.

4. *Helisoma anceps latchfordi* (Pilsbry). Meach Lake, Quebec, Canada.
   51, center tooth; 1-6, lateral teeth; 7-9, intermediate teeth; 10-26, marginal teeth. 60, an abnormal center tooth from another membrane, with accessory lateral cusps above the normal center cusps.

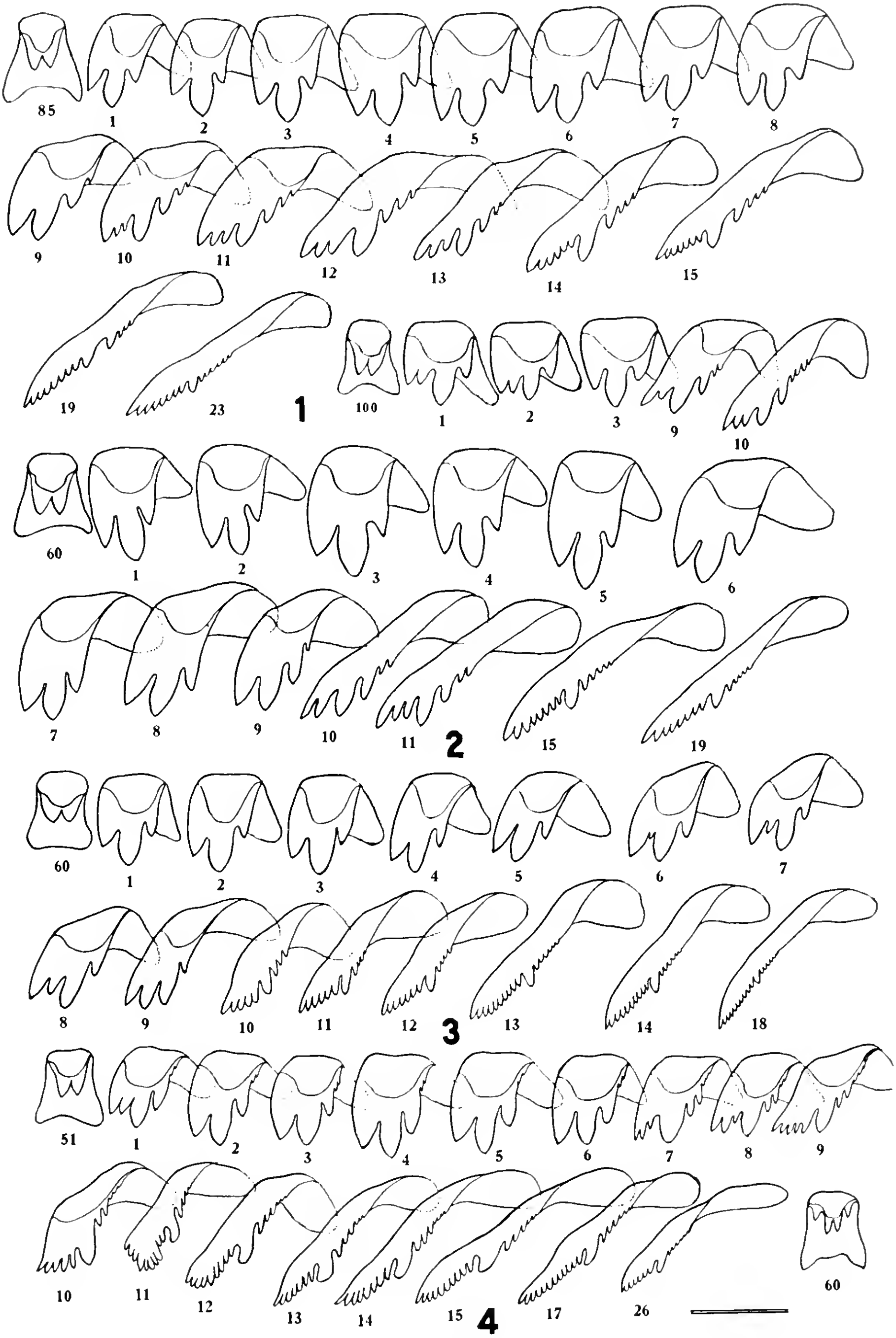
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PLATE 54

PLATE 55

Radulae of *Helisoma*

See remarks on plate 53. Line at bottom of plate indicates 25 microns in length.

1. *Helisoma trivolvis* (Say). Oneida Lake, New York.
    60, center tooth; 1-7, lateral teeth; 8-10, intermediate teeth; 11-18, marginal teeth.

2. *Helisoma trivolvis* (Say) = *pseudotrivolvis* F. C. Baker, near *lentum* Say. From Reelfoot Lake, Tennessee.
    150, center tooth; 1-7, lateral teeth; 8-10, intermediate teeth; 11-13, marginal teeth.

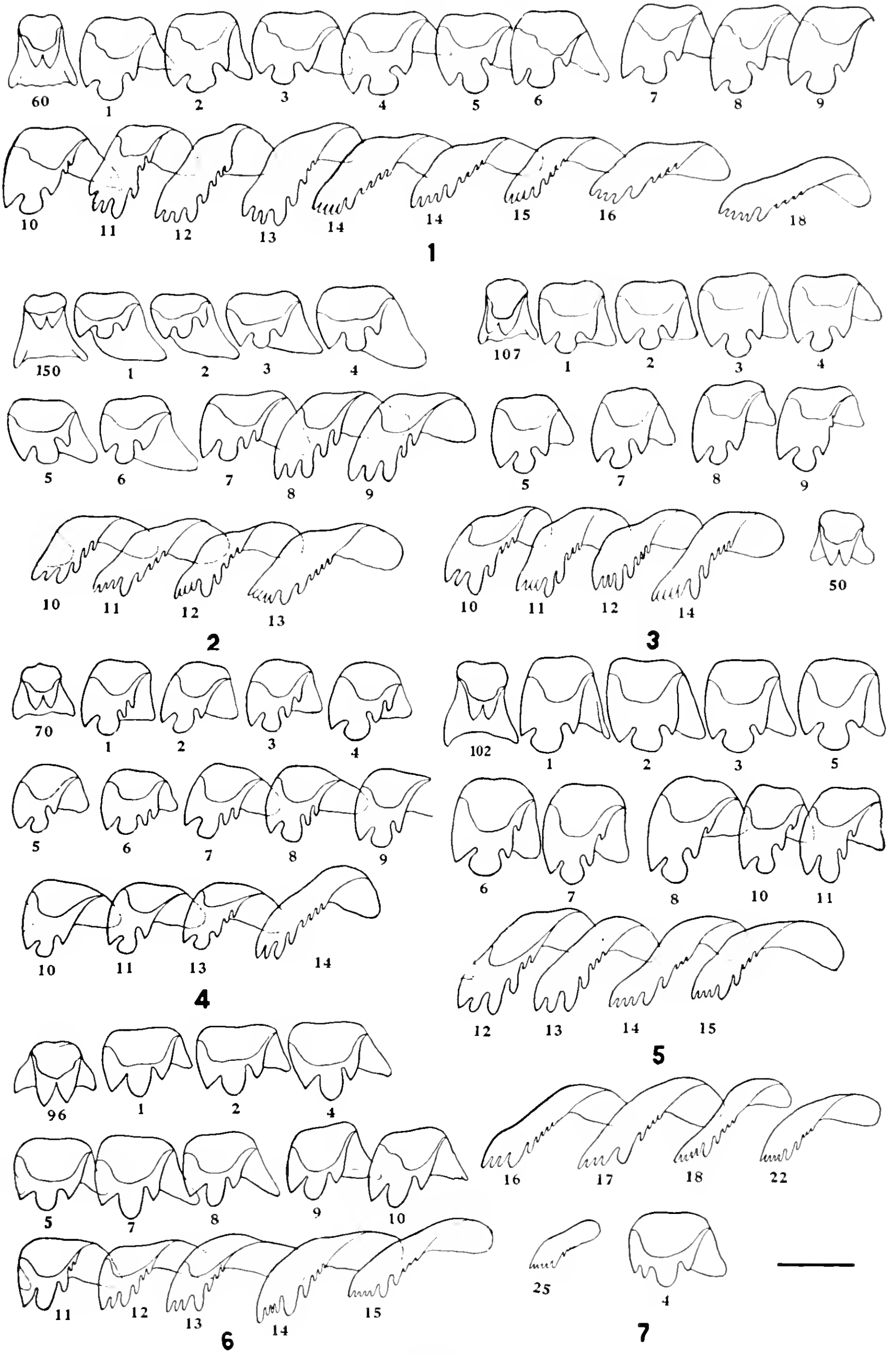
3. *Helisoma trivolvis lentum* (Say) = *pseudotrivolvis* F. C. Baker. Reelfoot Lake, Tennessee.
    107, center tooth; 1-7, lateral teeth; 8-10, intermediate teeth; 11-14, marginal teeth; 50, 50th center tooth of another row.

4. *Helisoma trivolvis* (Say). Sturgeon Bay, Wisconsin.
    70, center tooth; 1-6, lateral teeth; 7-11, intermediate teeth; 13, 14, marginal teeth.

5. *Helisoma chautauquense* F. C. Baker. Chautauqua Lake, New York.
    102, center tooth; 1-7, lateral teeth; 8-11, intermediate teeth; 12-15, marginal teeth.

6. *Helisoma trivolvis lentum* (Say). New Orleans, Louisiana.
    96, center tooth; 1-8, lateral teeth; 9-11, intermediate teeth; 12-15, marginal teeth.

7. *Helisoma trivolvis lentum* (Say). New Orleans, Louisiana.
    16-25, marginal teeth; 4, 4th lateral tooth from another row, with two entoconic cusps.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10 11 12 13 14 14 15 16 18
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10 11 12 13
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107 1 2 3 4
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70 1 2 3 4
5 6 7 8 9
10 11 13 14
4
102 1 2 3 5
6 7 8 10 11
12 13 14 15
16 17 18 22
5
96 1 2 4
5 7 8 9 10
11 12 13 14 15
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PLATE 55

PLATE 56

Radulae of *Helisoma*

See remarks on plate 53. Line at bottom of plate indicates 25 microns in length.

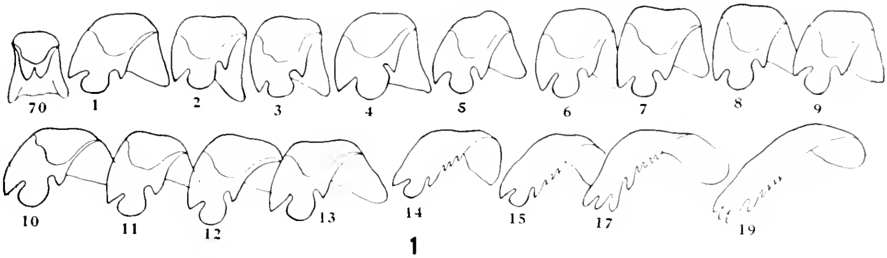
1. *Helisoma winslowi* (F. C. Baker). Little Arbor Vitae Lake, Wisconsin.
   70, center tooth; 1-13, lateral teeth; 14, 15, intermediate teeth; 17-19, marginal teeth.

2. *Helisoma trivolvis macrostomum* (Whiteaves). Bayfield, Wisconsin.
   53, center tooth; 1-8, lateral teeth; 9-13, intermediate teeth; 14-23, marginal teeth.

3. *Helisoma pilsbryi* (F. C. Baker). Chetek Lake, Wisconsin.
   100, center tooth; 1-8, lateral teeth; 10-12, intermediate teeth; 13-23, marginal teeth.

4. *Helisoma pilsbryi infracarinatum* F. C. Baker. Basswood River Rapids, Ontario.
   132, center tooth; 1-9, lateral teeth; 10-14, intermediate teeth; 15-21, marginal teeth.

5. *Helisoma pilsbryi infracarinatum* F. C. Baker. Rideau River, Ontario.
   Varying toward *pilsbryi*. 115, center tooth; 1-13, lateral teeth; 14, 15, intermediate teeth; 16-29, marginal teeth.



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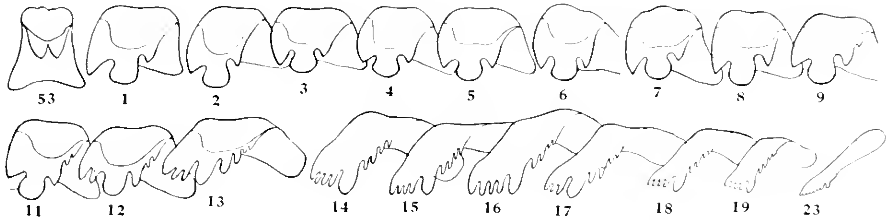

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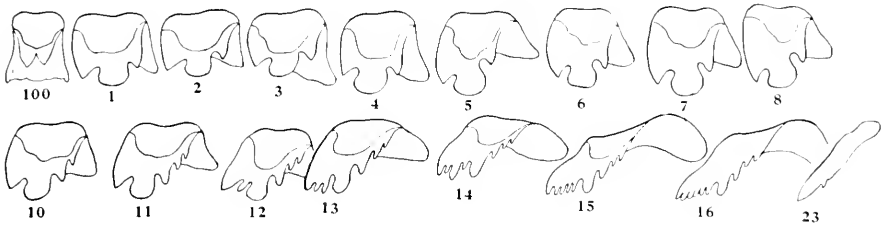

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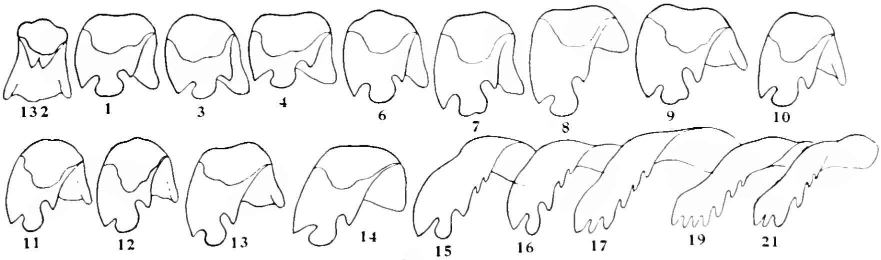

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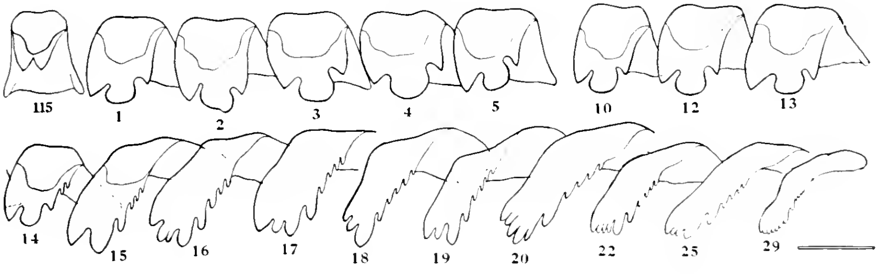

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PLATE 56

PLATE 57

Radulae of *Helisoma*

See remarks on plate 53. Line at bottom of plate indicates 25 microns in length.

1. *Helisoma truncatum* (Miles). Winnebago Lake, near Oshkosh, Wisconsin.

Normal membrane. 85, center tooth; 1-7, lateral teeth; 9-11, intermediate teeth; 13-20, marginal teeth.

2. *Helisoma truncatum* (Miles). Winnebago Lake, Wisconsin.

Abnormal membrane, with many split cusps on teeth. 90, center tooth; 1-8, lateral teeth, 6 and 7 with bifid entoconic cusps and 5, 6, and 7 with split ectoconic cusps; 9-11, intermediate teeth with modified ectocones; 12-21, marginal teeth.

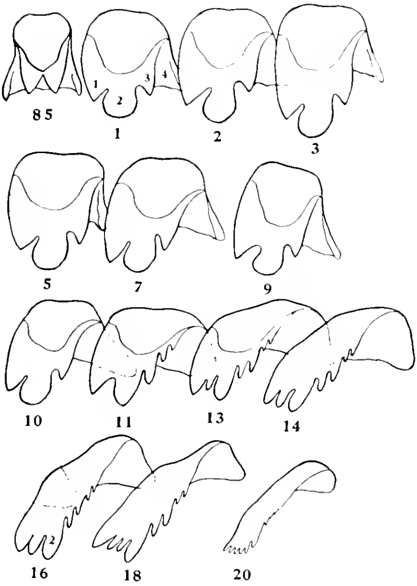
3. *Helisoma corpulentum* (Say). Lac la Croix, Ontario, Canada.

48, center tooth; 1-8, lateral teeth; 9-12, intermediate teeth; 13-25, marginal teeth.

4. *Helisoma magnificum* (Pilsbry). Near Wilmington, North Carolina.

90, center tooth; 1-14, lateral teeth; 16-23, intermediate teeth; 24-41, marginal teeth.

The small numerals on the first lateral of fig. 1 indicate the following parts of the tooth: 1, entocone or inner cusp; 2, mesocone or middle cusp; 3, ectocone or outer cusp; 4, base of attachment to radula membrane. In 16 of fig. 1, the small numeral 2 indicates the position of the mesocone in a marginal tooth.



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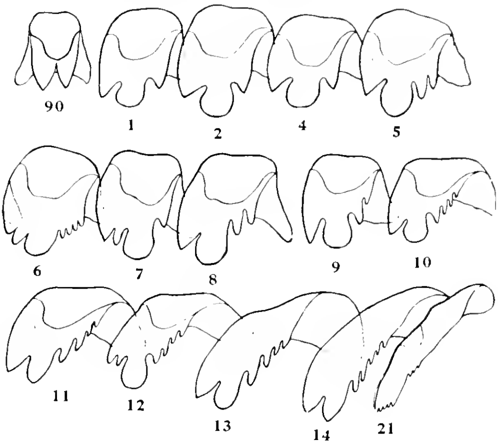

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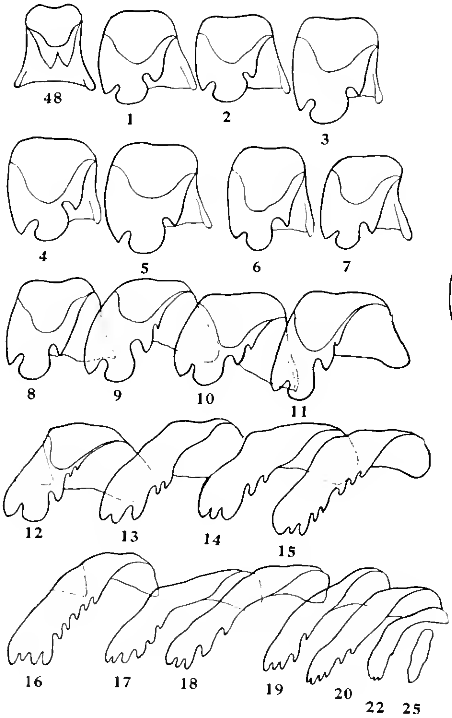

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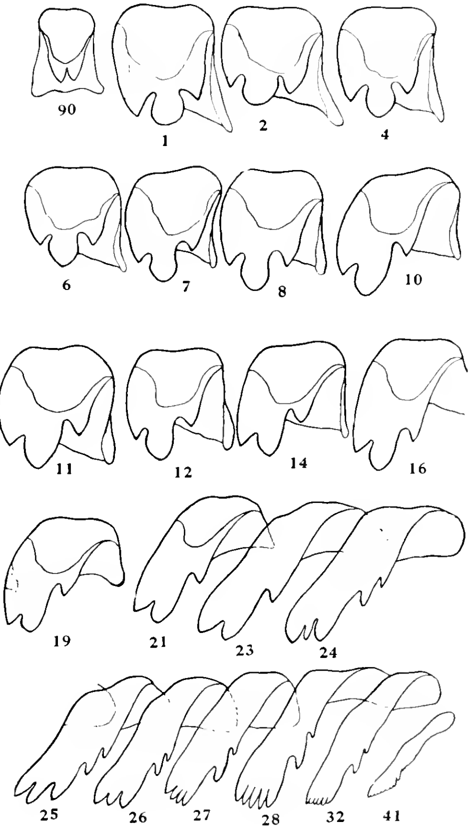

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PLATE 57

PLATE 58

Radulae of *Helisoma*

See remarks on plate 53. Line at bottom of plate indicates 25 microns in length.

1. *Helisoma whiteavesi* F. C. Baker. Mille Lacs, Ontario, Canada.

   105, center tooth; 1-16, lateral teeth; 17-19, intermediate teeth; 20-35, marginal teeth. 23, a pathologic tooth in another row. 12, a lateral tooth on the left side with split cusps.

2. *Helisoma corpulentum vermilionense* F. C. Baker. Vermilion Lake, Minnesota.

   101, center tooth; 1-7, lateral teeth; 9-12, intermediate teeth; 13-21, marginal teeth.

3. *Helisoma corpulentum multicostatum* F. C. Baker. Kahnipiminanikok Lake, Ontario, Canada.

   60, center tooth; 1-7, lateral teeth; 11-14, intermediate teeth; 15-41, marginal teeth.

4. *Helisoma plexatum* (Ingersoll). Teton River, near Rexburg, Idaho.

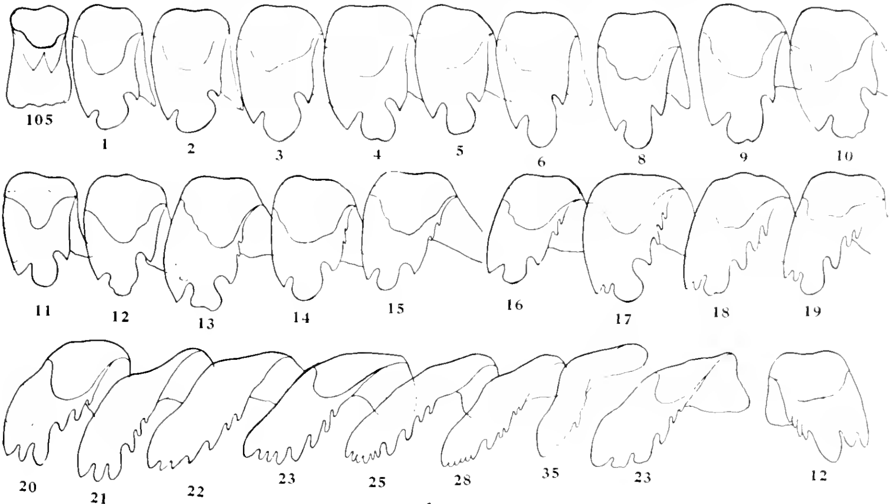
   44, center tooth; 1-8, lateral teeth, 1 and 4 with mesocones worn or pathologic; 10-13, intermediate teeth; 13-16, marginal teeth. The two 13 figures show how this tooth differed in two rows, being an intermediate tooth in one row and a marginal tooth in another row.

5 *Helisoma plexatum* (Ingersoll).

   The 120th row in another membrane from a Teton River specimen. 16-18, modified marginal teeth.

6. *Helisoma plexatum* (Ingersoll). Smartweed Lake, Colorado.

   13, a lateral tooth; 14-15, marginal teeth.



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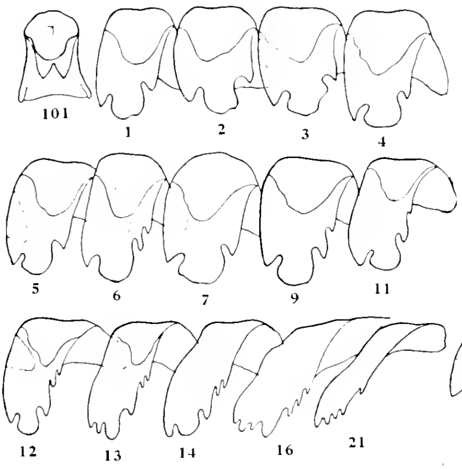

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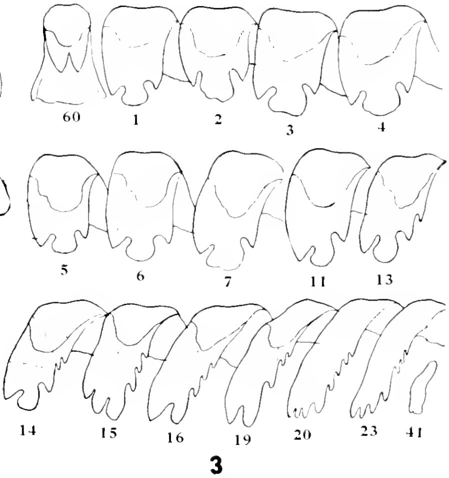

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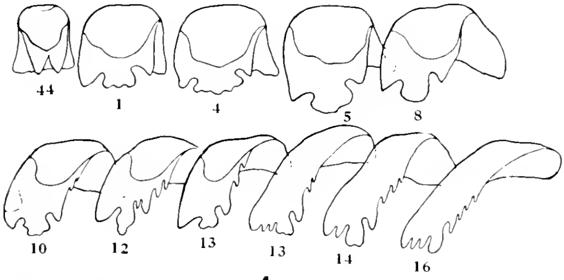

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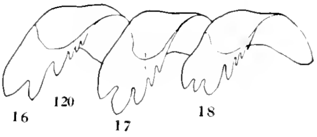

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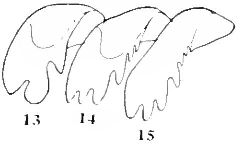

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PLATE 58

PLATE 59

Radulae of *Helisoma*

See remarks on plate 53. Line at bottom of plate indicates 25 microns in length.

1. *Helisoma plexatum* (Ingersoll). Grand Mesa, Colorado.
   60, center tooth; 1-12, lateral teeth; 13-17, intermediate teeth; 18-22, marginal teeth.

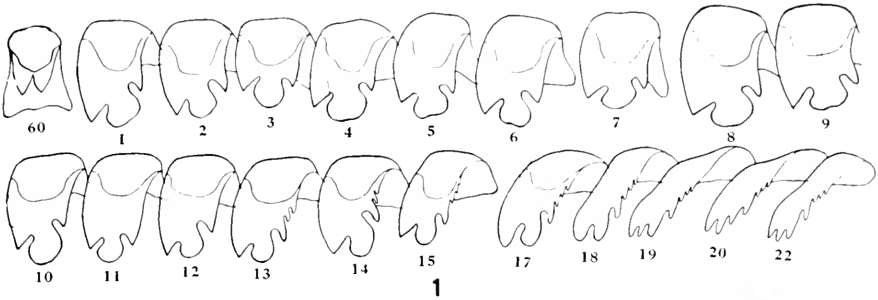
2. *Helisoma plexatum* (Ingersoll). Columbine Lake, Colorado.
   95, center tooth; 1-10, lateral teeth; 11-12, intermediate teeth; 13-15, marginal teeth.

3. *Helisoma tenue californiense* F. C. Baker. San Bernardino Mts., California.
   Normal teeth. 60, center tooth; 1-11, lateral teeth; 12, 13, intermediate teeth; 14-21, marginal teeth.

4. *Helisoma tenue californiense* F. C. Baker. San Bernardino Mts., California.
   Abnormal teeth, the lateral teeth with extra cusps on both entocones and ectocones and with mesocone much modified. 60, center tooth; 1-10, lateral teeth; 11, 12, intermediate teeth; 12-17, marginal teeth.

5. *Helisoma subcrenatum* (P. P. Carpenter). Variety. Pass Lake, Puget Sound, Washington.
   96, center tooth; 1-15, lateral teeth; 16-18, intermediate teeth; 19-28, marginal teeth.

6. *Helisoma tenue californiense* F. C. Baker. San Bernardino Mts., California.
   An abnormal 11th lateral tooth.



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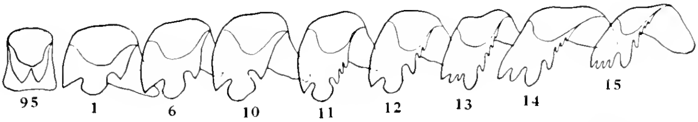

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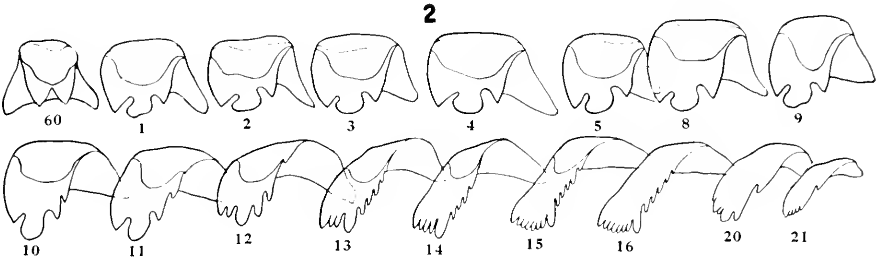

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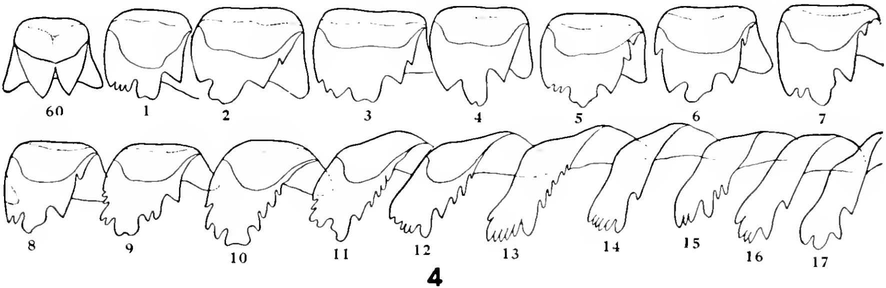

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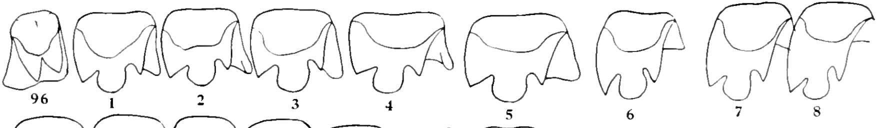

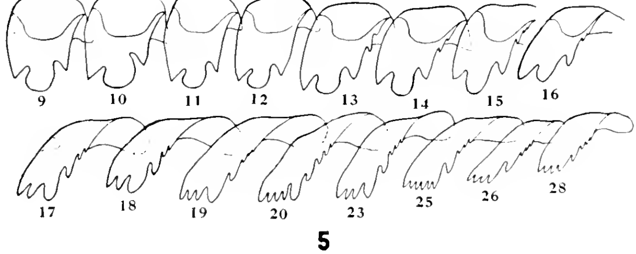

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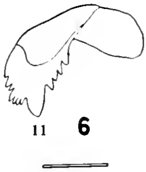

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PLATE 59

PLATE 60

Radulae of *Helisoma*

See remarks on plate 53. Line at lower right of plate indicates 25 microns in length.

1. *Helisoma subcrenatum* (P. P. Carpenter). Variety. Lost Lake, Puget Sound, Washington.

   73, center tooth; 1-7, lateral teeth; 12, 13, intermediate teeth; 15-20, marginal teeth.

2. *Helisoma subcrenatum* (P. P. Carpenter). Variety. Lost Lake, Puget Sound, Washington.

   88, abnormal center tooth; 5, lateral tooth with bicuspid entocone.

3. *Helisoma subcrenatum* (P. P. Carpenter). Skagit Co., Washington.

   90, center tooth; 1, 7, lateral teeth; 12, intermediate tooth; 17, 20, marginal teeth.

4. *Helisoma traskii* (Lea). Outlet of Kern Lake, California.

   82nd row, 9, intermediate tooth; 10, 11, marginal teeth.

5. *Helisoma traskii* (Lea). Outlet of Kern Lake, California.

   90, center tooth; 1-9, lateral teeth; 10, 11, intermediate teeth; 12-22, marginal teeth.

6. *Helisoma traskii* (Lea). Outlet of Kern Lake, California.

   80th row, 9, intermediate tooth; 10, first marginal tooth.

7. *Helisoma horni* (Tryon). Paul Lake, British Columbia.

   60, center tooth; 1-9, lateral teeth; 10-14, intermediate teeth; 15-32, marginal teeth. 4, fourth tooth in another row.

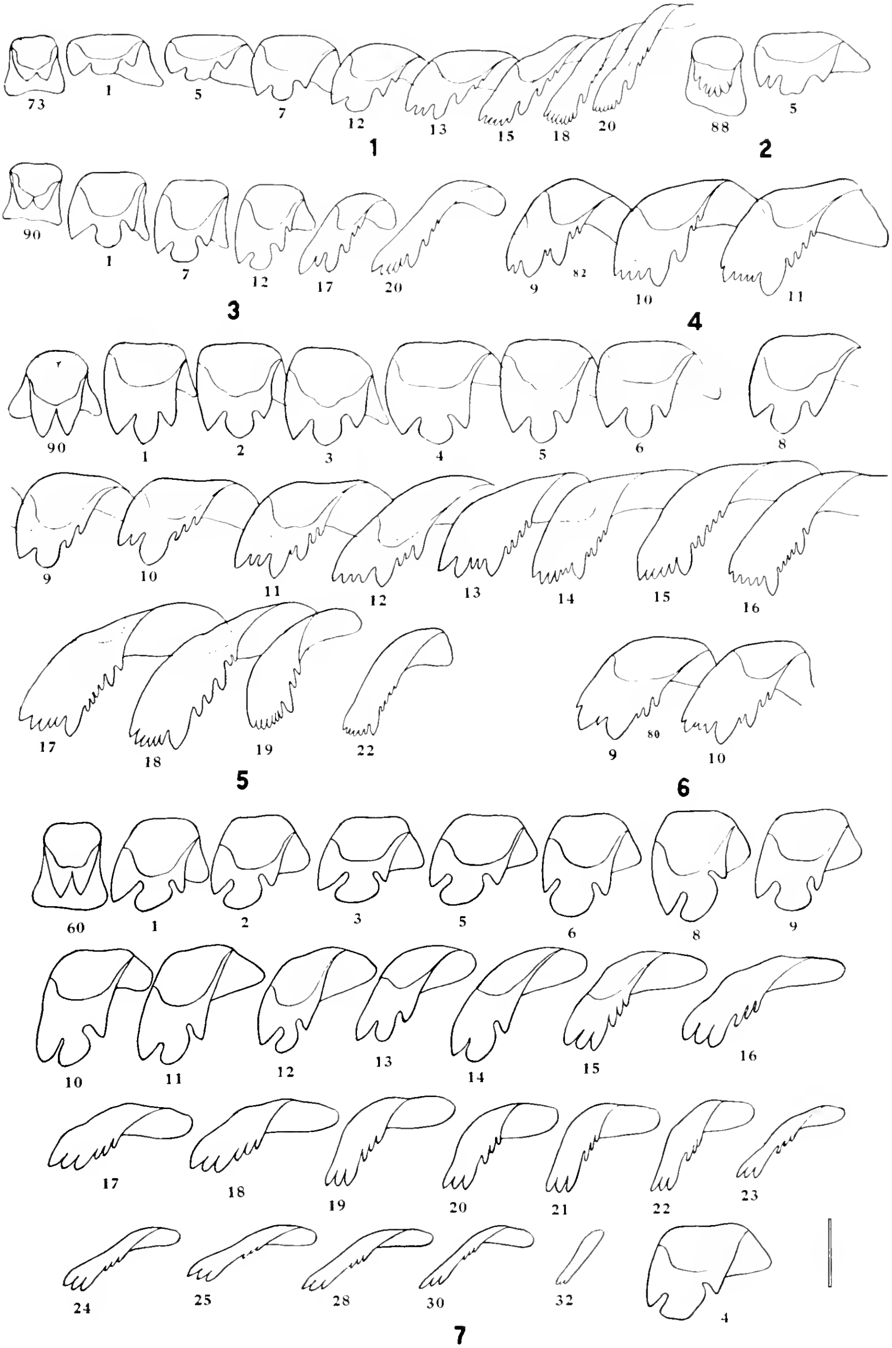
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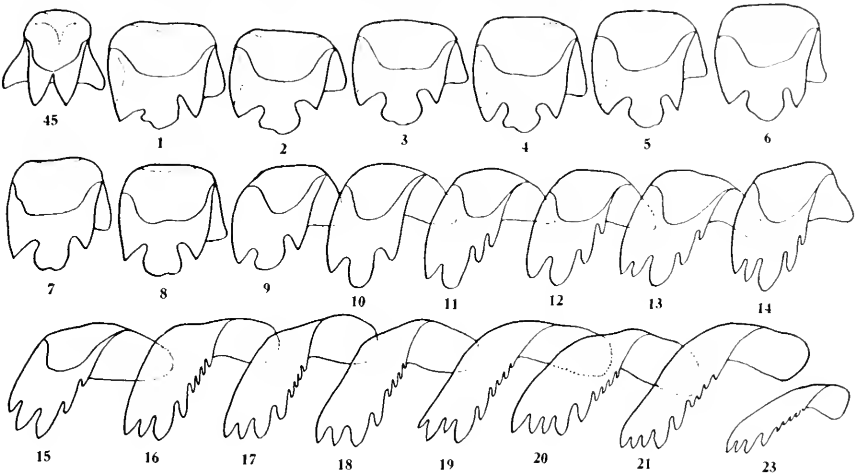
PLATE 60

PLATE 61

Radulae of *Helisoma*

See remarks on plate 53. Line at lower right of plate indicates 25 microns in length.

1. *Helisoma occidentale* (Cooper). Klamath Lake, Oregon.
   45, center tooth; 1-8, lateral teeth; 9-12, intermediate teeth; 13-23, marginal teeth.
2. *Helisoma subcrenatum* (P. P. Carpenter). Cottonwood Pass, Gypsum, Colorado.
   95, center tooth; 1-8, lateral teeth; 9-12, intermediate teeth; 13-20, marginal teeth.
3. *Helisoma oregonense* (Tryon). Tooele Co., Utah
   58, center tooth; 1-8, lateral teeth; 9, 10, intermediate teeth; 11-21, marginal teeth.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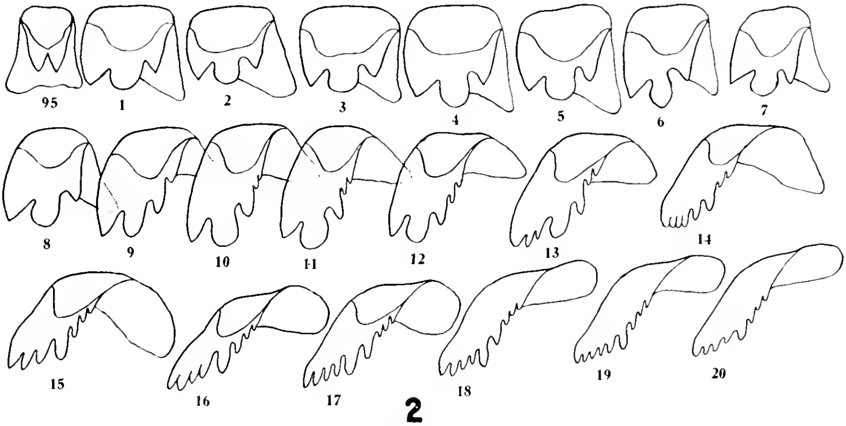
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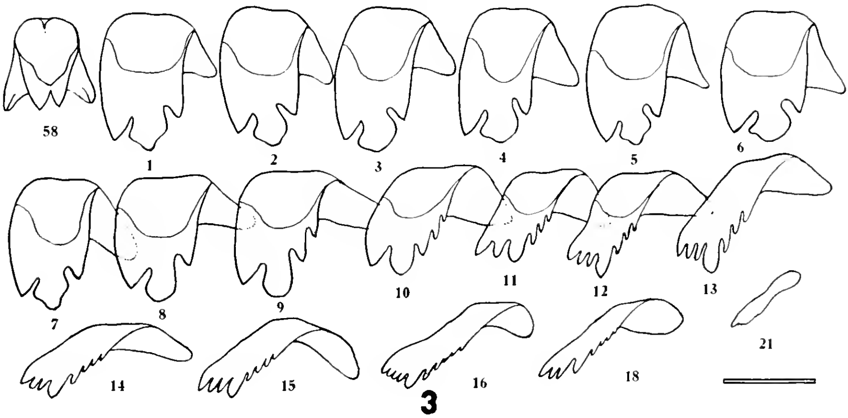
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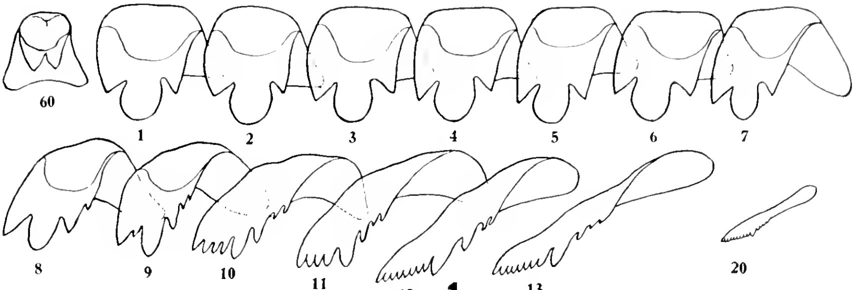
PLATE 61

PLATE 62

Radulae of *Helisoma*

See remarks on plate 53. Line at lower right of plate indicates 25 microns in length.

1. *Helisoma campanulatum* (Say). Oneida Lake, New York.
   60, center tooth; 1-7, lateral teeth; 8, 9, intermediate teeth; 10-20, marginal teeth.
2. *Helisoma campanulatum wisconsinense* (Winslow). Little Arbor Vitae Lake, Wisconsin.
   50, center tooth; 1-8, lateral teeth; 9, 10, intermediate teeth; 11-15, marginal teeth.
3. *Helisoma campanulatum canadense* F. C. Baker. Bamiji Lake, Ontario, Canada.
   52, center tooth; 1-8, lateral teeth; 9, 10, intermediate teeth; 11-20, marginal teeth.
4. *Helisoma campanulatum smithi* (F. C. Baker). Douglas Lake, Michigan.
   60, center tooth; 1-8, lateral teeth; 9, 10, intermediate teeth; 11-19, marginal teeth.



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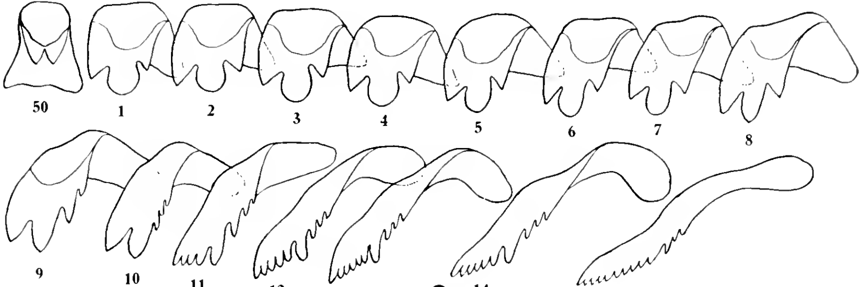

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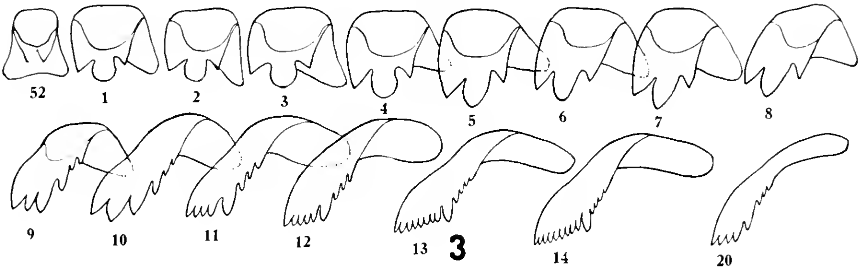

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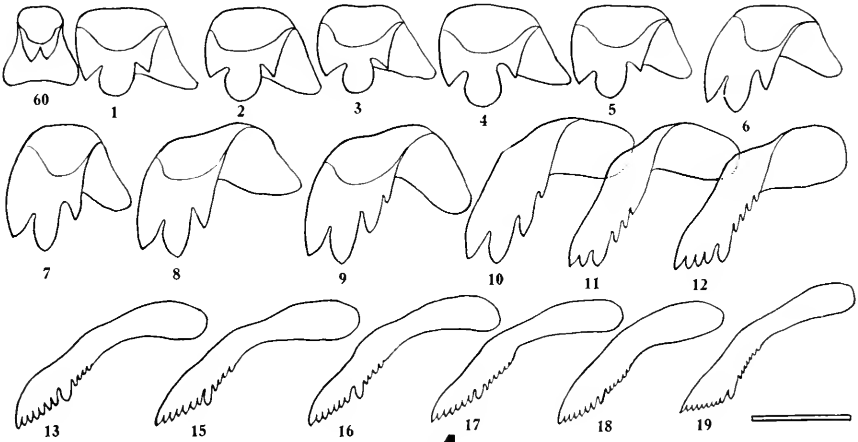

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PLATE 62

PLATE 63

Radulae of *Helisoma*

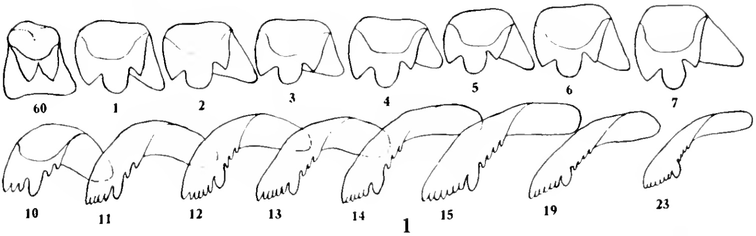
See remarks on plate 53. Line at lower right of plate indicates 25 microns in length.

1. *Helisoma trivolvis fallax* (Haldeman). Cambridge, Massachusetts.
   60, center tooth; 1-7, lateral teeth; 10, intermediate tooth; 11-23, marginal teeth.

2. *Helisoma tenue californiense* F. C. Baker. Shandon, California.
   77, center tooth; 1-11, lateral teeth; 12, intermediate tooth; 13-19, marginal teeth. 100th row. Numerals 1-11, lateral teeth with multiple cusps on entocone and ectocone.

3. *Helisoma trivolvis lentum* (Say). New Orleans, Louisiana.
   60, center tooth; 1-9, lateral teeth; 10, 11, intermediate teeth; 12-20, marginal teeth.

4. *Helisoma duryi eudiscus* Pilsbry. Silver Springs, Florida.
   84, center tooth; 1-10, lateral teeth; 11, 12, intermediate teeth; 12-22, marginal teeth.



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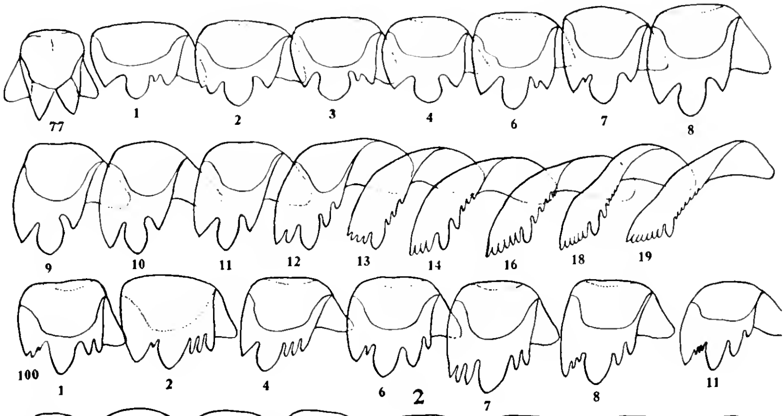

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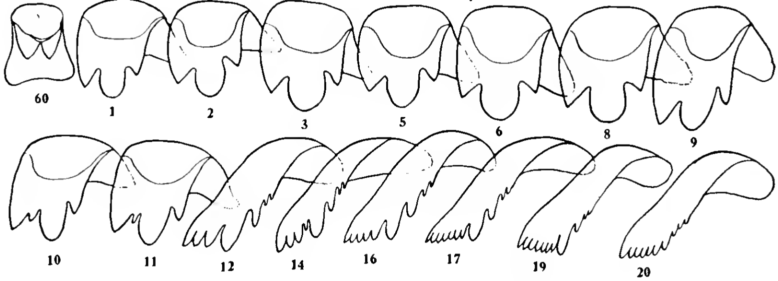

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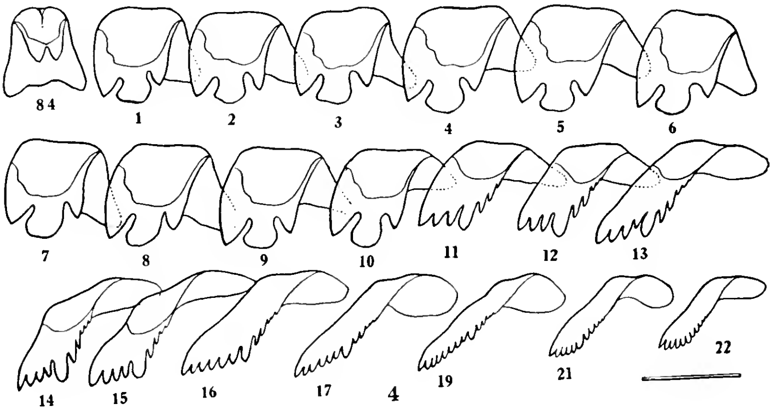

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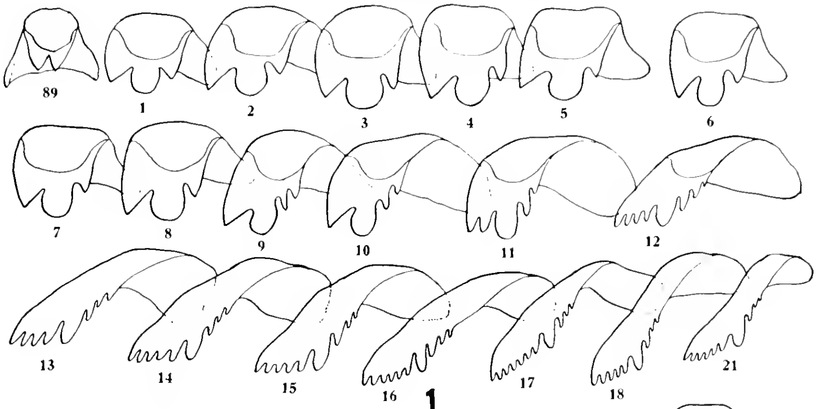
PLATE 63

PLATE 64

Radulae of *Helisoma*

See remarks on plate 53. Line at lower right of plate indicates 25 microns in length.

1. *Helisoma scalare* (Jay). Lake Butler, Florida.
   89, center tooth; 1-8, lateral teeth; 9-11, intermediate teeth; 12-21, marginal teeth.
2. *Helisoma scalare* (Jay). Lake Butler, Florida.
   86, center tooth of another specimen; 1-6, lateral teeth.
3. *Helisoma duryi normale* Pilsbry. Tamiami Trail, 40 miles west of Miami, Florida.
   110, center tooth; 1-11, lateral teeth; 12, intermediate tooth; 13-29, marginal teeth. 12, lower right, 12th tooth (marginal) in another row of teeth.
4. *Helisoma duryi normale* Pilsbry. Paines Prairie, Florida.
   55, center tooth; 1-9, lateral teeth; 10, intermediate tooth; 11-26, marginal teeth.
   140, center tooth; 1-10, lateral teeth; 11, intermediate tooth; 12-20, marginal teeth.



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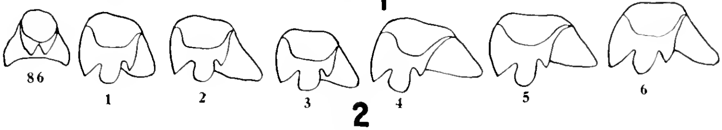

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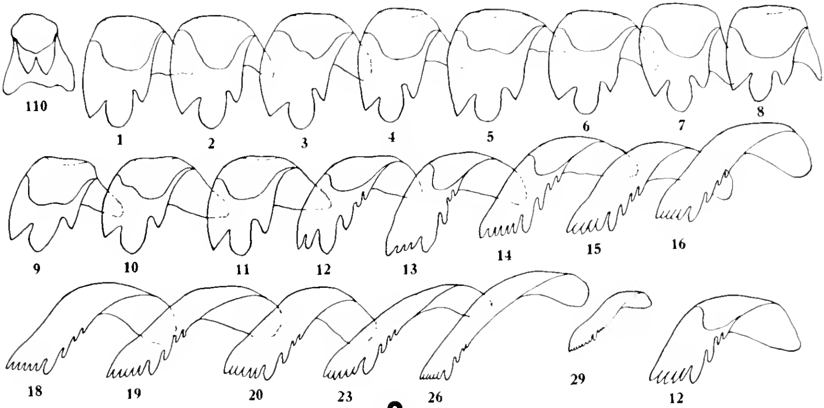

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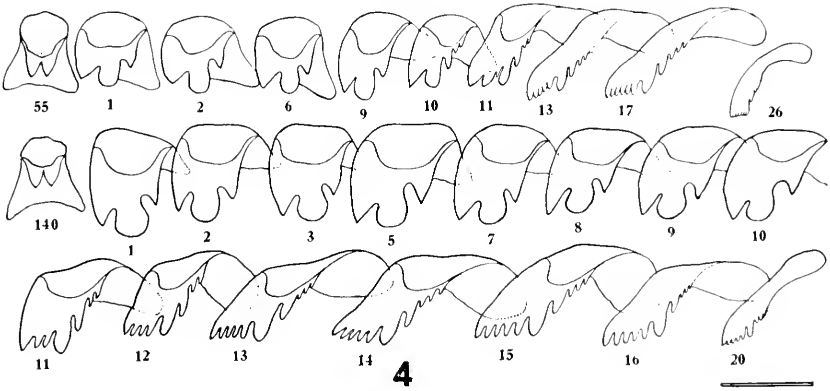

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PLATE 64

PLATE 65

Radulae of *Planorbula*, *Parapholyx*, and *Carinifex*

See remarks on plate 53. Line at lower left of plate indicates 25 microns in length.

1. *Planorbula armigera* (Say). Murphy Creek, near Madison, Wisconsin.

   128, center tooth; 1-6, lateral teeth; 9, 11, intermediate teeth; 12-19, marginal teeth.

2. *Planorbula jenksii* (H. F. Carpenter). Unionville, Connecticut.

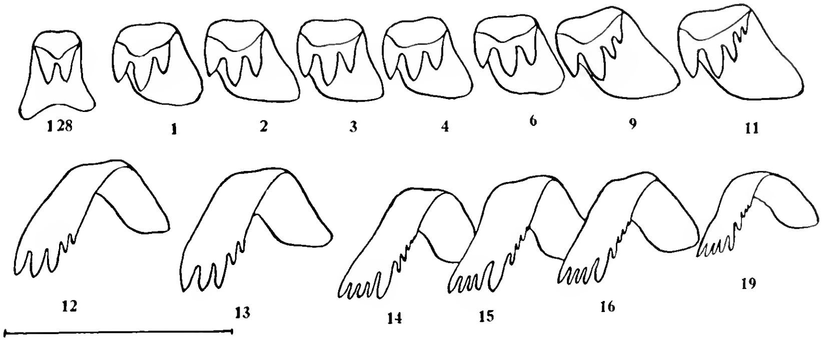
   105, center tooth; 1-5, lateral teeth; 9, 11, intermediate teeth; 12-19, marginal teeth.

3. *Parapholyx effusa klamathensis* F. C. Baker. Klamath Lake, Oregon.

   60, center tooth; 1-8 lateral teeth; 9-11, intermediate teeth; 13-19, marginal teeth.

4. *Carinifex jacksonensis* J. Henderson. Jackson Lake, Wyoming.

   120, center tooth; 1-10, lateral teeth; 12, intermediate tooth; 13-24, marginal teeth.



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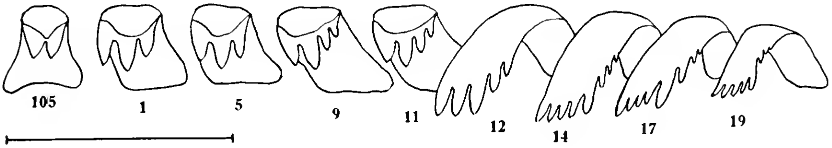

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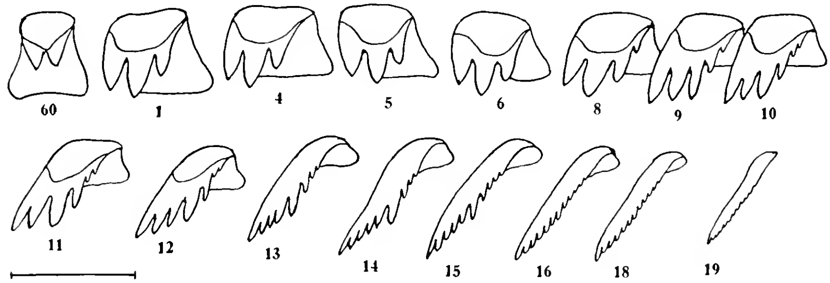

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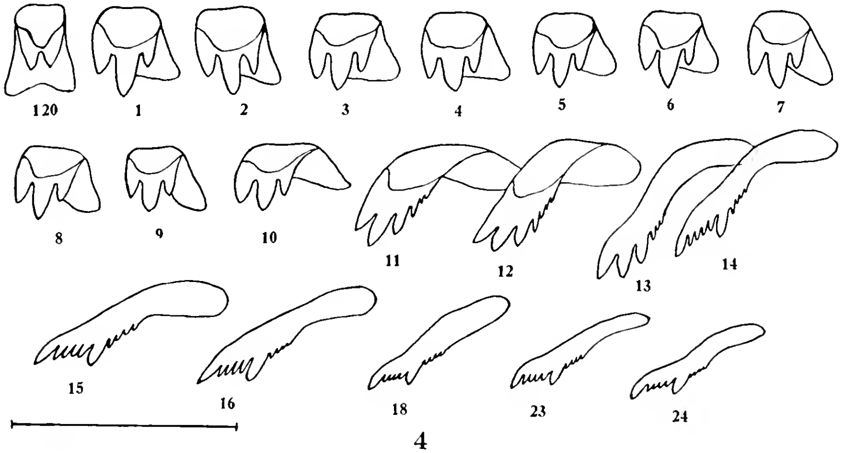

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PLATE 65

PLATE 66

Radulae of *Indoplanorbis* and *Planorbarius*

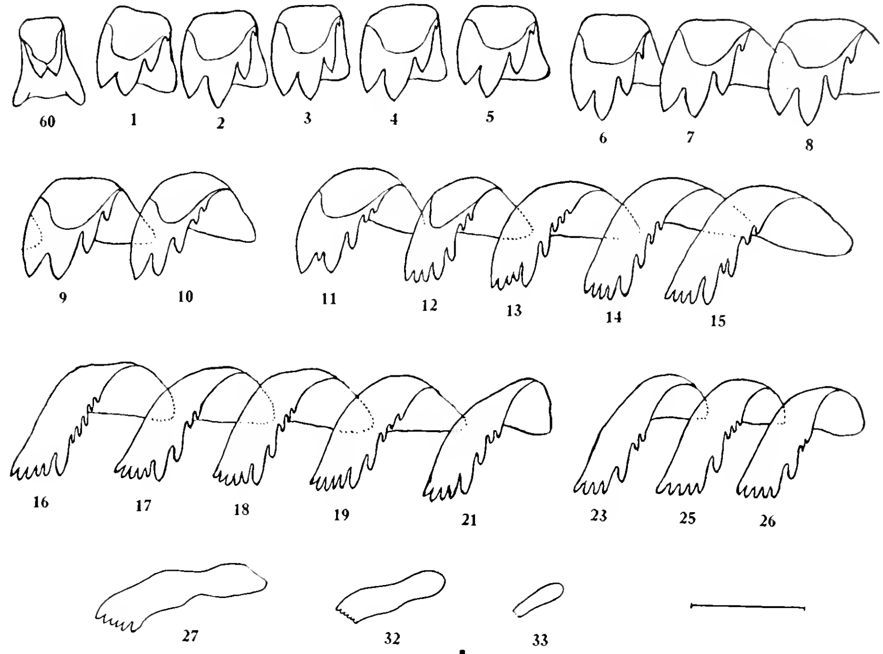
See remarks on plate 53. Line at lower right of plate indicates 25 microns in length.

1. *Indoplanorbis exustus* (Deshayes). North Shan State, Burma.

   60, center tooth; 1-5, lateral teeth; 6-10, intermediate teeth; 16-21, marginal teeth; 11, last intermediate tooth in another row; 12-15, marginal teeth in same row; 23-26, marginal teeth in same row; 27, 32, 33, outer marginal teeth in same row.

2. *Planorbarius corneus* (Linn.). Near Warsaw, Poland.

   60, center tooth; 1-9, lateral teeth; 10-14, intermediate teeth; 15-38, marginal teeth; 39-42, outer marginal teeth.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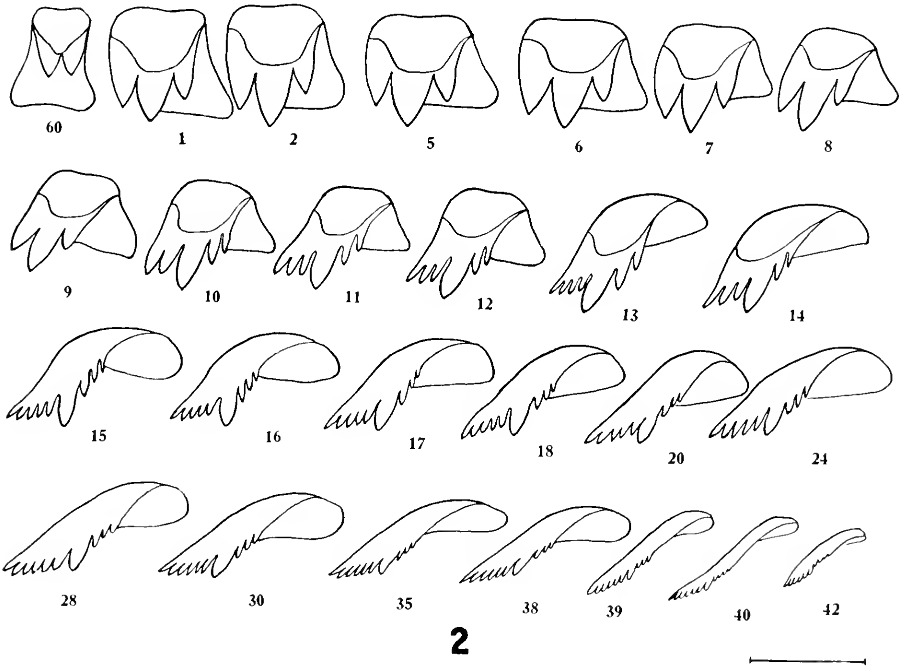
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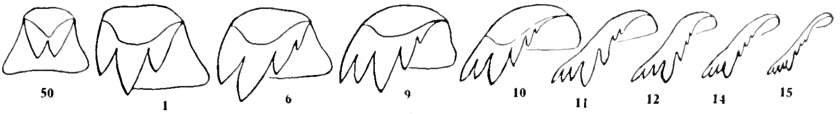
PLATE 66

PLATE 67

Radulae of Planorbidae

See remarks on plate 53. Line at lower right of plate indicates 25 microns in length. Line under fig. 6 is also for figs. 1 to 5.

1. *Promenetus exacuous* (Say). Wainwright Park, Alberta.
   50, center tooth; 1-6, lateral teeth; 9, 10, intermediate teeth; 11-15, marginal teeth.
2. *Promenetus umbilicatellus* (Cockerell). Wainwright Park, Alberta.
   60, center tooth; 1-6, lateral teeth; 9-11, intermediate teeth; 12-15, marginal teeth.
3. *Menetus cooperi callioglyptus* (Vanatta). Vancouver Island, British Columbia.
   55, center tooth; 1-8, lateral teeth; 9, 10, intermediate teeth; 11-15, marginal teeth.
4. *Menetus dilatatus* (Gould). Unionville, Connecticut.
   60, center tooth; 1-7, lateral teeth; 8-10, intermediate teeth; 11-14, marginal teeth.
5. *Menetus sampsoni* (Ancey). Stanton, Missouri.
   50, center tooth; 1-7, lateral teeth; 8, 10, intermediate teeth; 11-14, marginal teeth.
6. *Anisus spirorbis* (Linn.). Near Warsaw, Poland.
   45, center tooth; 1-10, lateral teeth; 11, intermediate tooth; 12-15, marginal teeth.
7. *Planorbis planorbis* (Linn.). Near Warsaw, Poland.
   60, center tooth; 1-9, lateral teeth; 11, intermediate tooth; 14-20, marginal teeth.
8. *Carinifex ponsonbyi* E. A. Smith. Klamath Lake, Oregon.
   115, center tooth; 1-6, lateral teeth; 7-10, intermediate teeth; 11-27, marginal teeth.



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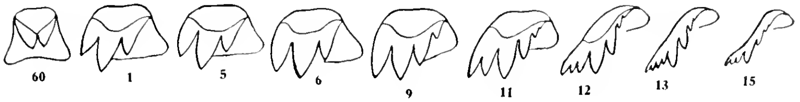

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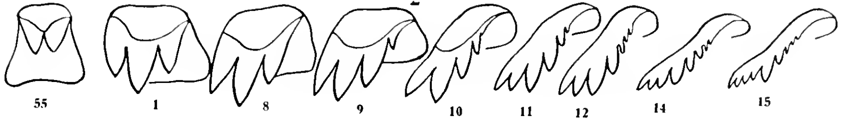

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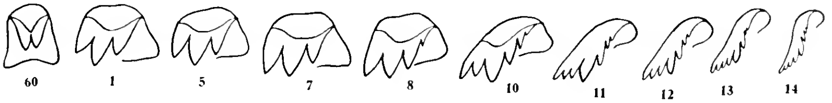

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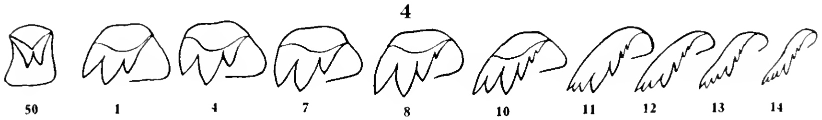

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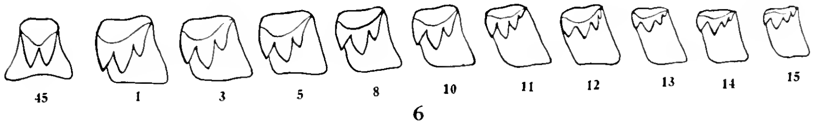

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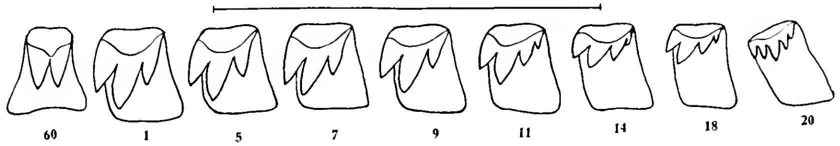

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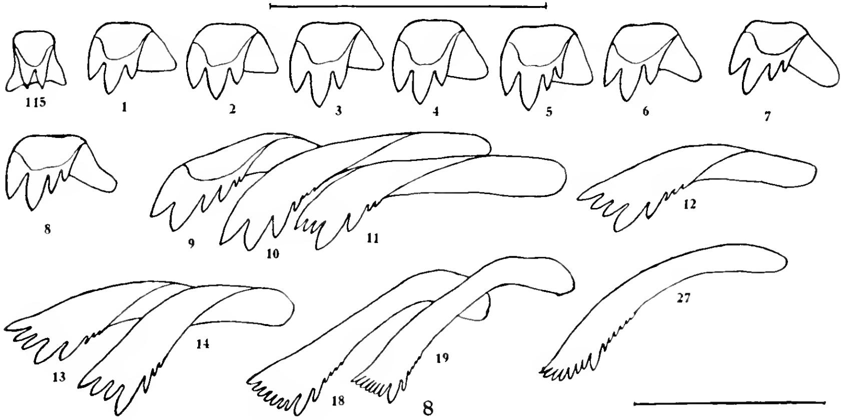

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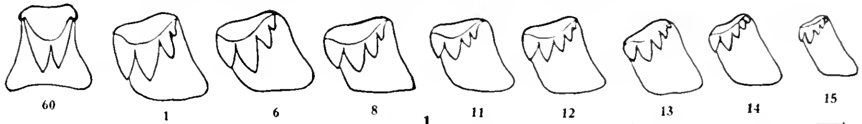
PLATE 67

PLATE 68

Radulae of Planorbidae

See remarks on plate 53. Line at lower right of plate indicates 25 microns in length for figs. 5-9; lines for figs. 1-4 are 10 microns in length.

1. *Bathyomphalus contortus* (Linn.). Near Warsaw, Poland.
   60, center tooth.
2. *Drepanotrema lucidum* (Pfeiffer). Havana, Cuba.
   50, center tooth; 1-8, lateral teeth; 13, 14, intermediate teeth; 15, marginal tooth.
3. *Drepanotrema anatinum* (Orbigny). Puerto Rico.
   50, center tooth; 1-5, lateral teeth; 7, 9, intermediate teeth; 13, marginal tooth.
4. *Drepanotrema hoffmani* F. C. Baker. Puerto Rico.
   52, center tooth; 1-6, lateral teeth; 8, intermediate tooth; 11-21, marginal teeth.
5. *Australorbis glabratus* (Say). Puerto Rico.
   60, center tooth; 1-13, lateral teeth; 14, 15, intermediate teeth; 16-26, marginal teeth.
6. *Tropicorbis riisei* (Dunker). Lares, Puerto Rico.
   50, center tooth; 1, lateral tooth; 5, 6, intermediate teeth; 7-12, marginal teeth.
7. *Tropicorbis obstructus* (Morelet). New Orleans, Louisiana.
   60, center tooth; 1-7, lateral teeth; 8, 9, intermediate teeth; 11-14, marginal teeth.
8. *Tropicorbis havanensis* (Pfeiffer). New Orleans, Louisiana.
   55, center tooth; 1, lateral tooth; 6-8, intermediate teeth; 10, 12, marginal teeth.
9. *Gyraulus albus* (Müller). Near Warsaw, Poland.
   60, center tooth; 1, 5, 8, lateral teeth; 10, intermediate tooth; 12, 13, marginal teeth.



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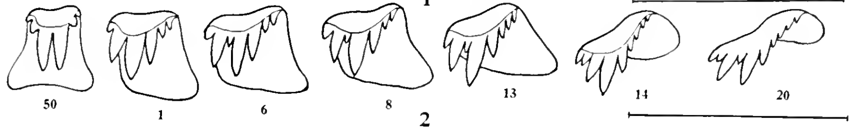

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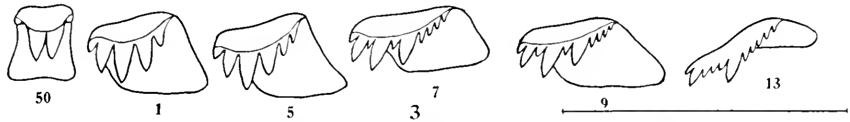

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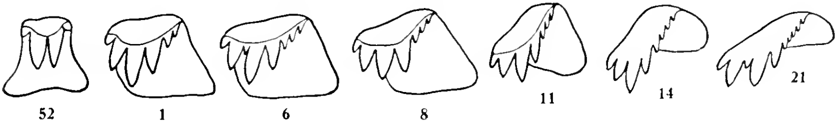

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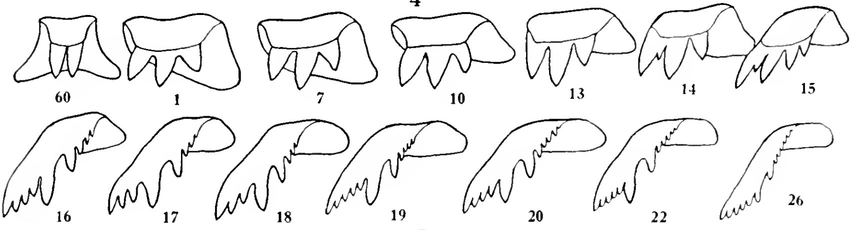

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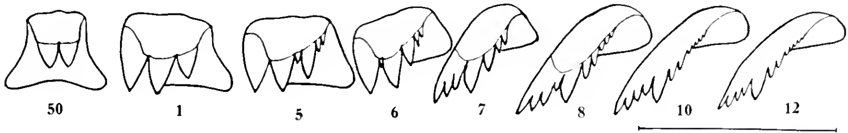

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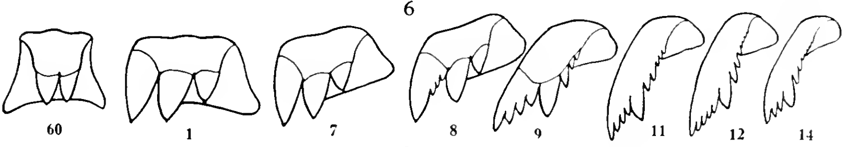

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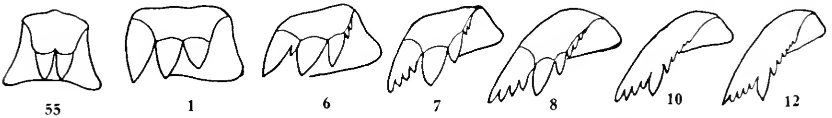

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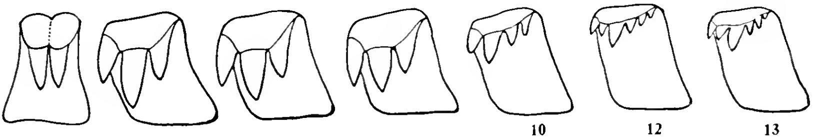

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PLATE 68

PLATE 69

Radulae of Planorbidae

See remarks on plate 53. Lines near figs. 1 to 5 indicate 25 microns in length; lines near figs. 6 to 9 indicate 10 microns in length.

1. *Gyraulus hirsutus* (Gould). Lake Nipissing, Ontario, Canada.
   50, center tooth; 1, lateral tooth; 9, 11, intermediate teeth; 12-16, marginal teeth.

2. *Gyraulus deflectus obliquus* (DeKay). Taylor Lake, Quebec, Canada.
   60, center tooth; 1, lateral tooth; 9-11, intermediate teeth; 13-18, marginal teeth.

3. *Gyraulus parvus* (Say). Winnebago Lake, near Oshkosh, Wisconsin.
   55, center tooth; 1, 5, lateral teeth; 6, intermediate tooth; 7-10, marginal teeth.

4. *Gyraulus similaris* (F. C. Baker). Tolland, Colorado.
   60, center tooth; 1, 6, lateral teeth; 8, 10, intermediate teeth; 13, 15, marginal teeth.

5. *Gyraulus vermicularis* (Gould). Near San Francisco, California.
   50, center tooth; 1-6, lateral teeth; 7-10, intermediate teeth; 11, marginal tooth.

6. *Armiger imbricatus* (Müller). Michigan.
   55, center tooth; 1-6, lateral teeth; 8, 10, intermediate teeth; 12, 13, marginal teeth.

7. *Segmentina nitida* (Müller). Near Warsaw, Poland.
   60, center tooth; 1-8, lateral teeth; 13-16, marginal teeth.

8. *Polypylis calathus* (Benson). North Shan State, Burma.
   50, center tooth; 1-8, lateral teeth; 13-18, marginal teeth.

9. *Intha capitis* Annandale. North Shan State, Burma.
   60, center tooth; 1-8, lateral teeth; 11, 12, marginal teeth.

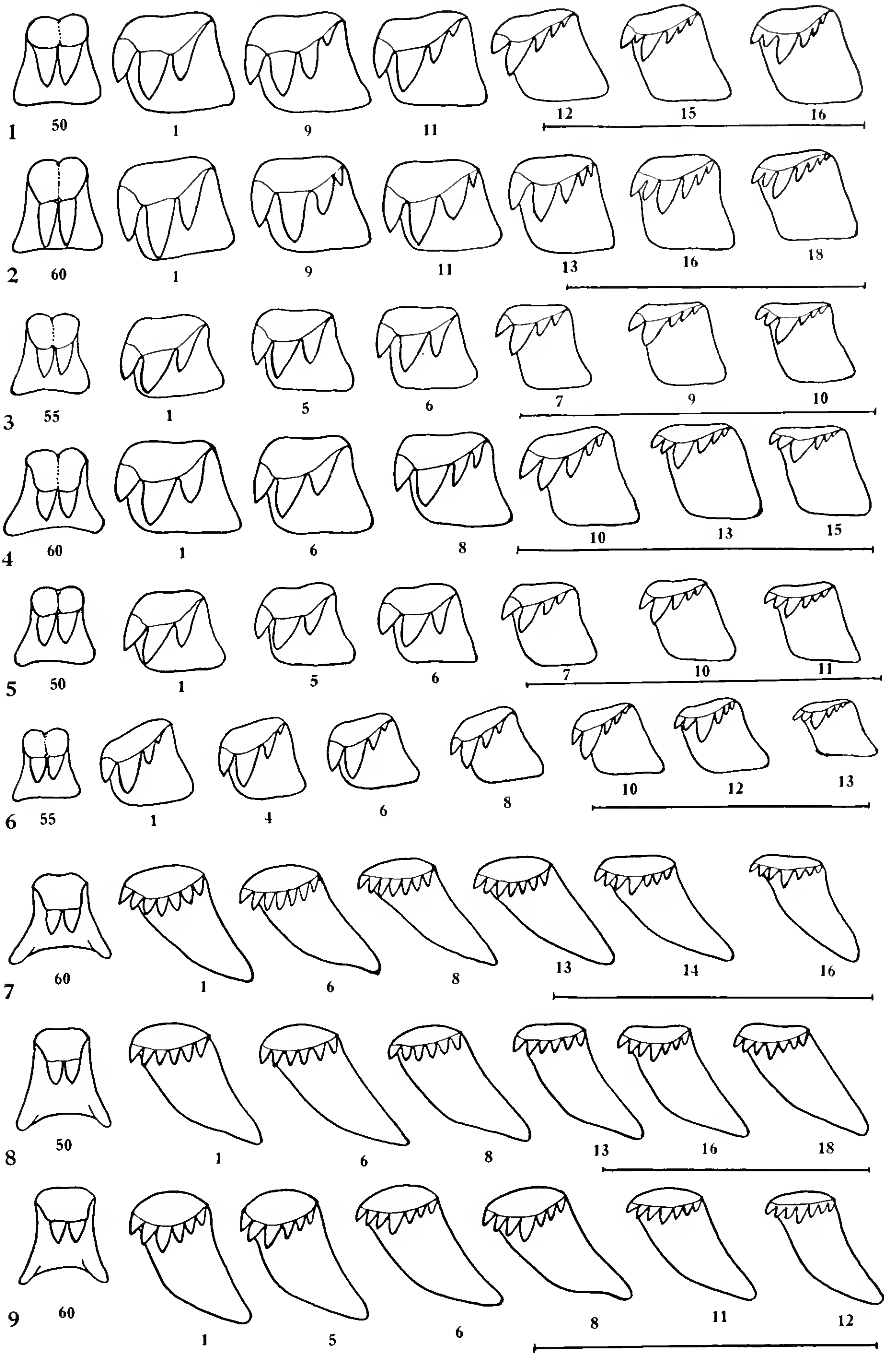
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PLATE 69

PLATE 70

Animals of Planorbidae

1. *Helisoma campanulatum* (Say). Canadian specimen. View as seen crawling up side of aquarium jar.
2. *Helisoma scalare* (Jay). March 13. Twelve hours out of egg.
3. *Helisoma scalare* (Jay). Lake Butler, Florida. Adult with shell 10 mm. long. Drawn from aquarium specimen.
4. *Tropicorbis havanensis* (Pfeiffer). New Orleans, Louisiana. Drawn from aquarium specimen. Shows pigmentation of mantle through shell.
5. *Gyraulus hirsutus* (Gould). Halfmoon Pond, near Alton Bay, Lake Winnipesaukee, New Hampshire. Head and tentacles of crawling animal.
6. *Helisoma trivolvis* (Say). Oneida Lake, New York. Young Animal.
7. *Helisoma trivolvis macrostomum* (Whiteaves). Near Bayfield, Wisconsin. Side view of crawling animal with parts indicated.
8. *Helisoma trivolvis fallax* (Haldeman). Cambridge, Massachusetts. Animal crawling up side of aquarium jar.
9. *Menetus dilatatus* (Gould). Unionville, Connecticut. Animal crawling on stick in aquarium jar. Side view.
10. *Menetus dilatatus* (Gould). Unionville, Connecticut. Top view of animal.
11. *Planorbula jenksii* (H. F. Carpenter). From pool near Lake Wentworth, New Hampshire. Animal crawling on bottom of aquarium jar.
12. *Helisoma subcrenatum* (P. P. Carpenter). Buccal sac with parts indicated.
13. *Gyraulus albus* (Müller). Buccal sac. The outline of the radula is shown in the radular sac and the buccal sac.

Line near figure indicates 1 mm. in length

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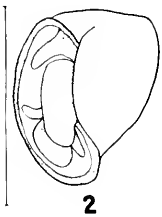

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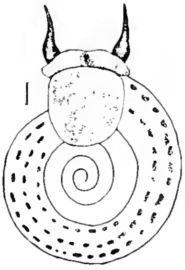

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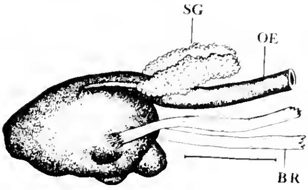

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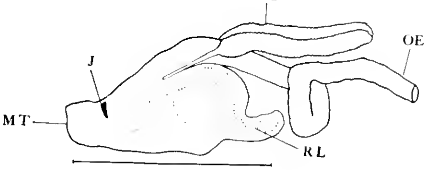

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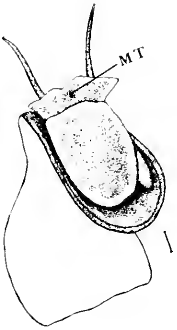

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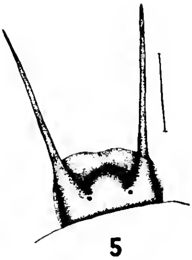

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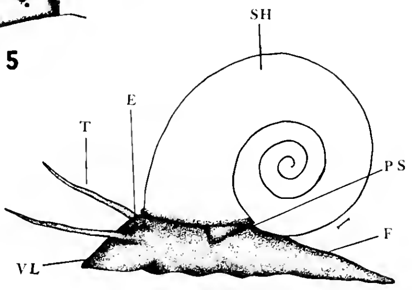

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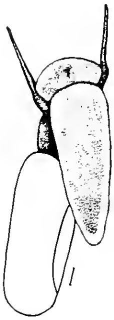

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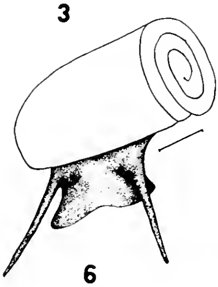

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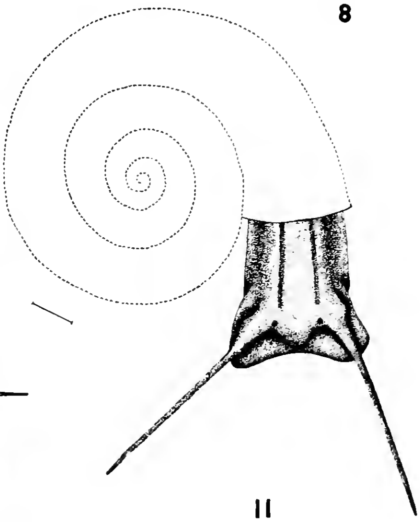

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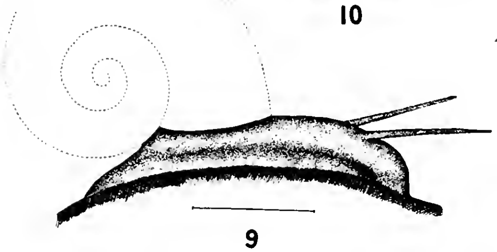

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PLATE 70

PLATE 71

Isidora and *Afroplanorbis*

1-6. *Isidora globosa* (Morelet). Copied from Connolly, Trans. Royal Soc. South Africa, XII, plate 8.

1. Posterior end of penis (verge) with its sheath split open, showing the junction of the vas deferens with the penis (verge). Fig. 11. × 11.
2. Alimentary canal and salivary glands seen from above. Fig. 12. × 6.
3. Reproductive organs (genitalia). Fig. 14. × 5.
4. Animal without its shell, seen from the left side. Fig. 13. × 3.
5. Pulmonary orifice, with the folded branchial tube, anus, etc., on the right of it. Fig. 8. × 5.
6. Posterior end of penis (vergic sac) showing penis papilla, this specimen exhibiting a different condition from that seen in fig. 1. Fig. 15. × 12.

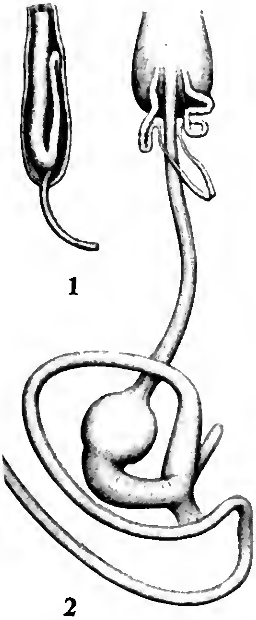
7-9. *Planorbis pfeifferi* Krauss (= *Afroplanorbis pfeifferi* (Krauss)). Copied from Connolly, as noted above, plate 8.

7. Lobes beneath the pulmonary orifice, seen from above. Fig. 17. × 8. Includes pseudobranch and rectum.
8. Buccal mass, salivary glands, oesophagus, stomach, caecum, and first loop of intestine. Fig. 19. × 6.
9. Reproductive organs (genitalia). Fig. 18. × 8.

10-12. *Planorbis adowensis* Bourg. (= *Afroplanorbis adowensis* (Bourg.)). Copied from Pilsbry, Proc. Acad. Nat. Sci. Phil., LXXXVI, p. 53.

10. Genitalia showing spermatheca, prostate, uterus, etc. Fig. G.
11. Male organ (penial complex) showing preputium and verge. Fig. F.
12. Preputium cut open to show pilasters and end of verge, the verge indicated by dotted lines. u.s. upper sac (vergic sac). Fig. H.

Figures are greatly enlarged



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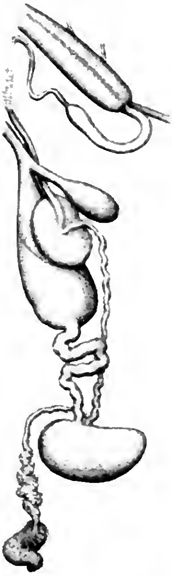

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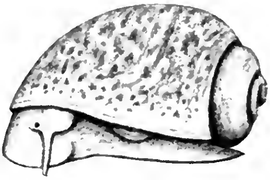

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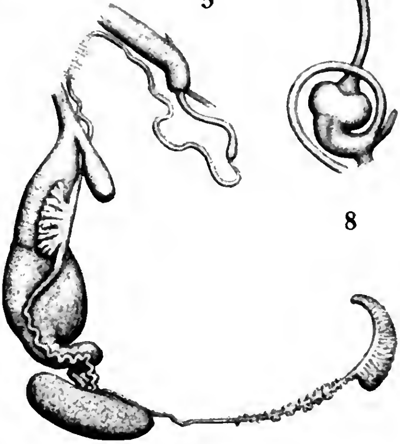

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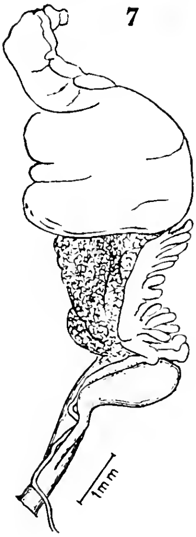

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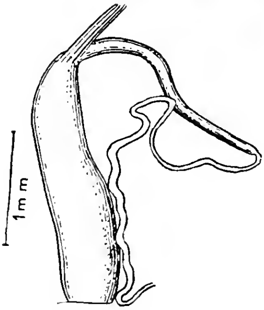

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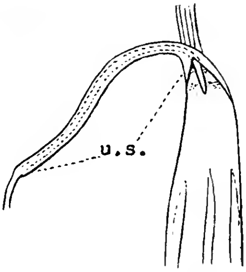

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PLATE 71

PLATE 72

Acrorbis petricola Odhner

Copied from Odhner's paper in Arkiv. för Zoologi, Band 29B, No. 14, two plates reduced to one plate in this volume.

1–3. *Acrorbis petricola* Odhner. Shell from below, front view, and from above.
4. Radula, one-half row on left side. × 1000.
5. Animal removed from shell to show organization, from above.
6. Head and foot of animal, fore view.
7. Buccal sac.
8. Digestive system, from above.
9. Penial complex.
10. Portion of genitalia.

Description of symbols used on this plate: a, flagellum (anhangsdrüse); b, spermatheca (bursa copulatrix); c, caecum, a blind sac; d, intestine; f, tentacle; g, ganglia in nerve collar; go, ovotestis (gonad); h, heart in pericardium; j, jaw; k, pseudobranch (kiemen falte); l, liver; m, stomach; n, kidney (niere); o, oesophagus; od, oviduct (in the figure this refers to the ovisperm duct); p, prostate; ph, buccal sac; ps, preputium (penissack, here including the whole penial complex, preputium and vergic sac); r, rectum; rp, penial retractors; s, salivary glands (speichel drüsen); t, radula sac (radula tasche); u, uterus; v, vas deferens.

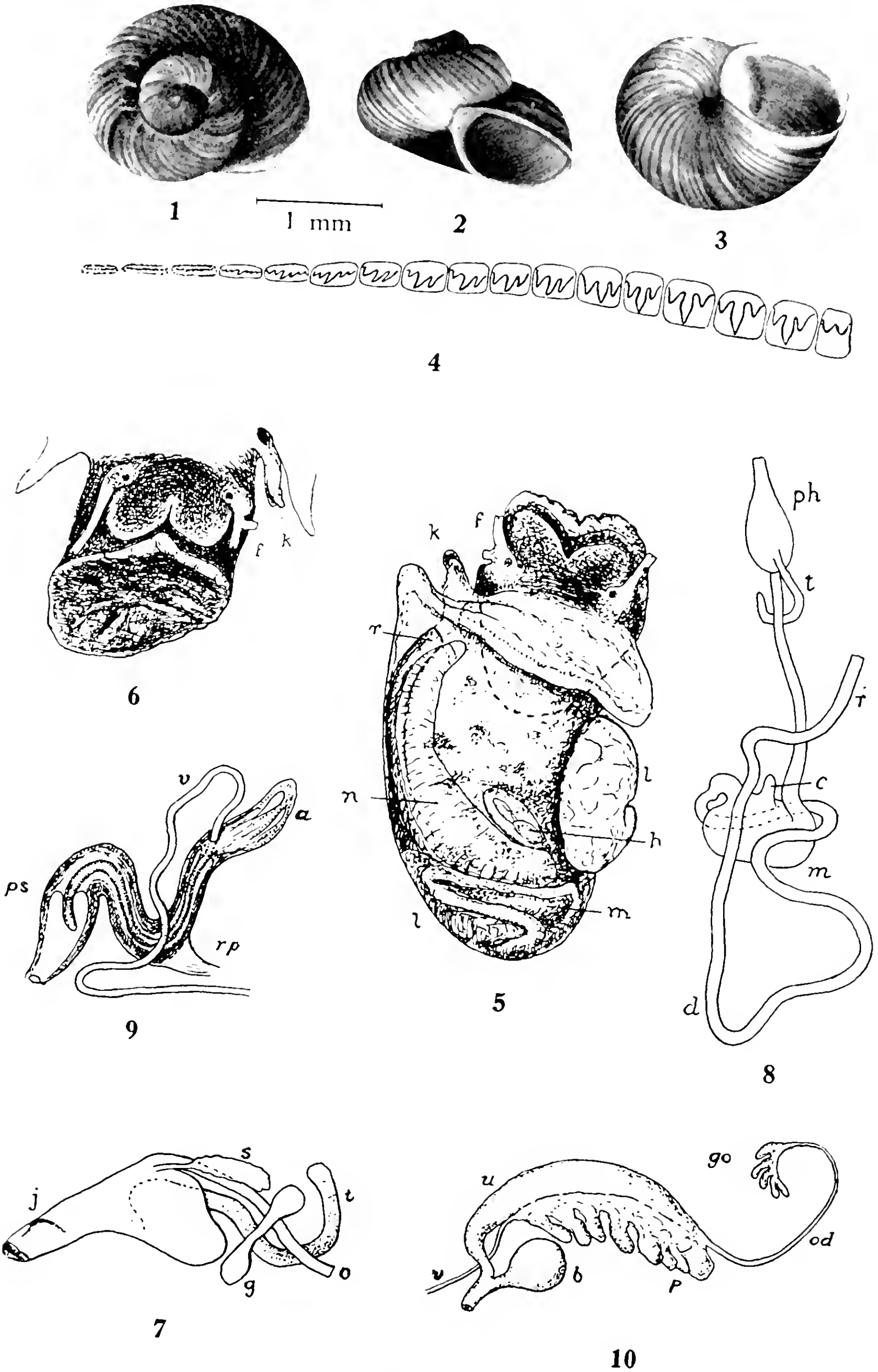
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PLATE 72

PLATE 73

Indoplanorbis exustus (Deshayes)

Genitalia copied from Larambergue, 1939b, p. 288

1. General view of genitalia (in French works the figures of both the animal and the shell are in reverse as compared with the position of American figures).
2. Penial complex (appareil copulateur) with vergic sac cut open to show length and nature of verge.
3. Transverse section of vas deferens (canal déférent).

Explanation of symbols used on the plates: Al, albumen gland; Bf, buccal sac; C, junction of preputium with vergic sac (col); C ⚥, ovisperm duct (canal hermaphrodite); Cd, vas deferens (canal déférent); G, preputium (gaine); G ⚥, ovotestis (glande hermaphrodite); Gn, nidamental gland (glande utérines); Od, oviduct; P, pilasters (piliers musculaires); Pc, spermatheca (poche copulatrice); Pe, verge (tube pénial); Pp, vergic sac (poche du pénis); Pr, prostate; R, retractor muscle (muscle retractéur); compare the insertions of this figure with the figures on plate 22 of this work; Sp, sperm duct (spermiducte); Ut, uterus; Va, vagina.

Vertical line indicates measurements in millimeters; horizontal line in microns.

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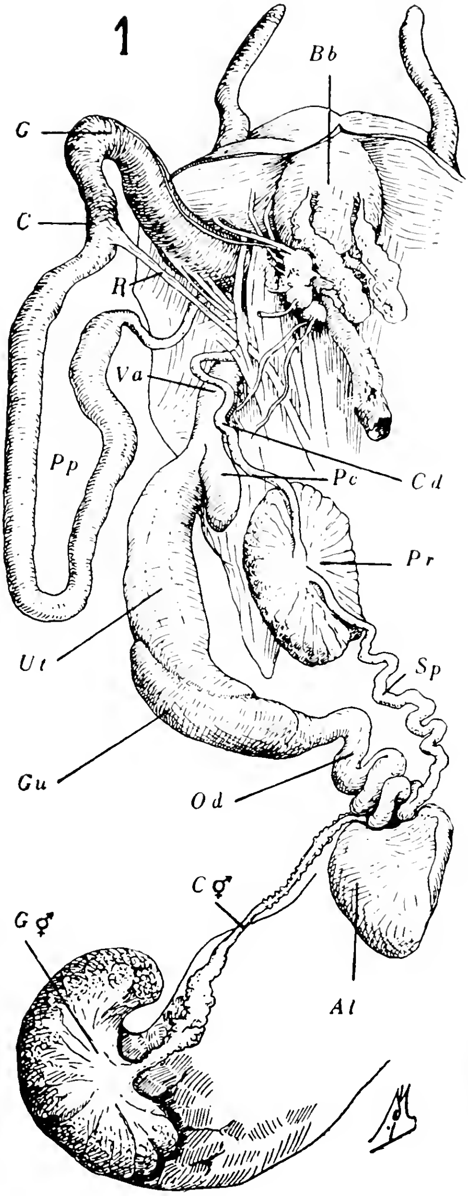

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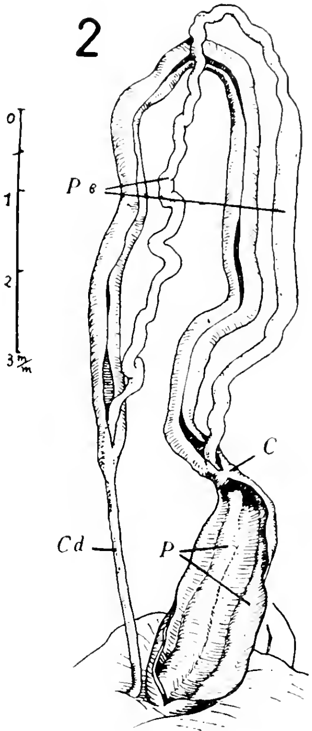

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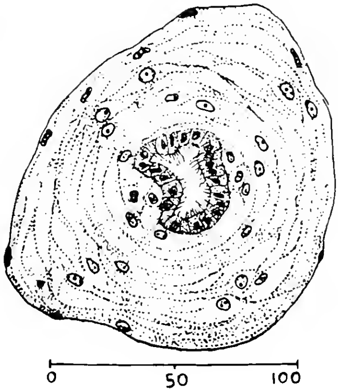


PLATE 73

PLATE 74

Indoplanorbis exustus (Deshayes)

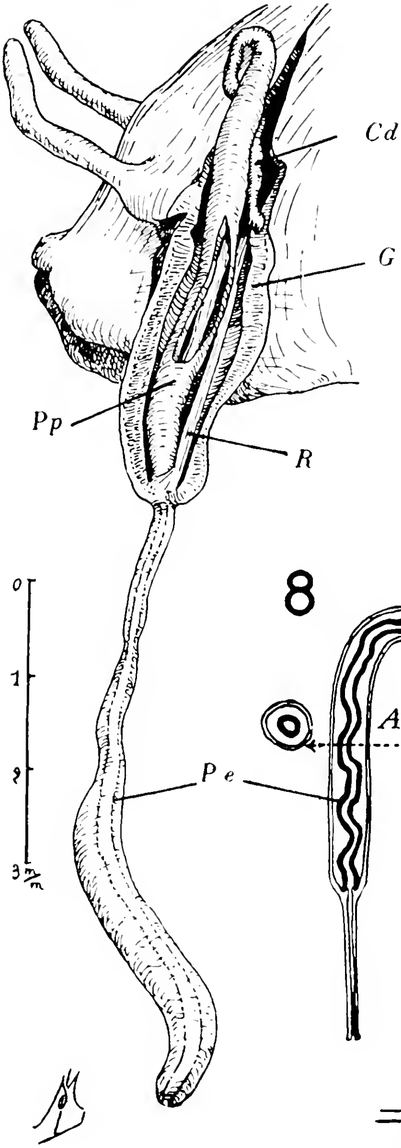
Genitalia copied from Larambergue, 1939b, p. 293

6. Individual with verge and preputium protruded from male genital opening, the latter cut open to show portion of verge not everted.
7. Two individuals of *Indoplanorbis* in coitus showing the extension of the penial complex from the body of the animal acting as male. Specimens anesthetized.
8. Schematic figure of penial complex retracted within the body of the animal.
9. Schematic figure of penial complex everted during copulation.

Explanation of symbols on the plate: Cd, vas deferens; G, preputium (gaine); Pe, verge (tube pénial); Pp, vergic sac (poche du pénis).

Vertical line indicates size in millimeters

6



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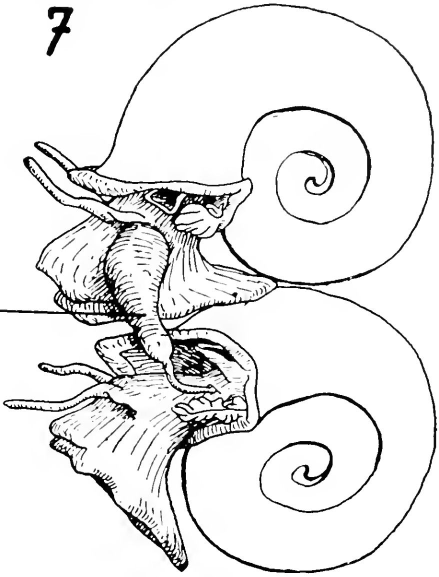

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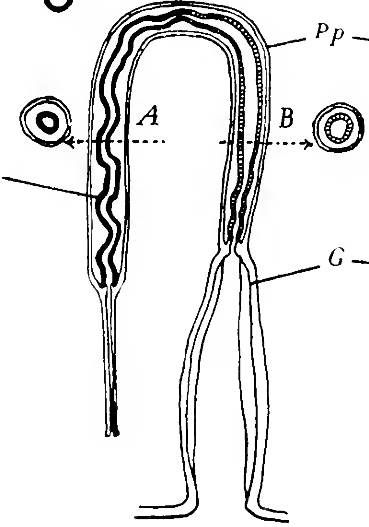

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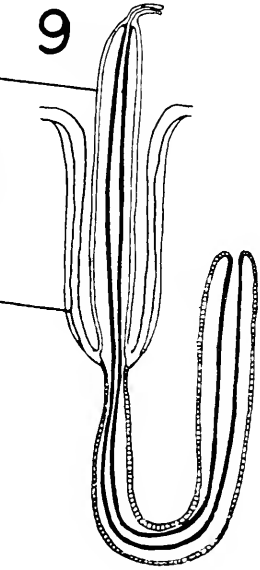

PLATE 74

PLATE 75

Bulinus contortus (Michaud)

Genitalia copied from Larambergue, 1939a, p. 93

4. General dissection of genitalia and fore part of body.
5. Penial complex cut open to show characteristics.
6. Carrefour of the genitalia.

Explanation of symbols on the plate: A, atrium; Al, albumen gland; Bb, buccal sac; C, junction of preputium with vergic sac (col); C ⚥, ovisperm duct (canal hermaphrodite); C Al, duct of albumen gland; Cd, vas deferens (canal déférent); G, preputium (gaine); G ⚥, ovotestis (glande hermaphrodite); Od, oviduct; P, pilasters (piliers musculaires); Pc, spermatheca (poche copulatrice); Pe, verge (pénis); Pp, vergic sac (poche du pénis); Pr, prostate; R, retractor muscle; Sp, sperm duct; Ut, uterus; Va, vagina.

Vertical line indicates size in millimeters

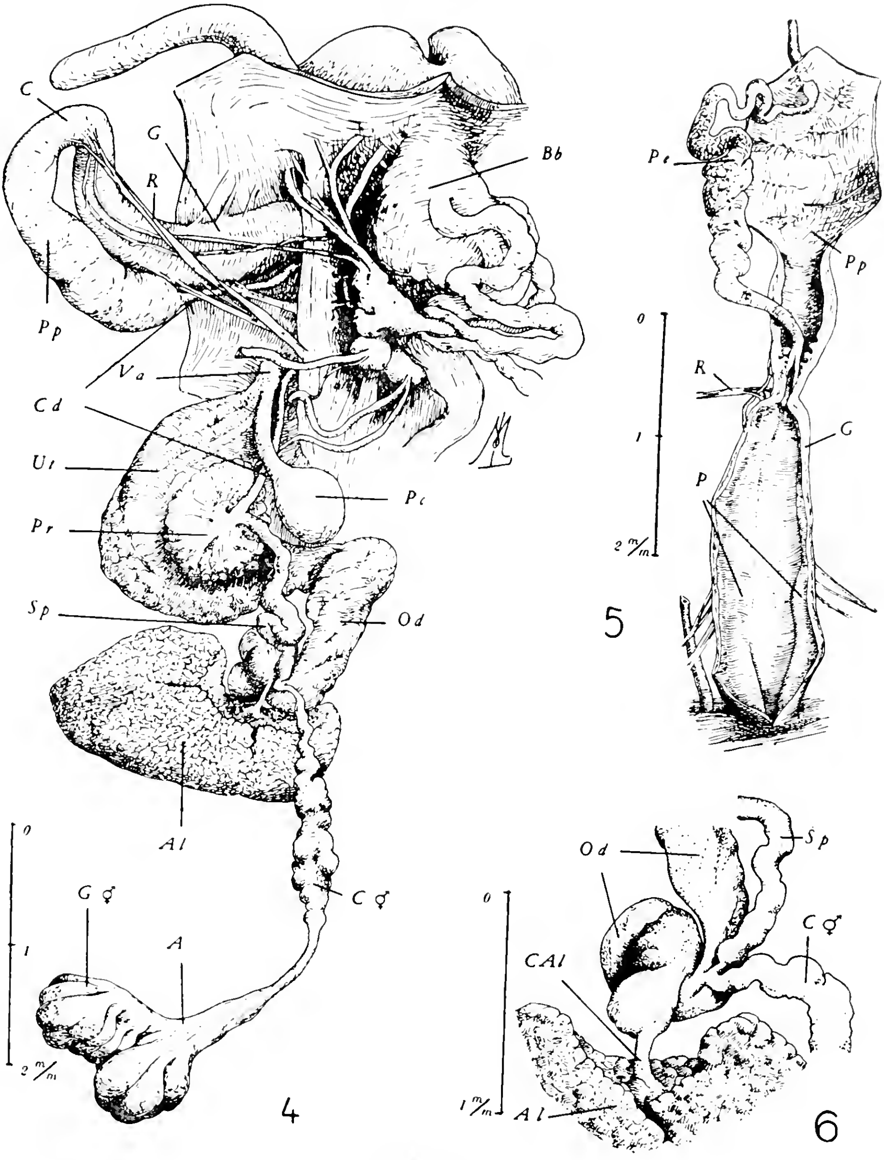
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PLATE 75

PLATE 76

Shells of Planorbidae

1. *Planorbis krambergeri* Halaváts. Resultate d. Wissens. Erforsch. des Balatonsee, plate 3, figs. 3a, 3b, 3c. ×6.
2. *Odontogyrorbis krambergeri* (Halaváts). Lörenthay, op. cit., Art. 3, plate 2, fig. 17. About ×5.
3. *Costorbis strauchianus* (Clessin). Conch. Cab., XVII, plate 31, fig. 5. ×3.
4. *Segmentina nitida* (Müller). Apertural lamellae. Greatly enlarged.
5. *Polypylis hemisphaerula* (Benson). Apertural lamellae. Greatly enlarged.
6. *Armiger crista* (Linn.). Forbes and Hanley, Hist. Brit. Moll., IV, plate 126, figs. 6, 7. About ×4.
7. *Tropicorbis obstructus* (Morelet). Lamellae on outer lip. Enlarged.
8. *Planorbula armigera* (Say). Lamellae on outer lip. Greatly enlarged.
9. *Planorbula wheatleyi* (Lea). Lamellae on outer lip. Greatly enlarged.
10. *Drepanotrema cultratum* (Orbigny). From Bolivar, Colombia. Penial complex. Pilsbry, 1934, fig. 6, E (after H. B. Baker); fl, flagellum; vd, vas deferens; pr, penial retractor, vide Pilsbry.
11. *Pompholopsis whitei* Call. Amer. Geol., I, p. 147, figs. 5-7.
12. *Vorticifex tryoni* (Meek). White, Proc. U.S. Nat. Mus., V, plate 5, figs. 5-7.
13. *Vorticifex binneyi* (Meek). Op. cit., figs. 8, 9.

Figures 11 to 13 are natural size

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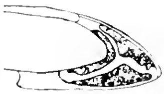

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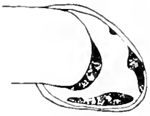

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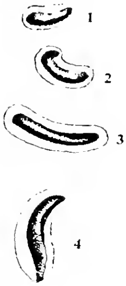

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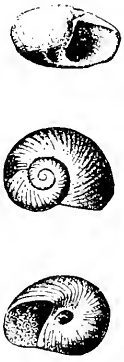

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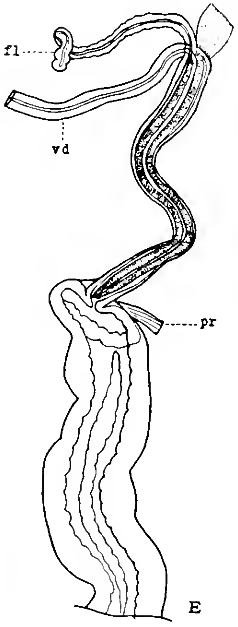

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PLATE 76

PLATE 77

Shells of Planorbidae

1–3. *Gyraulus albus* (Müller). Pond in park in Królikarnia, a suburb of Warsaw, Poland. Baker coll., 3968. ×4.

4–6. *Gyraulus parvus* (Say). Blue Pond, Wheatland Center Road, Monroe Co., New York. U.I., 41369. ×4.

7–9. *Tropicorbis orbiculus* (Morelet). Drift at falls, Valles, Mexico. U.I., 28525. ×2.

10–12. *Tropicorbis pallidus* (C. B. Adams). Kingston, Jamaica. U.I., 40466. ×4.

13–15. *Taphius andecolus* (Orb.). Lake Titicaca, Peru. U.I., 40595. ×1½.

16–18. *Anisus leucostomus* (Millet). Small pond in Bielany Park, Warsaw, Poland. Baker coll., 3969. ×4.

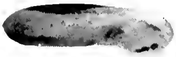
19. *Anisus vortex* (Linn.). Stream in meadow in Jab-Tonna, 18 km. northeast of Warsaw, Poland. Baker coll., 3971. ×2.

20–22. *Anisus spirorbis* (Linn.). Pond at Scarborough, England. Baker coll., 1234. ×4.

23–25. *Bathyomphalus contortus* (Linn.). Drewnica, 4 km. northeast of Warsaw, Poland. Baker coll., 3972. ×4.

26–28. *Planorbis planorbis* (Linn.). A pond 25 km. southeast of Warsaw, Poland. Baker coll., 3970. ×2.

29–31. *Australorbis glabratus* (Say). San Juan, Puerto Rico. M.C.Z., 65218. ×1½.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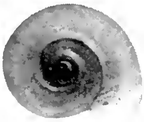
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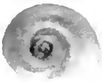
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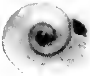
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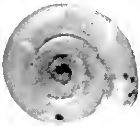
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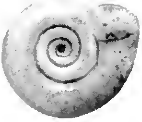
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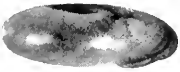
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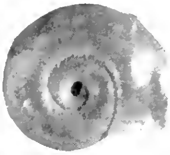
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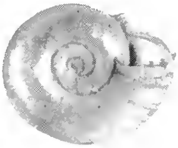
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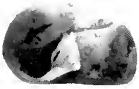
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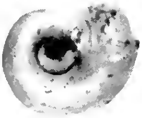
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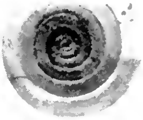
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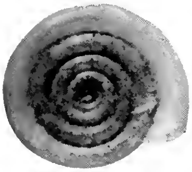
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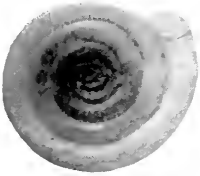
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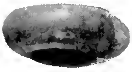
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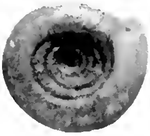
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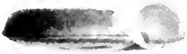
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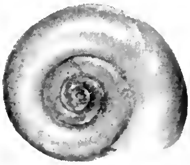
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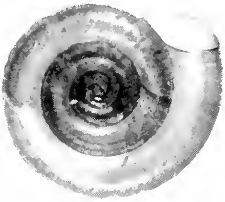
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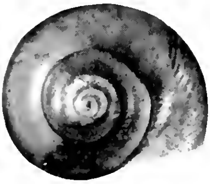
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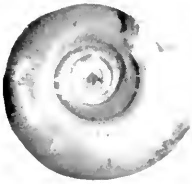
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PLATE 77

PLATE 78

Shells of Planorbidae

1, 2. *Tropicorbis melleus* (Lutz). Upper and under side of animal. From Lutz, fig. 5, a, c.

3. *Tropicorbis nigrilabris* (Lutz). Animal from above. Lutz, fig. 4, c.

4. *Tropicorbis nigrilabris* (Lutz). Animal from above, lighter in pigmentation than fig. 3. From Lutz, fig. 6, c, mislabeled *Planorbis nigricans* by Lutz. Figures 1-4 from Mem. Inst. Oswaldo Cruz, vol. 10, plate 16. Figures greatly enlarged.

5–7. *Helicorbis umbilicalis* (Benson). Figures 5, 6, Hongkong, China. Baker coll., 2756; fig. 7, Canton, China. Baker coll., 2751. ×3.

8–10. *Pingiella peipinensis* (Ping and Yen). Peiping, China. Baker coll., 3975. ×3.

11–13. *Drepanotrema lucidum* (Pfr.). Laguna del Bili, Alacranes Mts., Cuba. M.C.Z., 129991. ×3.

14–16. *Drepanotrema hoffmani* F. C. Baker. Isabela, Puerto Rico. Types. Baker coll., 3976. ×3.

17–19. *Drepanotrema cultratum* (Orb.). Painters Pond, Painters, Antigua. U.S.N.M., 272282. ×3.

20, 21. *Parapholyx effusa* (Lea). Sacramento River, California. Probably type lot. Lea coll., U.S.N.M., 121167. ×3.

22. *Parapholyx effusa* (Lea). Sacramento River, California. Lea coll., U.S.N.M., 121133. ×3.

23. *Carinifex newberryi* (Lea). Canoe Creek, California. U.S.N.M., 56405. ×3.

24. *Carinifex newberryi* (Lea). Canoe Creek, California. Type. Lea coll., U.S.N.M., 9256. ×3.

25–26. *Carinifex newberryi minor* Cooper. Clear Lake, California. Lea coll., U.S.N.M., 121025. ×3.

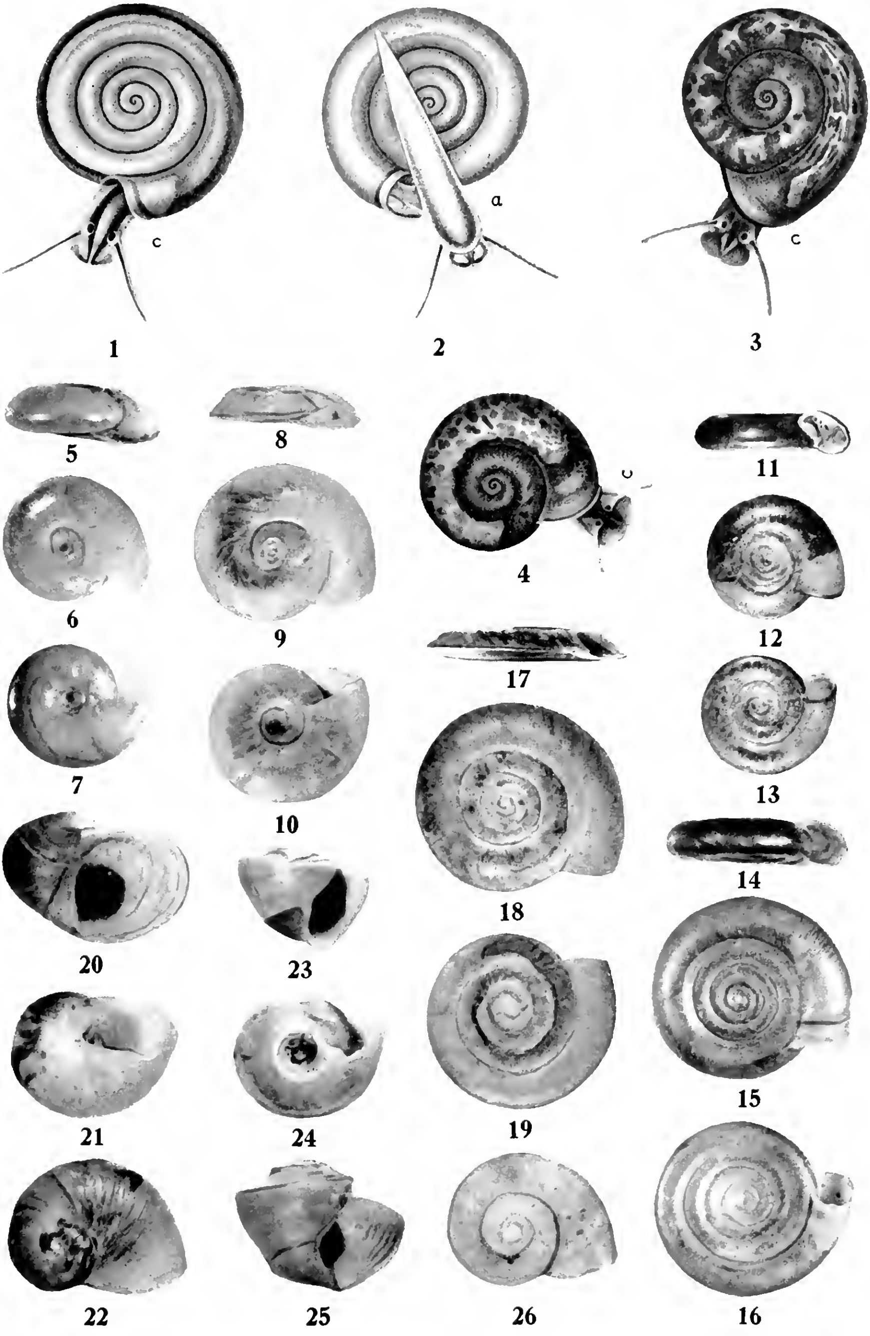

PLATE 78

PLATE 79

Shells of Planorbidae

1–3. *Segmentina nitida* (Müller). Swamp on a meadow in Czerniakow, a suburb of Warsaw, Poland. Baker coll., 3972. ×4.

4–6. *Hippeutis fontanus* (Lightfoot) = *complanatus* (Linn.). Damsells Mill Pond, Painswich, West Strand, England. Baker coll., 1256. ×6.

7–9. *Polypylis largilliarti* (Phil.) = *hemisphaerula* (Benson). Peiping, China. Baker coll., 5973. ×4.

10–12. *Platytaphius heteropleurus* (Pils. & Van.). Lake Titicaca, Peru. Baker coll., 3974. ×2.

13–15. *Menetus dilatatus* (Gould). Wrights Dike, Duxbury, Massachusetts. Baker coll., 3978. ×4.

16–18. *Drepanotrema anatinum* (Orb.). Figures 16, 17, Para, Brazil. U.S.N.M., 348535; fig. 18, Para, Brazil M.C.Z., 72832. ×5.

19–21. *Promenetus exacuous* (Say). Small brook west bank Cayuga Lake, near Cayuga, New York. Baker coll., 1140. ×4.

22–24. *Menetus opercularis* (Gould). San Francisco, California. U.S.N.M., 227303. ×4.

25–27. *Planorbula armigera* (Say). Thief River Falls, Minnesota. U.I., 27093. ×4.

28–30. *Planorbula wheatleyi* (Lea). Boligee, Alabama. Baker coll., 1140. ×4.

31, 32. *Perrinilla cordilleriana* (Hannibal). Truckee Lake Beds, Nevada. Hill near Hawthorne, on Belmont Stage Road, Nevada. Hannibal, Proc. Mal. Soc., X, plate 6, fig. 16, plate 8, fig. 34. About natural size.

33–35. *Indoplanorbis exustus* (Desh.). Figures 33, 34, Bombay, India. Baker coll., 1231; fig. 35, Calcutta, India, Baker coll., 2229. ×1½.


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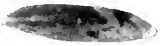
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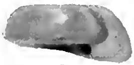
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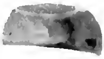
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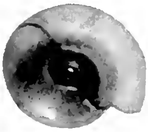
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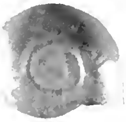
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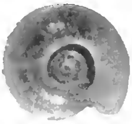
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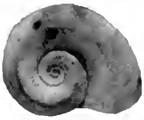
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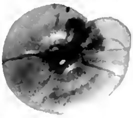
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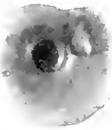
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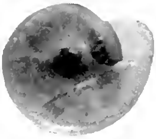
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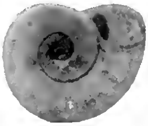
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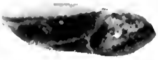
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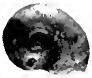
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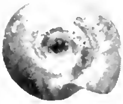
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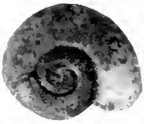
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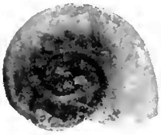
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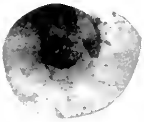
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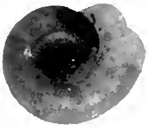
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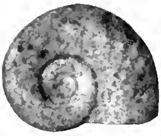
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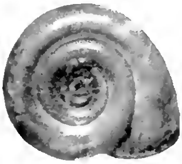
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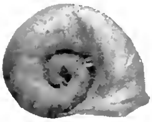
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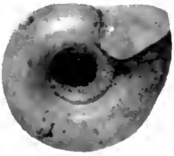
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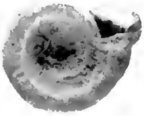
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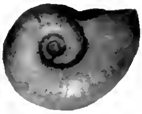
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PLATE 79

PLATE 80

Shells of Planorbidae

1–3. *Helisoma anceps* (Menke) = *Planorbis bicarinatus* Sowb. and *P. bicarinatus* Say. From Delaware River 1½ miles above Plum Point, New Jersey. Like Say's figures. U.I., Z25738. ×2.

4–6. *Helisoma anceps* (Menke). South Street Brook, Auburn, New York. Strongly carinated form. U.I., Z25934. ×2.

7–8. *Helisoma scalare* (Jay). Everglades, head of Miami River, Dade Co., Florida. Baker coll., 2371. ×2.

9. *Helisoma duryi seminole* Pilsbry. Lake Eustis, Florida. Physoid shell. Baker coll., 3977. ×2.

11–12. *Helisoma duryi normale* Pilsbry. Lake Pinsett, Florida. Typically planorboid shell. U.I., 41489. ×1½.

13–15. *Helisoma trivolvis* (Say). Braddocks Bay, near Rochester, New York. Lake Ontario. U.I., 29789. ×1½.

16–18. *Helisoma campanulatum* (Say). Thousand Island Park, St. Lawrence River, New York. U.I., 27112. ×1½.

19–21. *Helisoma multivolvis* (Case). Howe Lake, Marquette Co., Michigan. Baker coll., 1962. ×2.

22–24. *Planorbarius corneus* (Linn.). Rhone River, France. U.I., 25740. ×1½.

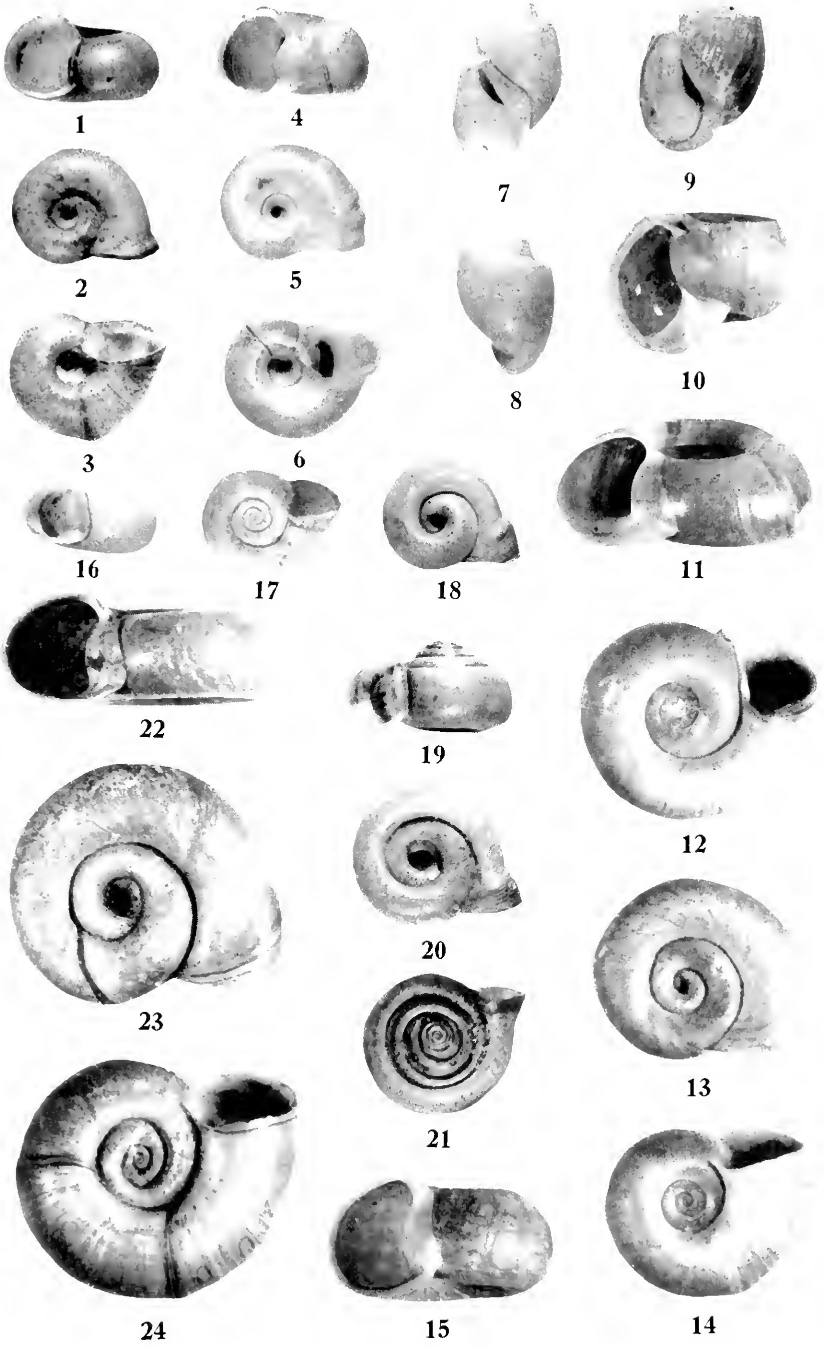

PLATE 80

PLATE 81

Shells of Planorbidae

1. *Poecilospira trochiformis* (Stahl). Steinheim, Germany. Showing extreme range of variation from short, flattened spire to long, conical spire. M.C.Z. ×2.
2. *Afroplanorbis adowensis* (Bourg.). Belgian Congo, Africa. Pilsbry and Bequaert, Bull. Amer. Mus. N.H., LIII, fig. 4, p. 118. ×1½.
3. *Afroplanorbis sudanicus* (Martens). Bahr-el-Ghazal, Africa. U.S.N.M., 215381. Pilsbry and Bequaert, op. cit., fig. 7, p. 122. ×1½.
4. *Biomphalaria smithi* Preston. Upper figures, specimen from Kabare, Lake Edward, Africa; lower figures, paratypes from Lake Edward. Pilsbry and Bequaert, op. cit., fig. 6, p. 121. ×1½.
5. *Paraplanorbis condoni* (Hanna). Vicinity of Warner Lake, eastern Oregon. Pliocene period. Hanna, Univ. Oregon Pub., I, No. 12, plate 1, figs. 1-3. About ×7.
6. *Planorbifex vanvlecki* (Arnold). North dome Kettleman Hills, King Co., California. Pliocene. Pilsbry, Proc. Acad. Nat. Sci. Phil., 86, plate 21, fig. 9, a, b, c. Reduced one-half from Pilsbry's figure. Line indicates 1 mm.
7. *Choanomphalus maacki* Gerstfeldt. Crosse and Fischer, Jour. de Conch., XXVII, plate 4, fig. 9.
8. *Choanomphalus valvatoides* Dybowski. Op. cit., plate 4, fig. 8.
9. *Choanomphalus schrenckii* Dybowski. Op. cit., plate 4, fig. 10. Line near figures 8-10 indicates natural size.
10. *Anisopsis calculus* (Sandberger). Land und Süss.-Conch. Vorwelt, taf. 1, figs. 7, 7a. (stark vergrössert).
11. *Anisopsis loryi* (Coquand). Op. cit., taf. 1, figs. 28, 28a, 28b.

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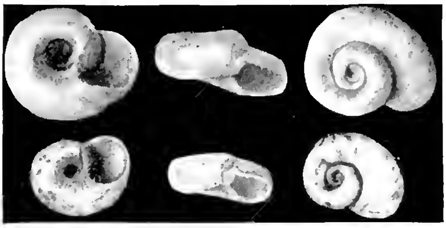

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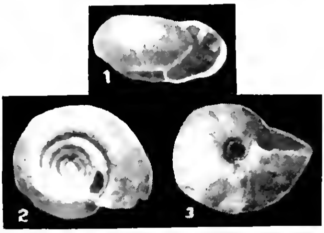

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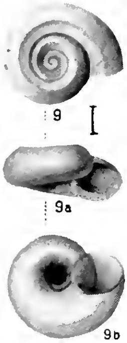

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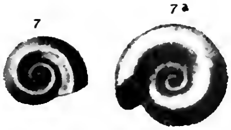

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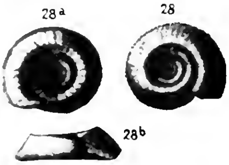

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PLATE 81

PLATE 82

Shells of Planorbidae

1, 2. *Helisoma anceps* (Menke). Ashland, Virginia. Resembling Menke's figure. B999.

3–5. *Helisoma anceps* (Menke). Below dam at Lake Junalaska, North Carolina. B1819.

6–8. *Helisoma anceps* (Menke). Long Lake, Alpena, Michigan. Resembling Rackett's figure of *Helix angulata*. B1001.

9–11. *Helisoma anceps* (Menke). Spring Grove, Dove Co., Alabama. Walker coll. Resembling Conrad's *Planorbis antrosa*. U.M., 67401.

12–15. *Helisoma anceps* (Menke). Potomac River, Fort Washington, Maryland. 14, resembling *unicarinatum*; 15, resembling *sayi*. U.S.N.M., 364718.

16, 17. *Helisoma anceps* (Menke). Blue Creek, Coeur d'Alene Mts., Idaho. U.M., 81780.

18, 19. *Helisoma anceps* (Menke). Portland, Oregon. Hemphill coll. C.A.S., 6875.

20–22. *Helisoma anceps striatum* (F. C. Baker). Bay View, Milwaukee, Wisconsin. From marl bed. B2851.

23–25. *Helisoma anceps shellense* F. C. Baker. Shell Lake, Washburn Co., Wisconsin. 23, paratype, U.I., Z19354; 24-25, type locality, U.I., Z13474.

26. *Helisoma anceps* (Menke). Portland, Oregon. U.C.M., 23143.

27–29. *Helisoma anceps minnesotense* (F. C. Baker). Frontenac, Minnesota. Types. B1002.

30. *Helisoma anceps* (Menke). Priests Lake, Bonnar Co., Idaho. U.M., 81798.

31. *Helisoma anceps corrugatum* (Currier). Northern part of Minnesota. B985.

32–34. *Helisoma anceps sayi* F. C. Baker. East Lake Okoboji, Iowa. Shimek coll., U.S.N.M., 476580.

Figures are enlarged approximately two diameters


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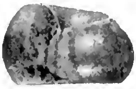
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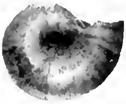
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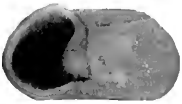
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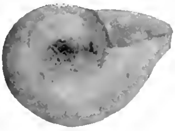
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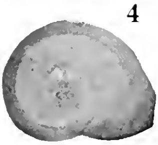
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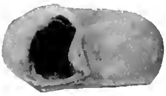
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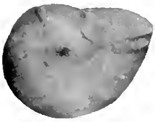
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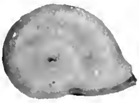
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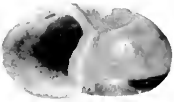
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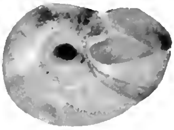
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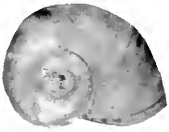
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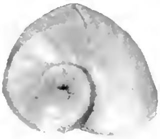
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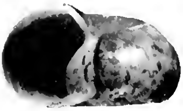
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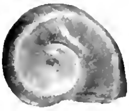
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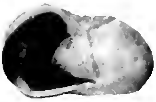
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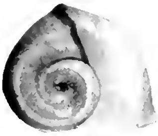
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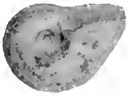
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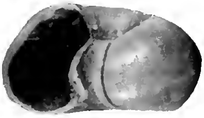
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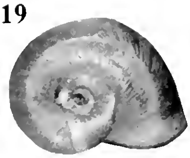
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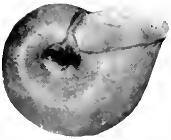
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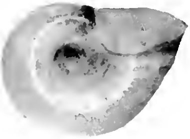
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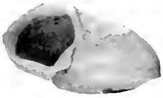
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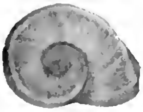
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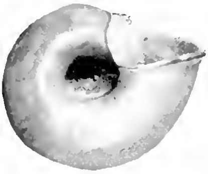
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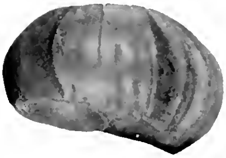
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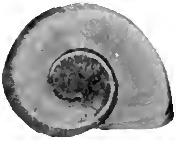
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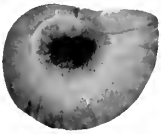
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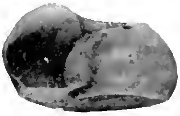
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PLATE 82

PLATE 83

Shells of Planorbidae

1–3. *Helisoma anceps sayi* F. C. Baker. Tomahawk Lake, Oneida Co., Wisconsin. Type locality. U.I., Z25736.

4–6. *Helisoma anceps sayi* F. C. Baker. West Lake Okoboji, Iowa. Shimek coll. Varying toward *anceps*. U.S.N.M., 475945.

7–9. *Helisoma anceps unicarinatum* (Haldeman). Plum Point, Delaware River, above Riverton, New Jersey. U.I., Z25938.

10–12. *Helisoma anceps unicarinatum* (Hald.). Cherokee River, Little River Station, Alabama. U.I., Z41055.

13–15. *Helisoma anceps unicarinatum* (Hald.). Blackstone River, above Courtland, West Virginia. Figure 13 resembles Haldeman's *angistomum*. U.S.N.M., 109888.

16–18. *Helisoma anceps politum* F. C. Baker. Honeywell Creek, Carleton Co., Ontario, Canada. F. R. Latchford coll. Holotype, fig. 16; paratypes, figs. 17, 18. U.S.N.M., 367426.

19-22. *Helisoma anceps bartschi* F. C. Baker. Brook at Great Falls, Virginia. Holotype, fig. 19; paratypes, figs. 20-22. U.S.N.M., 227858.

23–25. *Helisoma anceps* (Menke). Variety? Mouth of Yaqui River, Northwest Mexico. U.S.N.M., 53677.

26. *Helisoma anceps* (Menke). Variety? Potomac River. U.S.N.M., 364718.

27–29. *Helisoma anceps aroostookense* (Pilsbry). Woodland, Aroostook Co., Maine. Type locality. U.I., Z21015.

Figures are enlarged approximately two diameters

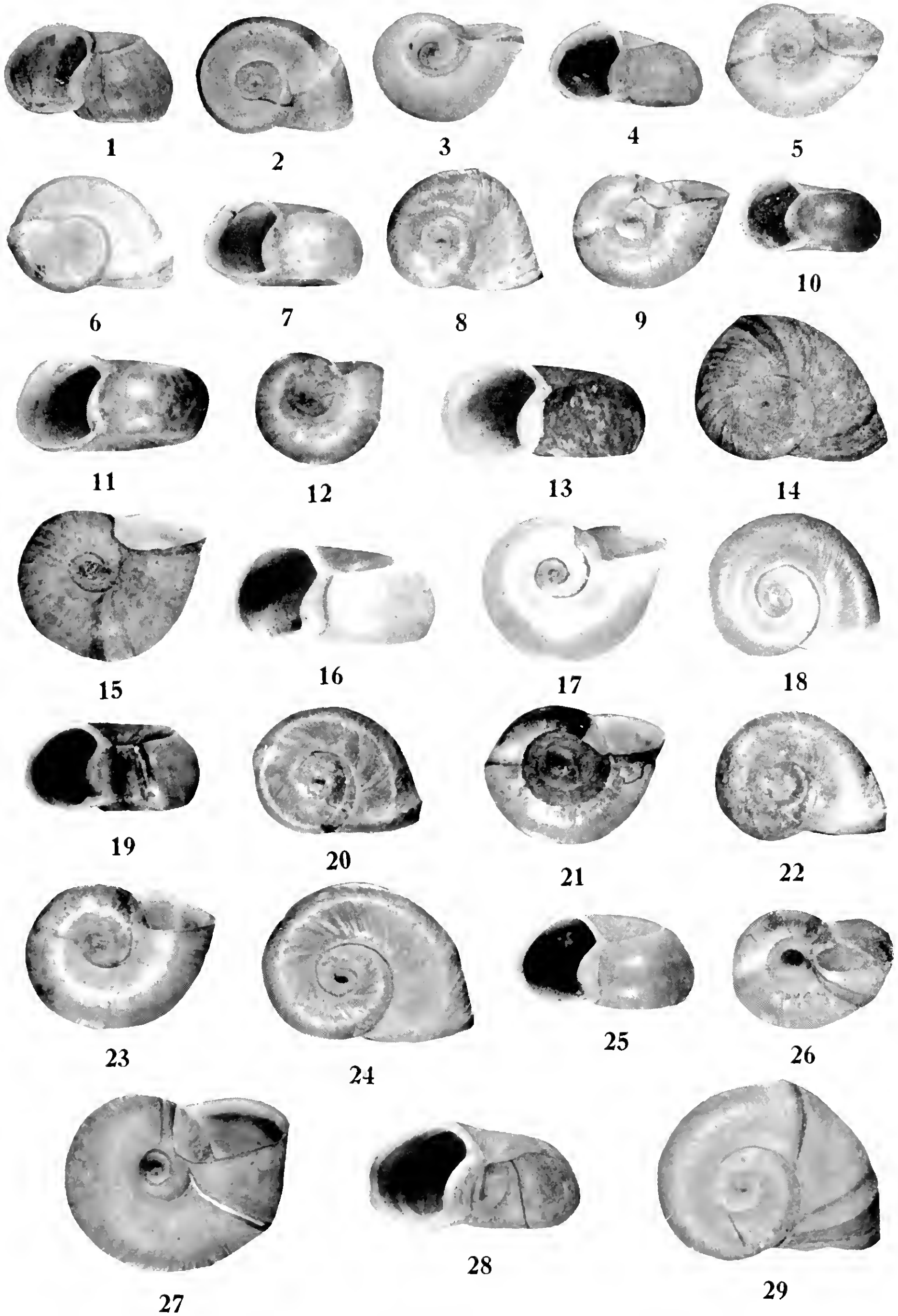


PLATE 83

PLATE 84

Shells of Planorbidae

1. *Helisoma anceps* (Menke). Immature shell. ×3½.
2. *Helisoma anceps percarinatum* (Walker). Immature shell. ×3½.
3. *Helisoma anceps portagense* (F. C. Baker). Immature shell. ×3½.
4. *Helisoma anceps royalense* (Walker). Immature shell. ×3½.
5. *Helisoma anceps sayi* F. C. Baker. Immature shell. ×3½.

6–8. *Helisoma anceps jordanense* (Winslow). Lake Charlevoix, NE of Jordan, Charlevoix Co., Michigan. Topotypes. U.M., 61589

9. *Helisoma anceps royalense* (Walker). Isle Royale, Michigan. Cotype. B. Walker. B995.

10–12. *Helisoma anceps rushi* F. C. Baker. Toad Island, Georgian Bay, Ontario. 10 holotype; 11-12 paratypes. U.I., Z25239.

13, 14. *Helisoma anceps royalense* (Walker). St. Joseph Lake, Ontario. U.I., Z30853.

15–17. *Helisoma anceps royalense* (Walker). Bamiji Lake, Ontario. U.I., Z30844.

18–20. *Helisoma eucosmius* (Bartsch). Types. Bull. U.S.N.M., 33, plate 57, figs. 1-3. ×4.

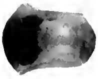
21. *Helisoma eucosmius* (Bartsch). Greenfield Pond, North Carolina. Paratype. U.S.N.M., 193890. ×3½.

22–24. *Helisoma eucosmius vaughani* (Bartsch). Types. Bull. U.S.N.M., 33, plate 57, figs. 4-6. ×4.

25. *Helisoma eucosmius vaughani* (Bartsch). Burke's Place, Louisiana. Paratype. U.S.N.M., 125719. ×3½.

26–28. *Helisoma anceps idahoense* F. C. Baker. Pend Oreille River, Sand Point, Idaho. Holotype. B1863.

All figures are enlarged about twice excepting those otherwise listed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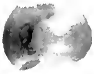
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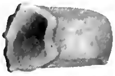
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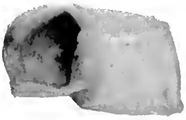
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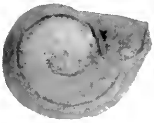
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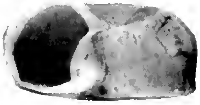
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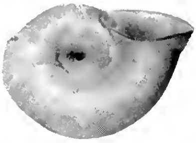
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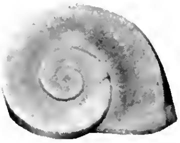
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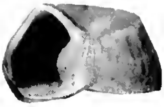
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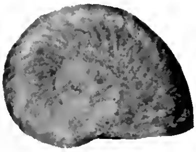
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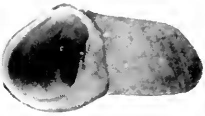
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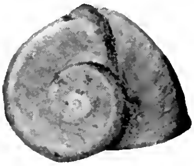
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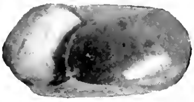
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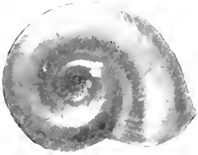
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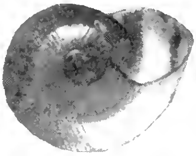
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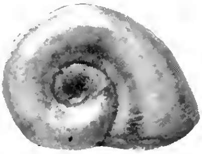
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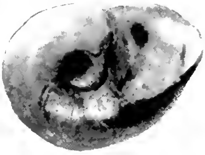
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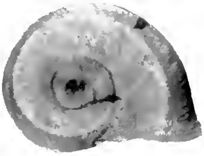
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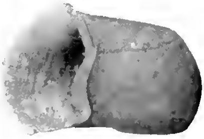
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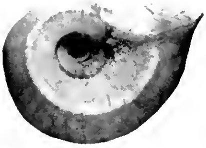
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PLATE 84

PLATE 85

Shells of Planorbidae

1–3. *Helisoma anceps portagense* (F. C. Baker). Portage Lake, Aroostook Co., Maine. Type locality. B988.

4. *Helisoma anceps portagense* (F. C. Baker). Meach Lake, Quebec, Canada. B3686.

5–7. *Helisoma anceps latchfordi* (Pilsbry). Meach Lake, Quebec, Canada. Type locality. Collected by Latchford. U.I., Z37203.

8–10. *Helisoma anceps percarinatum* (Walker). Crystal Lake, Benzie Co., Michigan. Type locality. B986.

11–13. *Helisoma anceps percarinatum* (Walker). Douglas Lake, Michigan. 12 ridged shell. U.I., Z26276.

14–16. *Helisoma anceps cahni* F. C. Baker. Big Muskallonge Lake, Vilas Co., Wisconsin. Types. U.I., Z21124.

17–19. *Helisoma trivolvis* (Say). Immature shells. ×3.

20–24. *Helisoma trivolvis* (Say). Showing regular increase in growth of shell. U.I., Z29134.

25–29. *Helisoma trivolvis* (Say). Braddock's Bay, near Rochester, New York. U.I., Z29789.

30. *Helisoma trivolvis* (Say). Elmira, Chemung Co., New York. U.I., Z34976.

All figures excepting 17-19 are enlarged about 1⅔ diameters

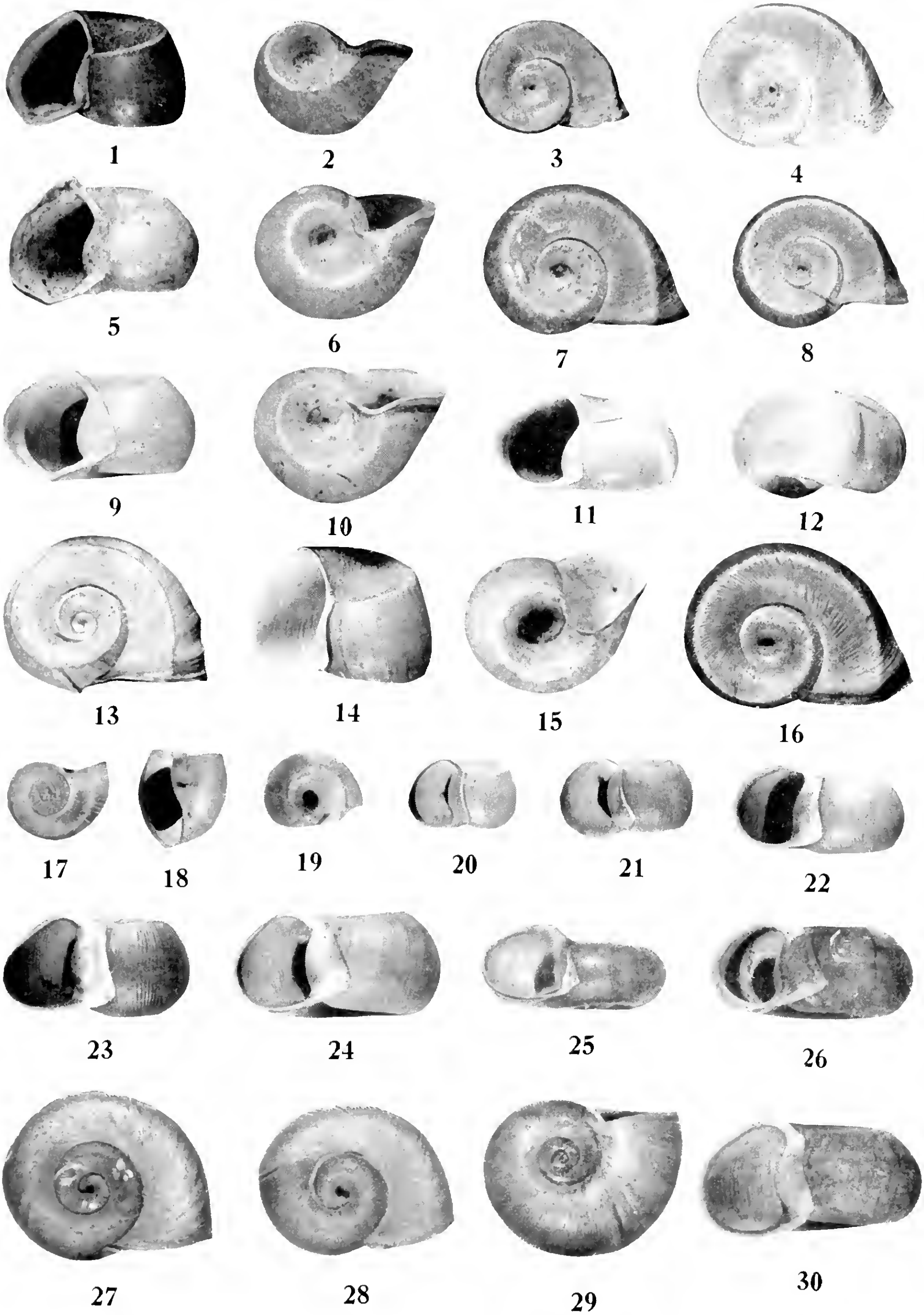
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PLATE 85

PLATE 86

Shells of Planorbidae

1. *Helisoma trivolvis* (Say). Indian River, Cheboygan Co., Michigan. (=*Planorbis. megastoma* DeKay.) U.I., Z32472.

2, 4. *Helisoma trivolvis* (Say). Salt Fork, near Urbana, Champaign Co., Illinois. (=*Planorbis pseudotrivolvis* F. C. Baker. 2, paratype; 4, holotype). U.I., Z11292.

3. *Helisoma trivolvis* (Say). Salt Fork, near Urbana, Illinois. (=*Planorbis pseudotrivolvis* F. C. Baker. Type locality.) B930.

5–8. *Helisoma trivolvis lentum* (Say). New Orleans, Louisiana. Type locality. U.I., Z30538.

9, 10, 13. *Helisoma trivolvis intertextum* (Sowerby). Manatee River, Florida. U.I., Z32367.

11, 12, 15. *Helisoma trivolvis intertextum* (Sowb.). Shoal Creek, Alabama. U.I., Z32365.

14. *Helisoma trivolvis intertextum* (Sowb.). Manatee River, Florida. B1085.

16. *Helisoma trivolvis chautauquense* F. C. Baker. Chautauqua Assembly, Chautauqua Lake, New York. Type locality. U.I., Z27842.

17. *Helisoma trivolvis chautauquense* F. C. Baker. Chautauqua Lake, New York. Holotype. U.I., Z23780.

18, 19. *Helisoma trivolvis chautauquense* F. C. Baker. Chautauqua Lake, New York. Paratypes. U.I., Z23780.

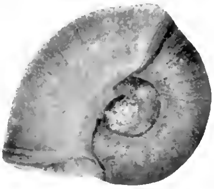
20. *Helisoma trivolvis* (Say). Enlargement of whorls on base. B3914. ×7.

21. *Helisoma trivolvis* (Say). (=*Planorbis pseudotrivolvis* F. C. Baker). Enlargement of whorls on base. B3915. ×7.

22. *Helisoma trivolvis lentum* (Say). Enlargement of whorls on base. B3916. ×7.

23. *Helisoma trivolvis intertextum* (Sowb.). Enlargement of whorls on base. B3917. ×7.

All figures, excepting those indicated otherwise, are
enlarged about 1⅔ diameters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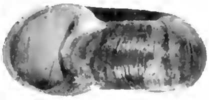
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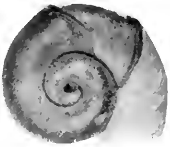
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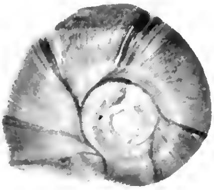
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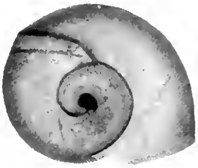
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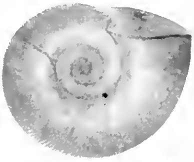
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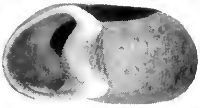
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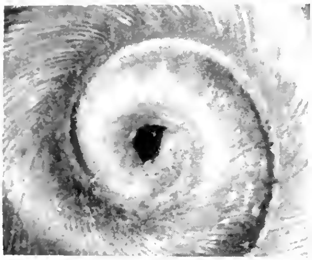
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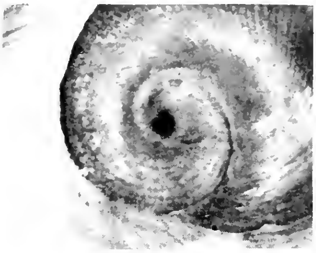
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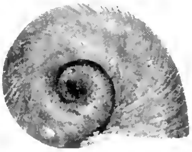
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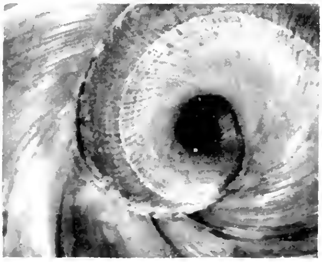
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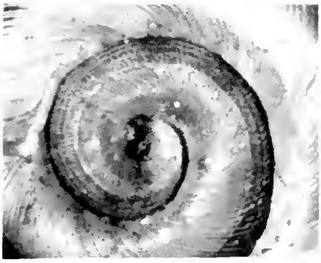
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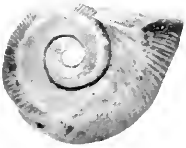
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PLATE 86

PLATE 87

Shells of Planorbidae

1–4. *Helisoma trivolvis fallax* (Haldeman). Milton Mills, Milton, Massachusetts. U.I., Z41108.

5–7. *Helisoma trivolvis fallax* (Haldeman). Green Lodge, Neponset, Massachusetts. B904.

8, 9. *Helisoma trivolvis fallax* (Haldeman). Fresh Pond, Cambridge, Massachusetts. U.S.N.M., 336571.

10. *Helisoma trivolvis fallax* (Haldeman). Port Elizabeth, Maine. U.S.N.M., 26449.

11–15. *Helisoma trivolvis marshalli* F. C. Baker. Washington, D.C. 13, holotype; 11-12, paratypes; 14-15, immature. U.S.N.M., 124989.

16. *Helisoma trivolvis marshalli* F. C. Baker. New Jersey. U.S.N.M., 504153.

17-20. *Helisoma trivolvis holstonense* F. C. Baker. Holston River, Smith Co., Virginia. 17, holotype; 18-20, paratypes. U.I., Z41443.

21. *Helisoma trivolvis lentum* (Say). New Orleans, Louisiana. Immature. Aquarium specimen. B3918.

22. *Helisoma trivolvis holstonense* F. C. Baker. Holston River, Virginia. Immature. U.I., Z41444.

23, 24. *Helisoma trivolvis holstonense* F. C. Baker. Holston River, Virginia. Variation in color. U.I., Z41444.

All figures are enlarged about two diameters

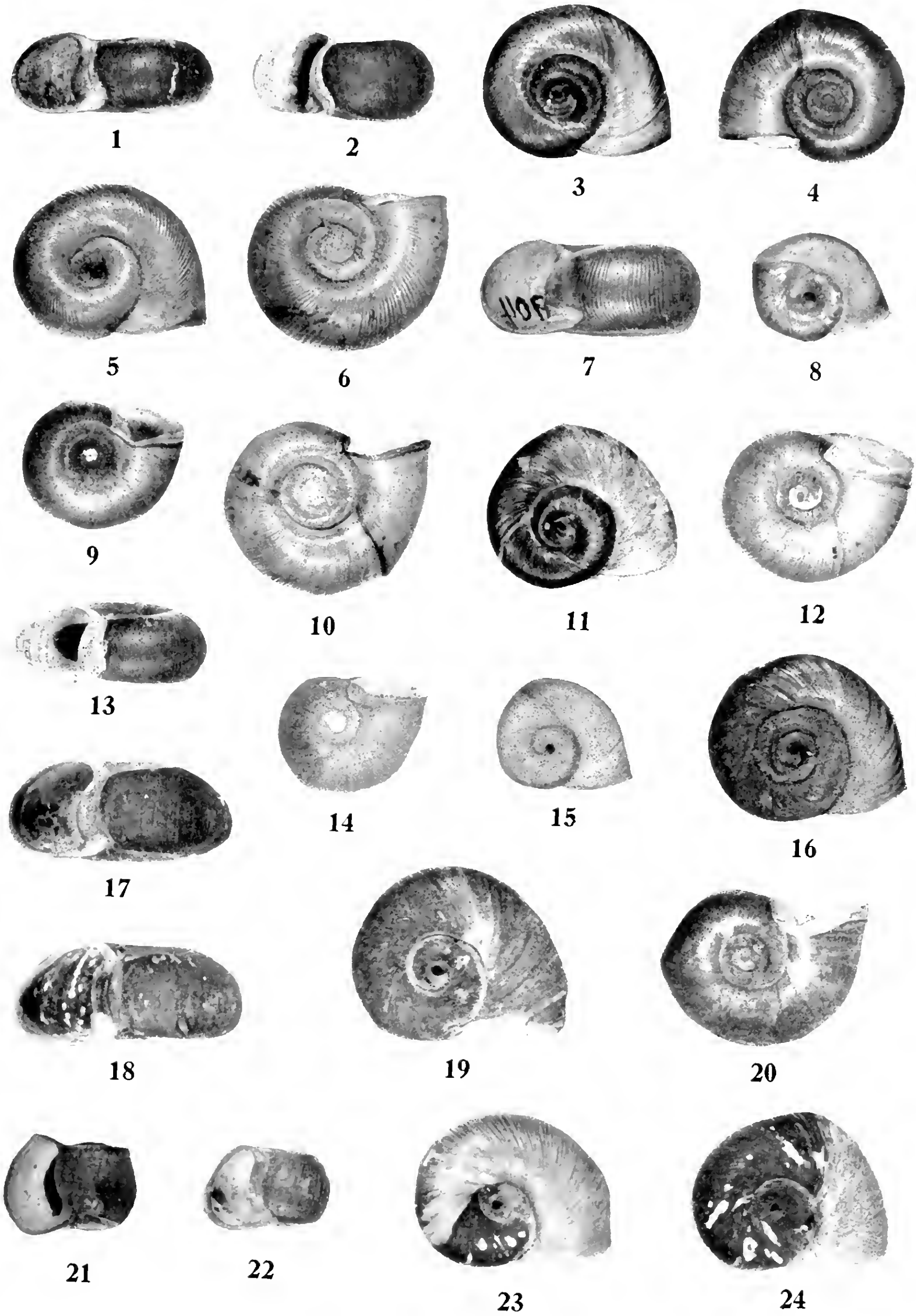

PLATE 87

PLATE 88

Shells of Planorbidae

1, 2. *Helisoma trivolvis trivolvis* (Say). Presque Isle, Michigan. Transition form toward *macrostomum*. U.I., Z26268.

3. *Helisoma trivolvis trivolvis* (Say). Winnebago Lake, near Oshkosh, Wisconsin. Large form, but typical. U.I., Z12791.

4–6. *Helisoma trivolvis macrostomum* (Whiteaves). Mile End Gate, near Montreal, Canada. National Museum of Canada. 4, lectotype, 3869; 5-6, paratypes, B3870.

7. *Helisoma trivolvis macrostomum* (Whiteaves). Bayfield, Wisconsin. In beach pool. U.I., Z13677a.

8–10. *Helisoma pilsbryi* (F. C. Baker). Tomahawk Lake, Oneida County, Wisconsin. Type locality. B843.

11–13. *Helisoma pilsbryi infracarinatum* F. C. Baker. Rideau River, near Ottawa, Canada. B3715.

14, 15. *Helisoma pilsbryi infracarinatum* F. C. Baker. Basswood River Rapids, Rainy River District, Ontario. 14, holotype, U.I., Z32361; 15, paratype, B2986.

16. *Helisoma pilsbryi infracarinatum* F. C. Baker. Basswood Lake, Ontario, Canada. U.I., Z41268.

All figures enlarged about 1½ diameters


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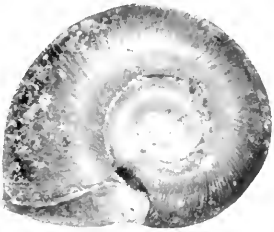
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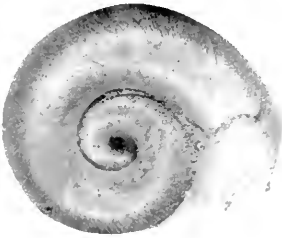
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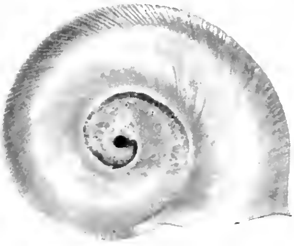
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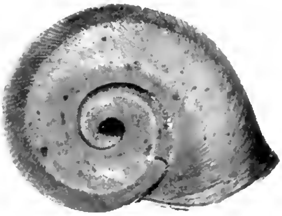
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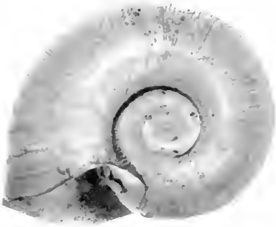
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PLATE 88

PLATE 89

Shells of Planorbidae

1–4. *Helisoma trivolvis lentum* (Say). Austin, Texas. Figure 3 varies toward *intertextum*. U.S.N.M., 252256.

5, 6. *Helisoma trivolvis intertextum* (Sowb.). Fort Smith, Arkansas. Variation toward *lentum* (fig. 6). U.S.N.M., 120965.

7. *Helisoma trivolvis intertextum* (Sowb.). South Carolina? Binney's fig. 179 of *Planorbis glabratus* (not of Say). U.S.N.M., 29219.

8. *Helisoma trivolvis intertextum* (Sowb.). Leon, Texas. U.S.N.M., 28210.

9, 10. *Helisoma trivolvis reticulatum* (Dall) (= *intertextum* Say). Salt Lake, Hilsborough Co., Florida. Types. U.S.N.M., 75421.

11. *Helisoma truncatum* (Miles). Saginaw Bay, Michigan. Type. Binney's fig. 202. U.S.N.M., 9010.

12. *Planorbis bellus* Lea (= *Helisoma trivolvis lentum* (Say)). Type. Tennessee. Lea Coll., U.S.N.M., 121178.

13–17. *Helisoma kennicotti* F. C. Baker. Lake Isle la Crosse, English River, Canada. 15, holotype; 16, 17, paratypes; 13, 14, immature. U.S.N.M., 29231 (old 9272).

18. *Helisoma subcrenatum* (Cpr.). Reservoir near Floweree, Montana. B3792.

19. *Helisoma subcrenatum* (Cpr.). Wainwright Park, Alberta. U.I., Z34689.

20. *Helisoma subcrenatum* (Cpr.). Fort Yukon, Alaska. U.S.N.M., 218908.

21. *Helisoma subcrenatum disjectum* (Cooper). Boise, Idaho. U.I., Z36335.

22. *Helisoma subcrenatum plexatum* (Ing.). Sagnache, Colorado. U.S.N.M., 535328.

23. *Helisoma occidentale* (Cooper). Klamath Falls, Oregon. U.S.N.M., 219750.

24. *Helisoma occidentale* (Cooper). Tule Lake, California. U.S.N.M., 160839a.

25. *Helisoma ammon* (Gould). Daggett, California. U.S.N.M., 349083.

26. *Helisoma ammon* (Gould). Spring Valley, San Mateo Co., California. U.M., 84105.

27. *Helisoma ammon* (Gould). Clear Lake, California. U.M., 81743.

28, 29. *Helisoma trivolvis* (Say). Aquarium specimens raised by Dr. E. G. Berry. Note resemblance to *Helisoma duryi seminole*. B3796.

Figures 18–29, immature.

All figures are enlarged a trifle less than two diameters

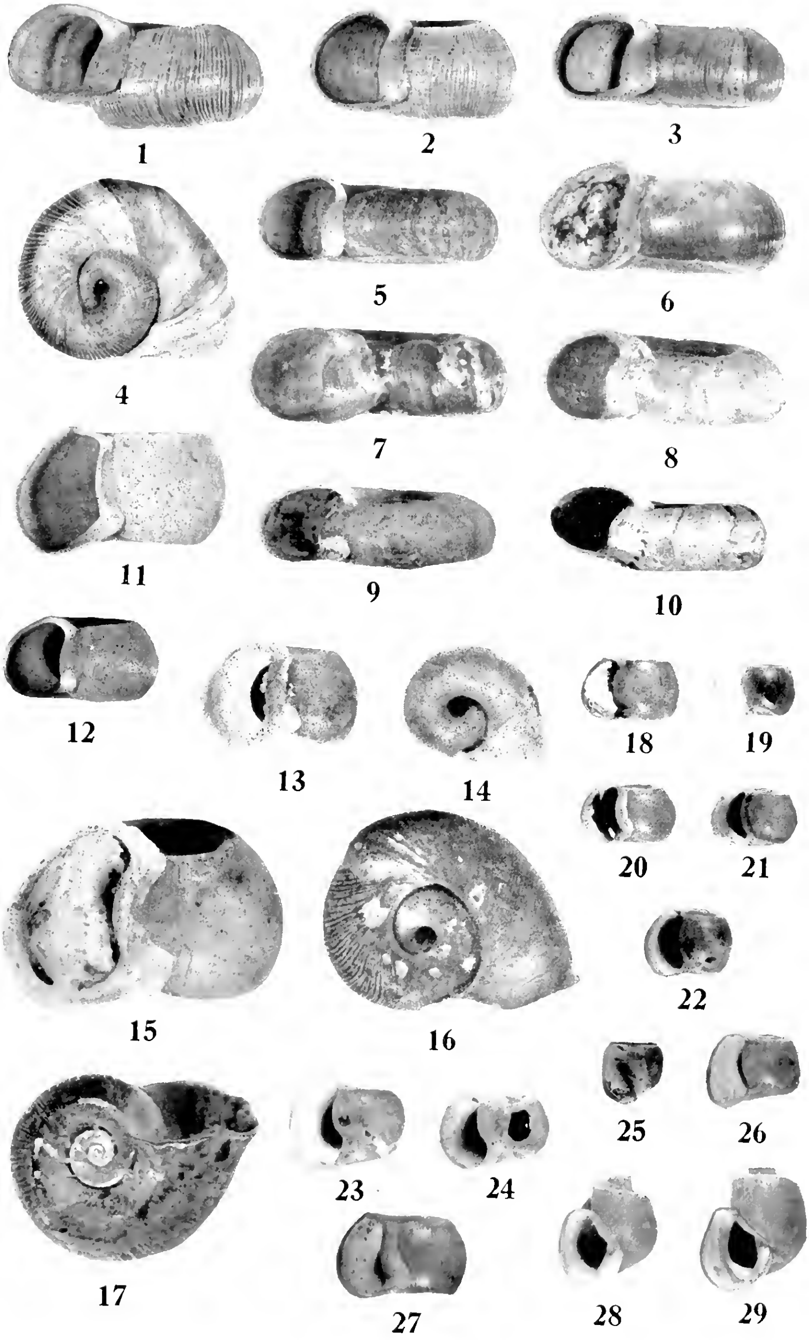


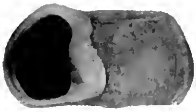
PLATE 89

PLATE 90

Shells of Planorbidae

1–4. *Helisoma truncatum* (Miles). Saginaw Bay, Michigan. Type locality. U.I., Z32515.
5–8. *Helisoma truncatum* (Miles). Spirit Lake, Iowa. U.S.N.M., 476566.
9. *Helisoma truncatum* (Miles). Spirit Lake, Iowa. U.S.N.M., 505847.
10. *Helisoma truncatum* (Miles). Sturgeon Bay, Door Co., Wisconsin. U.I., Z18455.
11, 12. *Helisoma truncatum* (Miles). Winnebago Lake, Wisconsin. U.I., Z12805.
13–15. *Helisoma subcrenatum disjectum* (Cooper). Tuolumne, California. B1090.
16–18. *Helisoma subcrenatum disjectum* (Cooper). Boise, Idaho. U.I., Z36335.
19–21. *Helisoma subcrenatum horni* (Tryon). Paul Lake, British Columbia. B3148.
22–24. *Helisoma subcrenatum* variety? Quamichan Lake, British Columbia. B1973.

All figures are enlarged a little less than two diameters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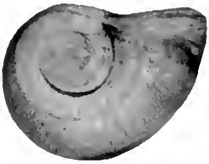
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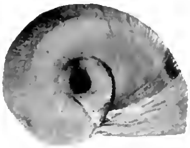
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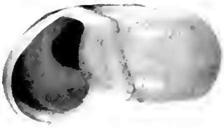
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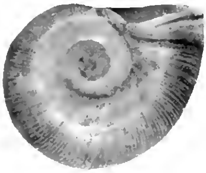
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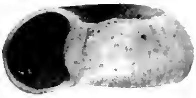
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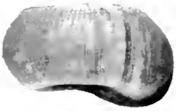
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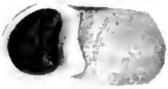
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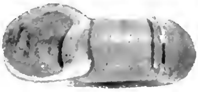
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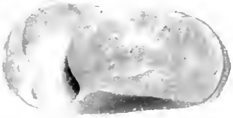
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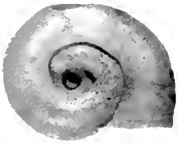
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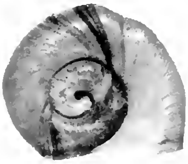
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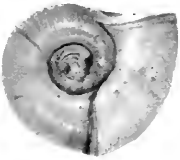
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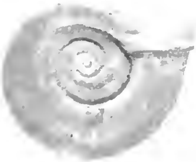
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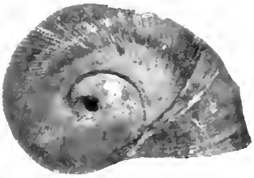
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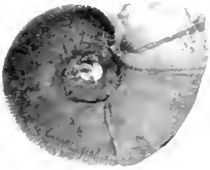
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PLATE 90

PLATE 91

Shells of Planorbidae

1–4. *Helisoma winslowi* (F. C. Baker). Little Arbor Vitae Lake, Vilas Co., Wisconsin. Paratypes. Figure 4, immature. × 3½. U.I., Z18637, Z19398.

5. *Helisoma pilsbryi* (F. C. Baker). Chetek Lake, Barron Co., Wisconsin. B.

6–8. *Helisoma pilsbryi preblei* F. C. Baker. Knee Lake, Manitoba. Figure 6, holotype; 7-8, paratypes. U.S.N.M., 180279.

9–12. *Helisoma subcrenatum* (Carpenter). Idaho. Shimek Coll., U.S.N.M., 504310.

13. *Helisoma subcrenatum* (Cpr.). Third Vermilion Lake, below warm sulphur cave, Alberta. Pathologic specimen. U.S.N.M., 272105.

14. *Helisoma subcrenatum* (Cpr.). Lake La Hoche, British Columbia. U.S.N.M., 43346.

15. *Helisoma subcrenatum* (Cpr.). Locomotive Springs, Kelton, Utah. U.S.N.M., 308926.

16, 18, 19. *Helisoma subcrenatum* variety? Utah Lake, 2 miles south of Lehi, Utah. B1894.

17. *Helisoma subcrenatum* variety? Same locality as above. Variation toward *subcrenatum*. B1894.

All figures, excepting 4, are enlarged about 1½ diameters


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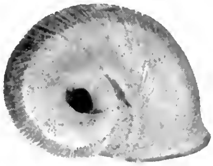
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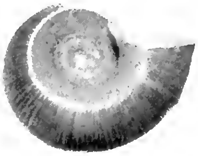
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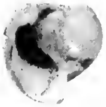
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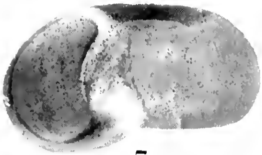
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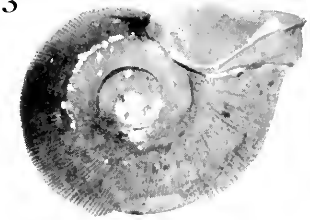
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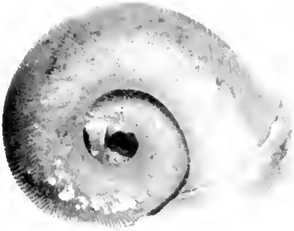
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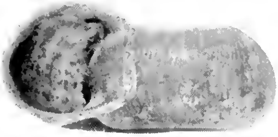
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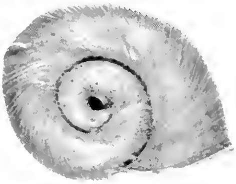
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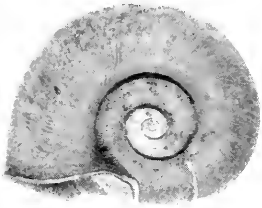
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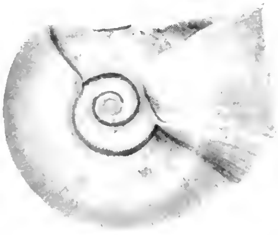
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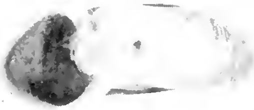
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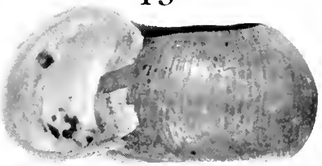
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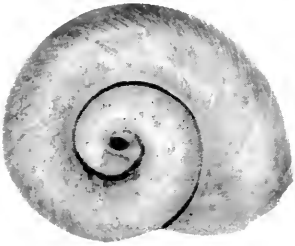
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PLATE 91

PLATE 92

Shells of Planorbidae

1, 2. *Helisoma subcrenatum* (Cpr.). Newton, Utah. B3046.

3 *Helisoma subcrenatum* (Cpr.). Stewart River, Yukon Dist., Alaska. U.S.N.M., 180281.

4. *Helisoma subcrenatum* (Cpr.). Cleary, Alaska. Fossil pits. U.S.N.M., 381941.

5. *Helisoma subcrenatum* (Cpr.). Great Slave Lake. Kennicott Coll., U.S.N.M., 9275.

6, 7. *Helisoma subcrenatum* (Cpr.). Wainwright Park, Alberta. B3919.

8–10. *Helisoma subcrenatum* (Cpr.). Fort Simpson, Mackenzie District, Canada. Kennicott Coll., U.S.N.M., 28378.

11, 12. *Helisoma subcrenatum* (Cpr.). Creek one mile west of Devon, Montana. Immature. B3793.

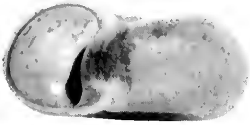
13–15. *Helisoma subcrenatum horni* (Tryon). Fort Yukon, Alaska. U.S.N.M., 218908.

16. *Helisoma subcrenatum horni* (Tryon). Dall River, Alaska. Varying toward *subcrenatum*. U.S.N.M., 180280.

17–22. *Helisoma subcrenatum plexatum* (Ingersoll). St. Mary Lake, Mineral Co., Colorado. Figure 17, lectotype, U.S.N.M., 420210; figs. 18-22, paratypes. U.S.N.M., 125130.

23. *Helisoma subcrenatum plexatum* (Ing.). Sagnache, Colorado. Immature. U.S.N.M., 535328

All figures are enlarged about 1½ diameters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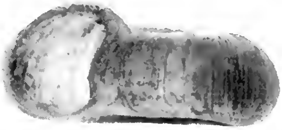
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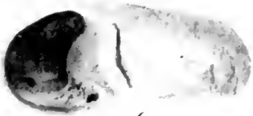
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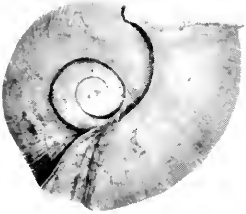
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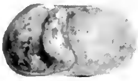
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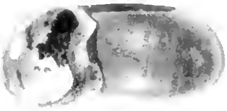
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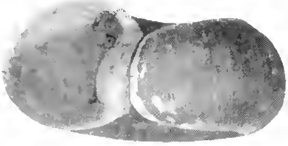
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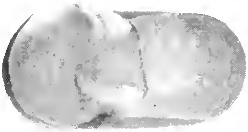
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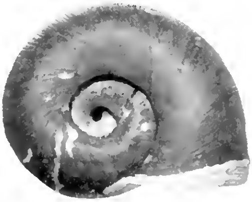
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PLATE 92

PLATE 93

Shells of Planorbidae

1–3. *Helisoma subcrenatum plexatum* (Ing.). Great Falls, Montana. U.S.N.M., 183037.

4. *Helisoma occidentale* (Cooper). Tule Lake, California. U.S.N.M., 160839a.

5. *Helisoma occidentale* (Cooper). 'Washington Territory.' Binney's fig. 193. U.S.N.M., 9120.

6. *Helisoma occidentale* (Cooper). Klamath Falls, Oregon. U.S.N.M., 219750.

7, 8. *Helisoma occidentale* (Cooper). Upper Klamath Lake, south boundary of reservation, Oregon. U.M., 62741.

9, 10. *Helisoma occidentale* (Cooper). Lower end Upper Klamath Lake, Oregon. B3246.

11, 12. *Helisoma occidentale* (Cooper). Slough at Wacos Bay, Klamath Lake, Oregon. B3069.

13, 14. *Helisoma occidentale* (Cooper). Upper Klamath Lake, Oregon. B3011.

15. *Helisoma occidentale* (Cooper). Upper Klamath Lake, south boundary of reservation. U.M., 62741.

16. *Helisoma occidentale depressum* F. C. Baker. Lower Klamath Lake, Oregon. Holotype. B3239.

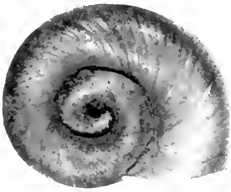
17, 18. *Helisoma occidentale depressum* F. C. Baker. Lower Klamath Lake, Oregon. Paratypes. B3240.

19, 20. *Helisoma binneyi* (Tryon). Portland, Oregon. Stanford Univ., B3220.

21, 22. *Helisoma binneyi* (Tryon). Lake Whatcom, Washington. B853.

23–26. *Helisoma binneyi* (Tryon). Holders Lake, Nanaimo, British Columbia. U.M., 81750.

All figures are enlarged about 1½ diameters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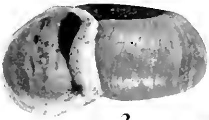
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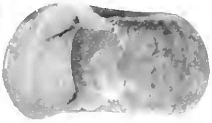
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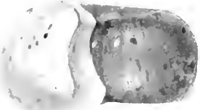
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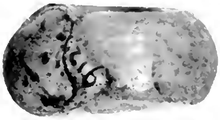
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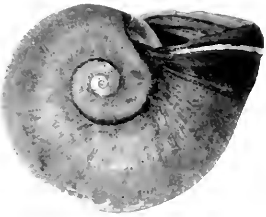
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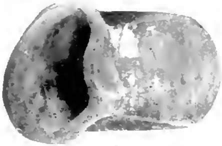
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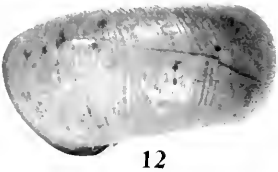
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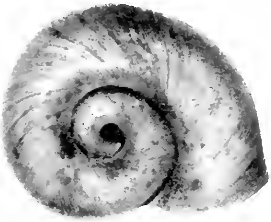
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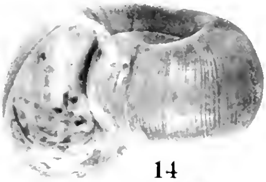
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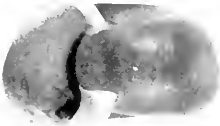
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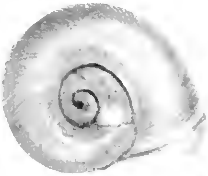
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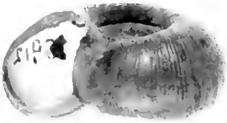
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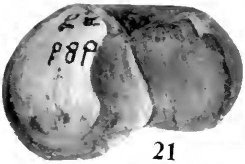
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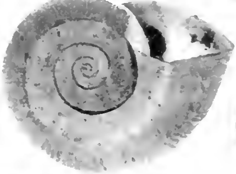
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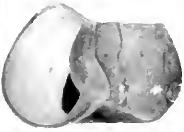
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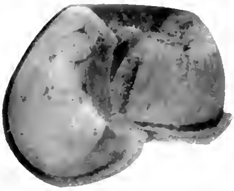
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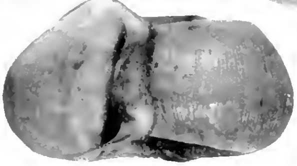
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PLATE 93

PLATE 94

Shells of Planorbidae

1–5. *Helisoma binneyi randolphi* F. C. Baker. Seattle, Washington. Figure 1, holotype; 2-4, paratypes; 5, immature. U.S.N.M., 504360.

6–8. *Helisoma binneyi randolphi* F. C. Baker. Green Lake, Seattle, Washington. About half grown. U.S.N.M., 474779.

9–11. *Helisoma binneyi* (Tryon). Astoria, Oregon. B1888.

12, 13. *Helisoma binneyi* (Tryon). Portland, Oregon. Immature. U.I., Z35295.

14. *Helisoma ammon* (Gould). Spring Valley, San Mateo Co., California. Immature. U.M., 84105.

15. *Helisoma ammon* (Gould). Near Cerritos, Los Angeles Co., California. Immature. U.S.N.M., 174051.

16. *Helisoma binneyi* (Tryon). Astoria, Oregon. Back view of shell. U.I., Z18459.

17. *Helisoma ammon* (Gould). Monterey, Monterey Co., California. Back view of shell. U.M., 81746.

18. *Helisoma binneyi* (Tryon). Oregon. Type. Gould's figure of *Planorbis corpulentum* Say, U.S. Ex. Exped., plate 8, fig. 130. U.S.N.M., 5530.

19. *Helisoma binneyi* (Tryon). Columbia River, Oregon. Binney's fig. 191 of *Planorbis corpulentum* Say. U.S.N.M., 8119.

20, 21. *Helisoma ammon* (Gould). Hollister, San Benito Co., California. U.M., 81748.

22–24. *Helisoma ammon* (Gould). Stockton, San Joachin Co., California. B3246.

25, 26. *Helisoma ammon* (Gould). San Joachin River, California. U.M., 81749.

27. *Helisoma ammon* (Gould). San Diego, California. U.M., 35676.

28. *Helisoma ammon* (Gould). Stockton, San Joachin Co., California. Immature. U.M., 81571.

All figures are enlarged about 1½ diameters

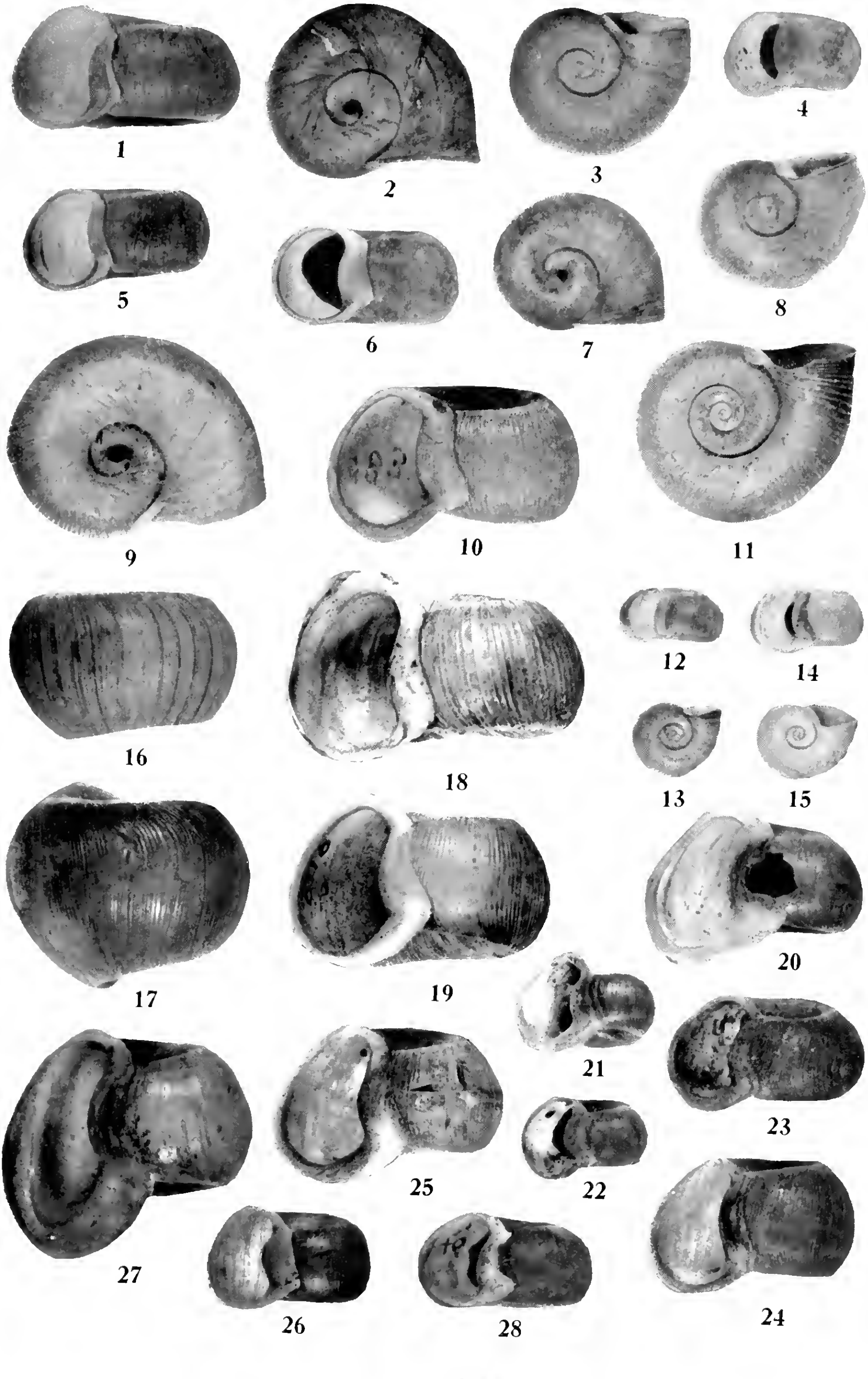

PLATE 94

PLATE 95

Shells of Planorbidae

1–5. *Helisoma ammon* (Gould). Mountain Lake near San Francisco, California. Immature form. B3288.

6–9. *Helisoma ammon* (Gould). Clear Lake, California. Stages of growth. U.M., 81743.

10, 11. *Helisoma ammon* (Gould). Clear Lake, California. U.M., 81752.

12–14. *Helisoma ammon* (Gould). Watsonville, Santa Cruz Co., California. U.M., 81747.

15. *Helisoma ammon* (Gould). Kern Lake, Tulare Co., California. Cooper Coll., B9124.

16. *Helisoma ammon* (Gould). Point Happy, Indio, California. U.I., Z35624.

17–19. *Helisoma traskii* (Lea). Bakersfield, Kern Co., California. Immature. U.M., 81754.

20, 21. *Helisoma traskii* (Lea). Kern Lake, Tulare Co., California. Type of Lea, figured by Binney, 188. Lea Coll., U.S.N.M., 121000.

22. *Helisoma traskii* (Lea). California? U.S.N.M., 47616.

23–25. *Helisoma traskii* (Lea). Buena Vista Canal, draining Buena Vista Lake, which drained Kern Lake, California. More depressed than Lea's type. B3066.

All figures are enlarged about 1½ diameters


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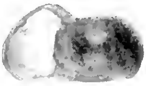
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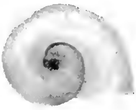
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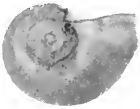
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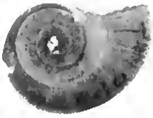
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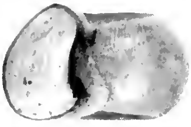
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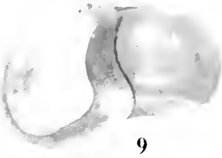
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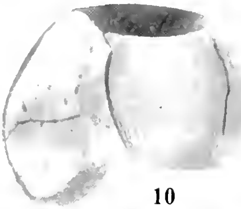
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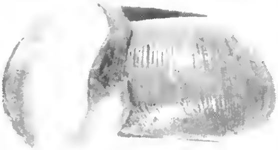
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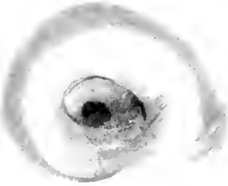
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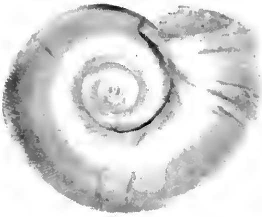
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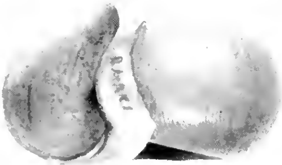
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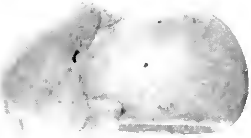
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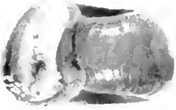
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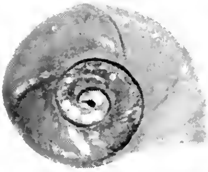
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PLATE 95

PLATE 96

Shells of Planorbidae

1–3. *Helisoma oregonense* (Tryon). Pueblo Valley on boundary of Oregon, sixty miles west of east boundary. Type locality. B1096.

4, 5. *Helisoma oregonense* (Tryon). Nevada. Stearns Coll. U.M., 35679.

6–8. *Helisoma oregonense* (Tryon). Sixteen miles northwest of Gerbach, Nevada. M.C.Z., 92410.

9–12. *Helisoma oregonense* (Tryon). Variation. Tooele Co., Utah, in salt spring. B3920.

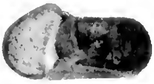
13–17. *Helisoma subcrenatum perdisjectum* F. C. Baker. Yellowstone Lake, Wyoming. Figure 13, holotype; 14-17, paratypes. U.S.N.M., 30207a.

18–22. *Helisoma anceps anticostianum* F. C. Baker. English Bay, Anticosti Island. Fig. 18, holotype; 19-22, paratypes. M.C.Z., 48285.

23–30. *Helisoma anceps* (Menke). Chevanus Pond, north of Knoxville, Tennessee. Figures 24, 25, 29, normal *anceps*; figs. 26, 27, 28, 30, the *angistomus* form of Haldeman; fig. 23, immature. M.C.Z., 46502.

31–34. *Helisoma magnificum* (Pilsbry). Greenfield Pond, near Wilmington, North Carolina. Type locality. Bartsch's figs. Proc. U. S. Nat. Mus., 33, plate 57, figs. 7-9. U.S.N.M., 193321.

Figures 1-30 are enlarged about two diameters;
figs. 31-34 are about natural size.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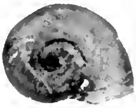
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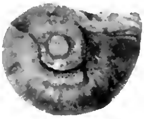
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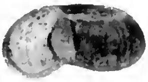
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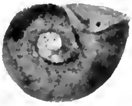
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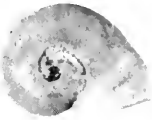
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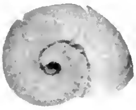
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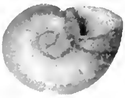
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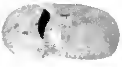
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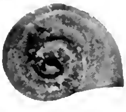
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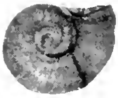
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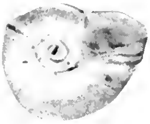
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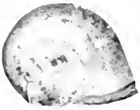
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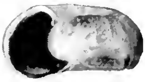
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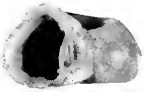
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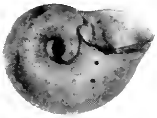
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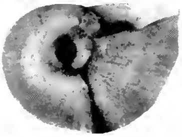
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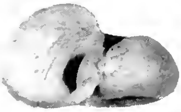
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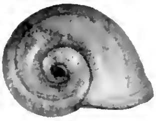
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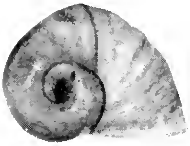
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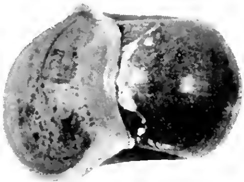
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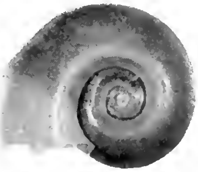
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PLATE 96

PLATE 97

Shells of Planorbidae

1–4. *Helisoma tenue* (Philippi). Platpa near City of Mexico, Mexico. Type locality. U.S.N.M., 160175.

5. *Helisoma tenue* (Philippi). Laguna de Tamos, near Tampico, Vera Cruz, Mexico. U.S.N.M., 467437.

6. *Helisoma tenue* (Philippi). Toluca, Mexico. U.S.N.M., 185942.

7, 8. *Helisoma tenue* (Philippi). Lake Texcoco, near City of Mexico, Mexico. M.C.Z.

9. *Helisoma tenue* (Philippi). Vera Cruz. Strebel Coll. U.S.N.M., 10585.

10. *Helisoma tenue* (Philippi). Sources of Rio Lerma, Valley of Toluca, Mexico. U.S.N.M., 467433.

11. *Helisoma tenue* (Philippi). Orizaba, Mexico. U.S.N.M., 22009.

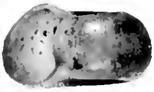
12. *Helisoma tenue bourcardi* (C. and F.). City of Mexico, Mexico. U.S.N.M., 8506.

13–17. *Helisoma tenue bourcardi* (C. and F.). City of Mexico, Mexico. U.S.N.M., 26453.

18–25. *Helisoma tenue exaggeratum* (von Martens). Lake Patzcuaro, State of Michoacan, Mexico. Type locality. U.S.N.M., 467462.

26–28. *Helisoma tenue applanatum* (von Martens). Lanos River, Chichuachua, Mexico. U.S.N.M., 16252.

All figures are enlarged about 1½ diameters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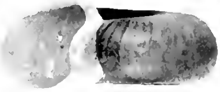
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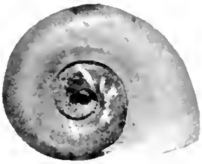
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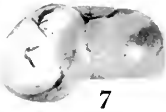
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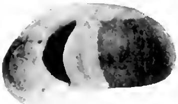
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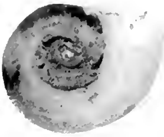
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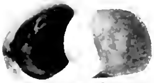
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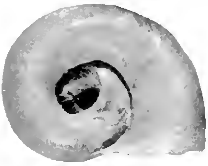
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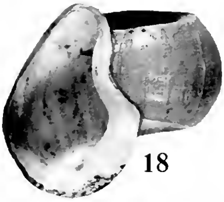
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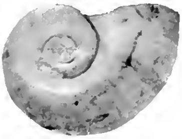
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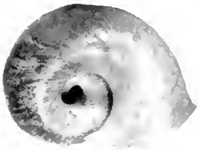
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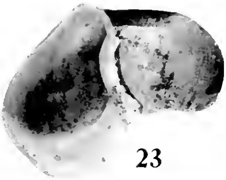
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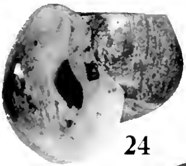
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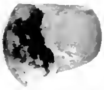
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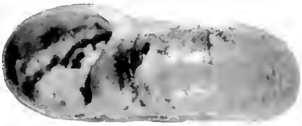
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PLATE 97

PLATE 98

Shells of Planorbidae

1. *Helisoma tenue applanatum* (von Martens). Orizaba, Mexico. Strebel Coll. U.S.N.M., 10538.

2–6. *Helisoma tenue applanatum* (von Martens). Yaqui River, near Ciudad Obregon, Sonora, Mexico. U.S.N.M., 467429.

7, 8. *Helisoma tenue applanatum* (von Martens). Mazatlan, Mexico. Lea Coll. U.S.N.M., 121192.

9–13. *Helisoma tenue sinuosum* (Bonnet). Santa Cruz River, Tucson, Arizona. In stream bed. U.S.N.M., 130237.

14. *Helisoma tenue sinuosum* (Bonnet). Soroyta Creek, Sonora, Mexico. U.S.N.M., 130229.

15. *Helisoma tenue sinuosum* (Bonnet). Albuquerque, New Mexico. 5000 ft. altitude. U.S.N.M., 134552.

16, 17. *Helisoma tenue californiense* F. C. Baker. Santa Cruz, California. U.S.N.M., 47571.

18. *Helisoma tenue californiense* F. C. Baker. Santa Cruz, California. U.S.N.M., 47572.

19–21. *Helisoma tenue californiense* F. C. Baker. Crystal Creek, San Jose, California. U.S.N.M., 32111.

22. *Helisoma tenue californiense* F. C. Baker. Santa Cruz Mts., 4 miles from Los Gatos, California. U.S.N.M., 75437.

23, 24. *Helisoma tenue californiense* F. C. Baker. Guadeloupe Creek, San Jose, California. Paratypes. B3262.

25. *Helisoma tenue sinuosum* (Bonnet). Rio Grande, El Paso, Texas. Immature. U.S.N.M., 130239.

26. *Helisoma tenue californiense* F. C. Baker. Bixby, Los Angeles Co., California. Immature. B3227.

Figures 25 and 26 show differences in spire whorls and sculpture of the two varieties

All figures are enlarged about 1½ diameters

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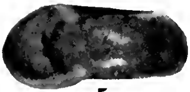

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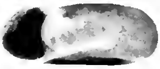

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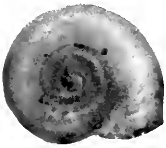

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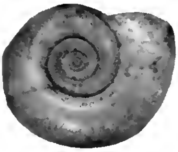

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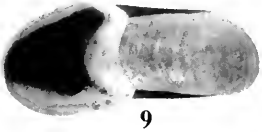

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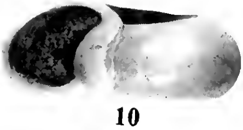

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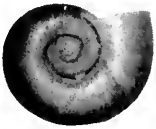

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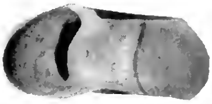

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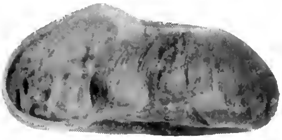

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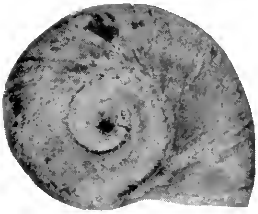

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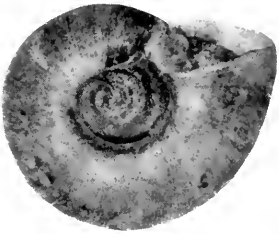

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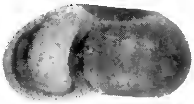

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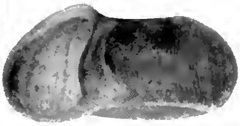

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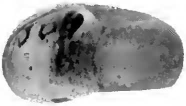

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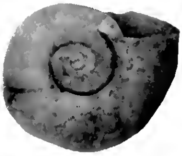

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PLATE 98

PLATE 99

Shells of Planorbidae

1. *Helisoma tenue applanatum* (von Martens). Near Vallecitos, Lower California. Immature. U.S.N.M., 162654.

2, 3. *Helisoma tenue applanatum* (von Martens). Yaqui River, near Ciudad Obregon, Mexico. Immature. U.S.N.M., 467429.

4–8. *Helisoma tenue sinuosum* (Bonnet). Santa Cruz River, Tucson, Arizona. Immature. U.S.N.M., 130237.

9, 10. *Helisoma tenue sinuosum* (Bonnet). Rio Grande, El Paso, Texas. Immature. U.S.N.M., 130239.

11–15. *Helisoma tenue californiense* F. C. Baker. Bixby, Los Angeles Co., California. Immature. U.S.N.M., 174048.

16–19. *Helisoma tenue strebelianum* (F. and C.). Penasco, 5 miles north of San Luis Potosi, Mexico. Immature. U.S.N.M., 251815.

20–24. *Helisoma caribaeum guatemalense* (Clessin). Reservoirs 4 miles north of Guatemala City, Guatemala. U.M., 83490.

25. *Helisoma tenue strebelianum* (F. and C.). Tamaulipus, Mexico. U.S.N.M., 109916.

26. *Helisoma tenue strebelianum* (F. and C.). Coy River, San Luis Potosi, Mexico. B3921.

27–30. *Helisoma tenue strebelianum* (F. and C.). Alta Mira, Tamaulipus, Mexico. U.S.N.M., 251807.

31. *Helisoma caribaeum* (Orb.). Naranjo, Guatemala. Varying toward *Helisoma caribaeum guatemalense*. U.M., 83487.

32–36. *Helisoma caribaeum guatemalense* (Clessin). Nicaragua. U.M., 83485.

All figures are enlarged about 1½ diameters


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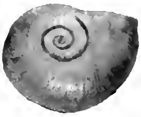
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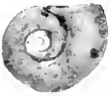
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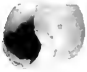
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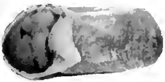
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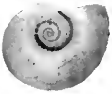
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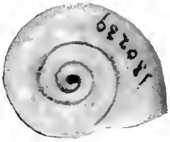
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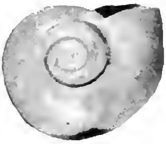
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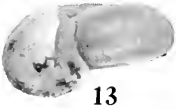
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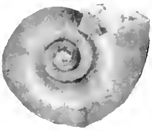
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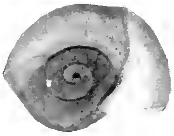
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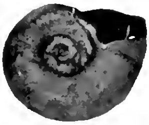
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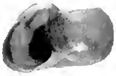
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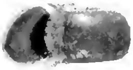
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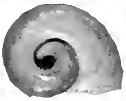
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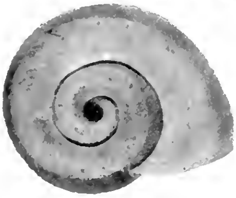
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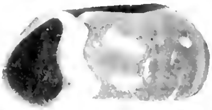
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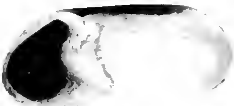
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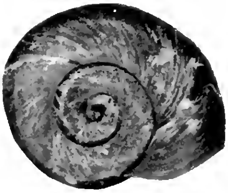
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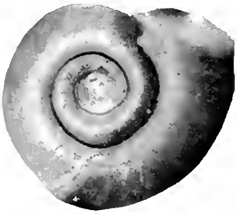
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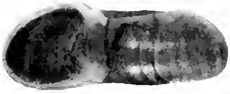
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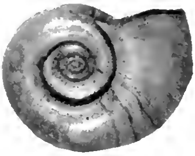
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PLATE 99

PLATE 100

Shells of Planorbidae

1, 2, 5. *Helisoma caribaeum* (Orb.). Cuba. U.M., 83491.

3, 4. *Helisoma caribaeum* (Orb.). Punta de la Junta, Cuba. U.S.N.M., 11204.

6–10. *Helisoma caribaeum* (Orb.). Panama. U.M., 83492.

11–13. *Helisoma caribaeum* (Orb.). Somorrostro, Havana, Cuba. B3075.

14–17. *Helisoma caribaeum* (Orb.). Vera Cruz, Mexico. U.S.N.M., 210882.

18–20. *Helisoma wyldii salvini* (Tristram). Guatemala. U.S.N.M., 121023.

21–24. *Helisoma wyldii* (Tristram). San Carlos, Nicaragua. U.S.N.M., 354295.

25–27. *Helisoma wyldii* (Tristram). Lake Olomega, San Salvador. U.S.N.M., 360392

28. *Helisoma wyldii* (Tristram). Lake Metapan, San Salvador. U.S.N.M., 360391.

29, 30. *Helisoma wyldii* (Tristram). Lake Guija, San Salvador. U.S.N.M., 360390.

31. *Helisoma tumens* (Cpr.). Mazatlan, Mexico. U.S.N.M., 46967.

32, 33. *Helisoma tumens* (Cpr.). Mazatlan, Mexico. U.S.N.M., 47517.

34–37. *Helisoma tumens* (Cpr.). Mazatlan, Mexico. B2284.

All figures are enlarged about $1\frac{1}{2}$ diameters

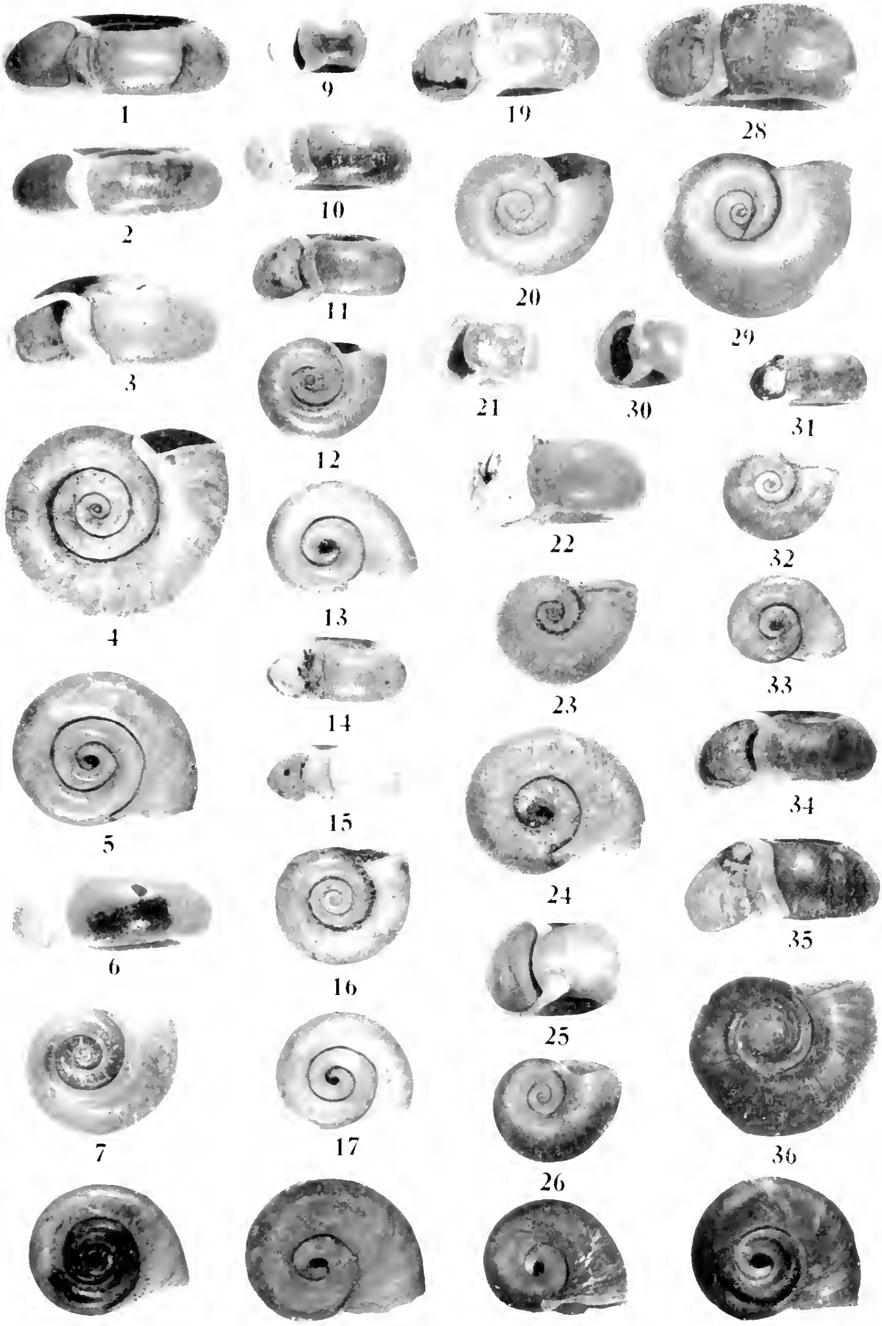
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PLATE 100

PLATE 101

Shells of Planorbidae

1. *Helisoma foveale* (Menke). Jamaica. U.S.N.M., 74762.

2. *Helisoma foveale* (Menke). Jamaica. U.S.N.M., 90479.

3, 4, 6. *Helisoma foveale* (Menke). Kingston, Jamaica. U.S.N.M., 454058.

5. *Helisoma foveale* (Menke). Kingston, Jamaica. U.S.N.M., 74762.

7. *Helisoma magnificum* (Pilsbry). Young, born in captivity. Parent from type locality. U.S.N.M.

8, 9. *Helisoma costaricense* (Preston). Catalina, Guanacaste, Costa Rica. Cotype. B2132.

10. *Helisoma costaricense* (Preston). Catalina, Guanacaste, Costa Rica. Figured type. U.S.N.M., 202522.

11, 12. *Helisoma anceps idahoense* F. C. Baker. Foot of Elbow or Lindbergh Lake, Mission Mts., Montana. M.C.Z.

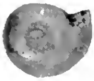
13. *Helisoma subcrenatum* variety? Utah Lake, Utah. U.S.N.M., 29332.

14. *Helisoma subcrenatum* (Cpr.). Oregon. From Nuttall in Lea Coll. U.S.N.M., 120986.

15. *Helisoma caribaeum* (Orb.). Cuba. To show rounded inner whorls. U.M., 83491. ×6.

16. *Helisoma tenue applanatum* (von Martens). To show flat inner whorls. U.S.N.M., 10538.

All figures, excepting 15 and 16, are enlarged about 1½ diameters



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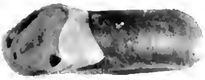

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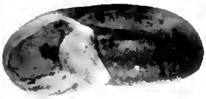

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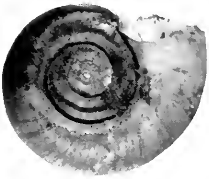

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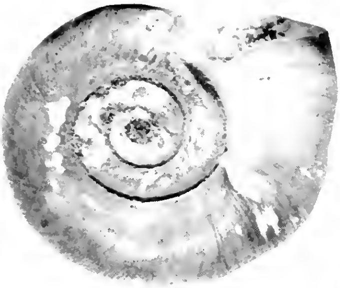

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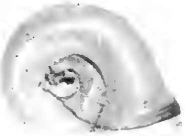

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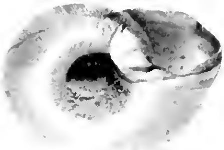

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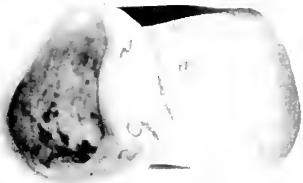

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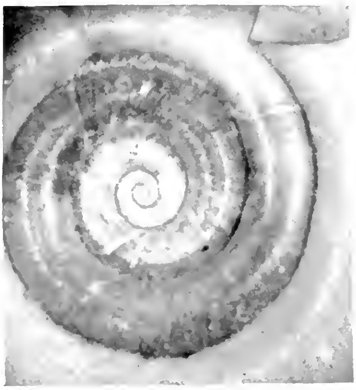

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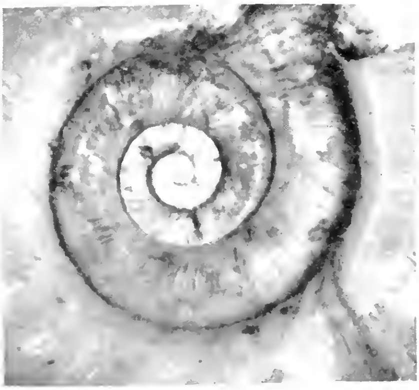

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PLATE 101

PLATE 102

Shells of Planorbidae

1. *Helisoma tenue chapalense* (Pilsbry). Proc. Acad. Sci. Phil., 1920, p. 193, fig. 1. Enlarged.

2. *Helisoma contrerasi* (Pilsbry). Proc. Acad. Sci. Phil., 1920, p. 193, fig. 2. Enlarged.

3, 4. *Helisoma contrerasi* (Pilsbry). Lake Chapala, near Guadalajara, Mexico. U.S.N.M., 225863.

5–10. *Helisoma tenue chapalense* (Pilsbry). Oaxaca, Mexico. U.S.N.M., 117952.

11, 12. *Helisoma scalare* (Jay). Caloosatchee Pliocene formation, Florida. B1106.

13, 14. *Helisoma scalare* (Jay). Lake Griffin, near Leesburg, Florida. B1438.

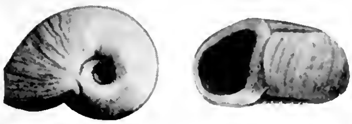
15–18. *Helisoma scalare* (Jay). Head of Miami River, Everglades, Dade Co., Florida. B2969.

19, 20. *Helisoma scalare* (Jay). Everglades, Florida. B3002.

21. *Helisoma duryi seminole* Pilsbry. Everglades, Florida. B2962.

22, 23. *Helisoma duryi seminole* Pilsbry. Sumter Co., Florida. B2965.

All figures, excepting 1 and 2, are enlarged about two diameters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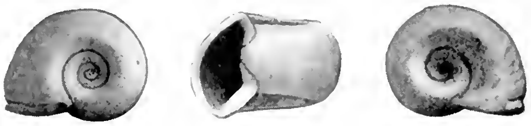
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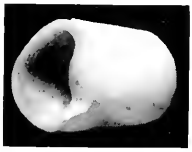
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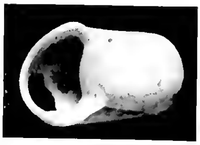
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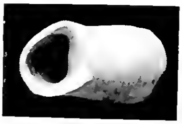
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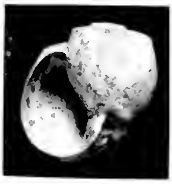
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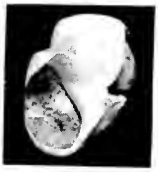
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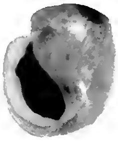
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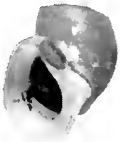
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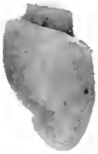
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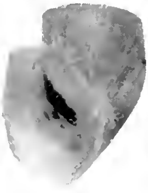
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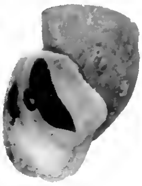
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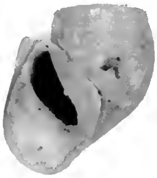
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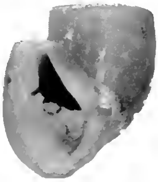
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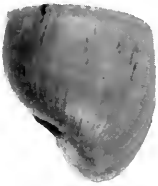
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PLATE 102

PLATE 103

Shells of Planorbidae

1, 2. *Helisoma duryi seminole* Pilsbry. Everglades, Florida. B2962.

3–5, 8, 9. *Helisoma duryi seminole* Pilsbry. Lake Eustis, Lake Co., Florida. Paratypes. B2960.

6, 7. *Helisoma duryi seminole* Pilsbry. Lake Eustis, Lake Co., Florida. U.I., Z32368.

10, 11. *Helisoma duryi seminole* Pilsbry. Okechobee Lake, near More Haven, Florida. M.C.Z., 43311.

12. *Helisoma duryi seminole* Pilsbry. Lake Apopka, Florida. M.C.Z., 71599.

13. *Helisoma duryi seminole* Pilsbry. Lake Apopka, Florida. M.C.Z., 71598.

14–18. *Helisoma duryi seminole* Pilsbry. Survey, Lee Co., Florida. M.C.Z., 68236.

19. *Helisoma duryi seminole* Pilsbry. Sumter Co., Florida. U.I., Z32364.

20–30. *Helisoma duryi* (Wetherby). Near West Palm Beach, Florida. M.C.Z., 82856.

31. *Helisoma duryi* (Wetherby). Miami, Florida. U.S.N.M., 153412.

These figures show the great variation in form of spire and shape of shell of the *duryi* complex, especially the form *seminole*.

All figures are enlarged about 1½ diameters

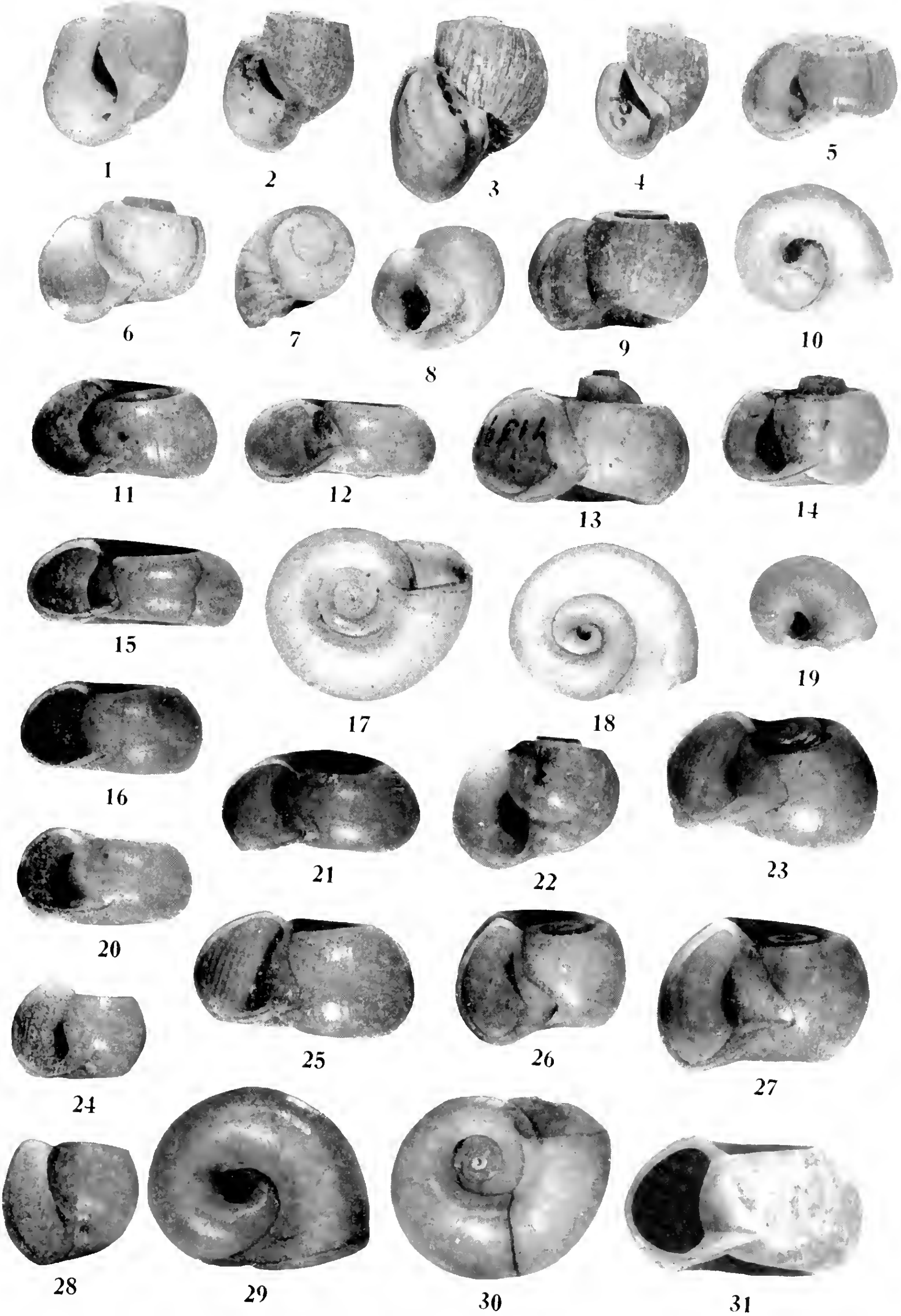
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PLATE 103

PLATE 104

Shells of Planorbidae

1–3. *Helisoma duryi* (Wetherby). Kissimmee River, Florida. Variation toward variety *normale*. U.S.N.M., 168921.

4–7. *Helisoma duryi* (Wetherby). Near West Palm Beach, Palm Beach Co., Florida. Variation toward variety *normale*. M.C.Z., 45103.

8–16. *Helisoma duryi normale* Pilsbry. One mile north of Oil well, Pinecrest, Everglades, Florida. U.I., Z34637.

17. *Helisoma duryi normale* Pilsbry. Canal west of Boynton, Palm Beach Co., Florida. Malleated base. M.C.Z., 76659.

18–22. *Helisoma duryi normale* Pilsbry. Magnolia, Florida. M.C.Z., 87505.

All figures are enlarged about $1\frac{1}{2}$ diameters


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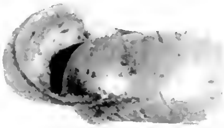
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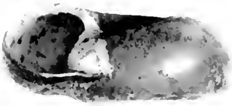
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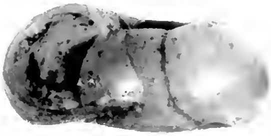
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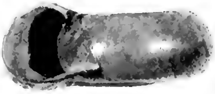
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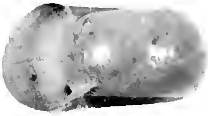
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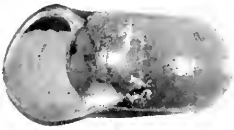
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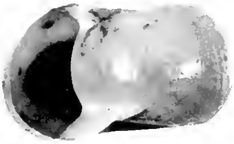
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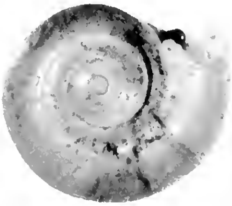
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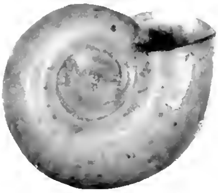
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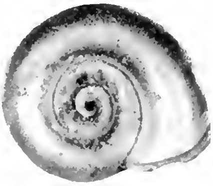
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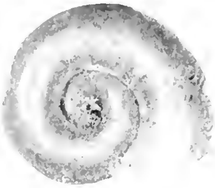
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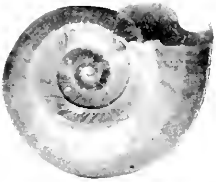
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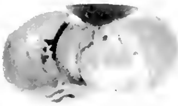
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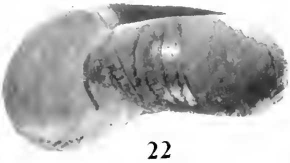
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PLATE 104

PLATE 105

Shells of Planorbidae

1–3. *Helisoma duryi normale* Pilsbry. Everglades 40 miles from Ft. Meyers, Florida. M.C.Z., 71020.

4–8. *Helisoma duryi intercalare* (Pilsbry). East shore Lake Okeechobee, Palm Beach Co., Florida. M.C.Z.

9. *Helisoma duryi intercalare* (Pilsbry). Beecher Spring, Wakulla, Wakulla Co., Florida. U.S.N.M., 153079.

10, 11. *Helisoma duryi intercalare* (Pilsbry). Lake Jessup, Florida. U.S.N.M., 167040.

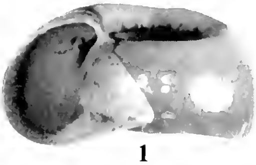
12, 13. *Helisoma duryi intercalare* form *alternatum* Pilsbry. Blue Creek, Lake Co., Florida. Type locality. M.C.Z., 83729.

14–16. *Helisoma duryi eudiscus* Pilsbry. Head of Miami River, near Miami, Dade Co., Florida. Paratypes. B3074.

17–19. *Helisoma duryi eudiscus* Pilsbry. Silver Springs, Marion Co., Florida. Varying toward *intercalare*. B3073.

20–27. *Helisoma duryi preglabratum* (Marshall). Canal, Palm Beach Co., Florida. Type locality. M.C.Z., 46572.

All figures are enlarged about $1\frac{1}{2}$ diameters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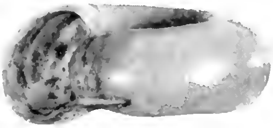
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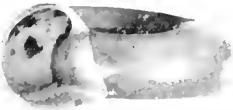
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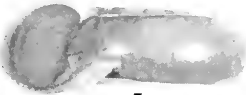
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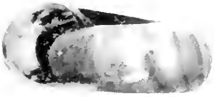
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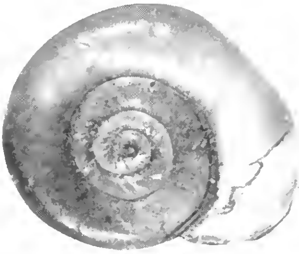
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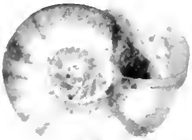
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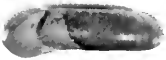
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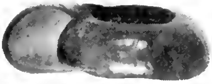
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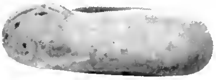
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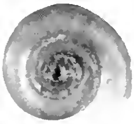
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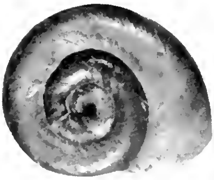
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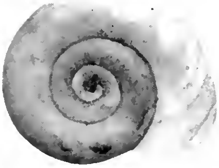
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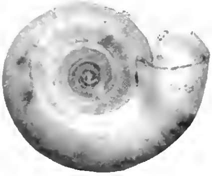
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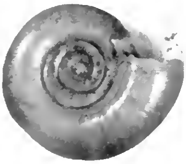
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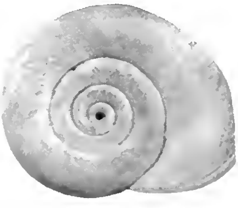
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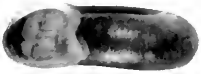
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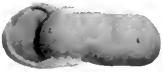
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PLATE 105

PLATE 106

Shells of Planorbidae

1–3. *Helisoma duryi seminole* Pilsbry. Florida. U.S.N.M., 99301.

4\. *Helisoma conanti* Dall. Caloosahatchee River, Florida. U.I., Z40570.

5–7. *Helisoma conanti* Dall. Caloosahatchee River, Florida. B1107.

8\. *Helisoma disstoni* (Dall). Vero, St. Lucia Co., Florida. U.S.N.M., 331971.

9–11. *Helisoma* species? Asecibo, Puerto Rico. U.S.N.M., 535394.

12–15. *Helisoma disstoni* (Dall). Canal, Palm Beach Co., Florida. M.C.Z., 99182.

16\. *Helisoma corpulentum multicostatum* F. C. Baker. Lake Kahnipiminanikok, Ontario, Canada. Young. U.I., Z32628.

17\. *Helisoma corpulentum* (Say). Lac la Croix, Ontaria, Canada. Young. U.I., Z32626.

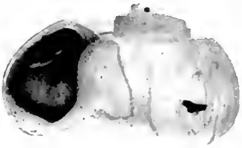
18\. *Helisoma whiteavesi* F. C. Baker. Lac des Mille Lacs, Ontario, Canada. Holotype. U.I., Z32311.

19, 20. *Helisoma whiteavesi* F. C. Baker. Lac des Mille Lacs, Ontario, Canada. Paratypes. U.I., Z32312.

21\. *Helisoma whiteavesi* F. C. Baker. Lac des Mille Lacs, Ontario, Canada. Paratype, Immature. U.I., Z32313.

22\. *Helisoma corpulentum* (Say). Kettle Falls, Rainy River District, Ontario, Canada. Began as a *corpulentum* and on last whorl changed form of shell toward that of *multicostatum*. U.S.N.M., 361737.

All figures are enlarged about 1½ diameters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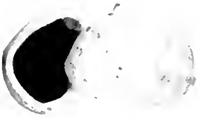
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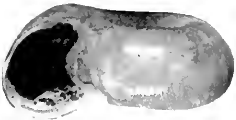
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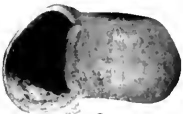
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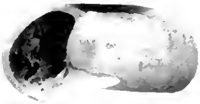
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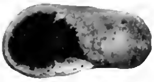
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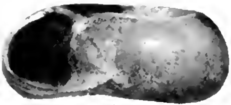
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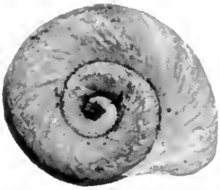
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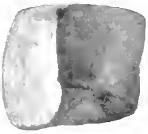
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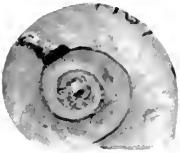
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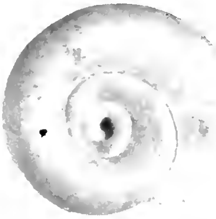
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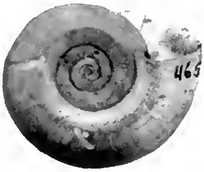

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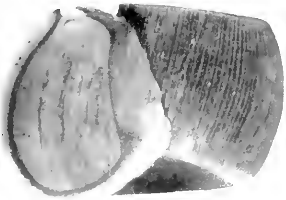
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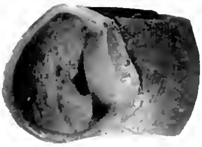
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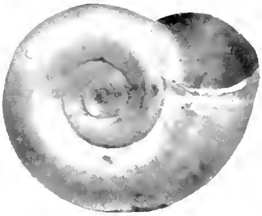
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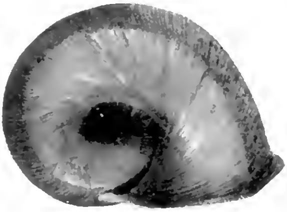
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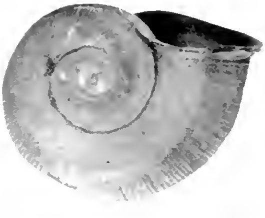
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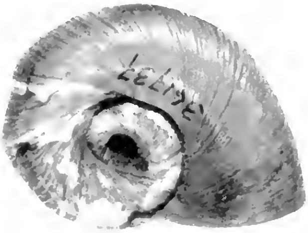
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PLATE 106

PLATE 107

Shells of Planorbidae

1–4. *Helisoma corpulentum* (Say). Lac la Croix, Ontario, Canada. U.I., Z32296.

5. *Helisoma corpulentum* (Say). Rainy Lake, Ontario, Canada. A type locality. B1101.

6. *Helisoma corpulentum* (Say). Rabbit Point, west of Sabaskong Bay, Lake of the Woods, Canada. A type locality. Resembles Say's figure. U.I., Z41286.

7. *Helisoma corpulentum* (Say). Lac la Croix, Ontario, Canada. U.I., Z32626.

8. *Helisoma corpulentum vermilionense* F. C. Baker. Vermilion Lake, St. Louis Co., Minnesota. Holotype. B3021.

9, 10. *Helisoma corpulentum vermilionense* F. C. Baker. Vermilion Lake, Minnesota. Paratypes. B3014.

11. *Helisoma corpulentum vermilionense* F. C. Baker. Vermilion Lake, Minnesota. Paratype, immature. U.I., Z32518.

12. *Helisoma corpulentum multicostatum* F. C. Baker. Lake Kahnipiminanikok, Ontario, Canada. Holotype. U.I., Z32308.

13. *Helisoma corpulentum* (Say). Lac la Croix, Ontario, Canada. Young. U.I., Z32626.

14. *Helisoma corpulentum vermilionense* F. C. Baker. Vermilion Lake, Minnesota. Young. U.I., Z32627.

15. *Helisoma whiteavesi* F. C. Baker. Lac des Mille Lacs, Canada. Young. U.I., Z32312.

16–18. *Helisoma corpulentum multicostatum* F. C. Baker. Kahnipiminanikok Lake, Ontario, Canada. Paratypes. U.I., Z32307.

19. *Helisoma corpulentum multicostatum* F. C. Baker. Knife Lake, Minnesota. U.I., Z29828.

20. *Helisoma corpulentum multicostatum* F. C. Baker. Bemidji Lake, Beltrami Co., Minnesota. U.I., Z32475.

21. *Helisoma corpulentum multicostatum* F. C. Baker. Kahnipiminanikok Lake, Ontario, Canada. Immature. U.I., Z32628.

All figures are enlarged about 1½ diameters


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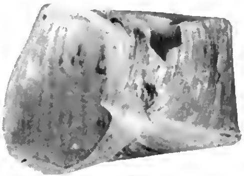
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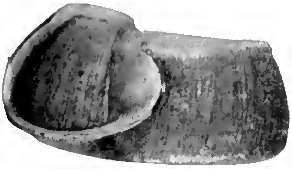
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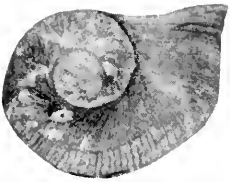
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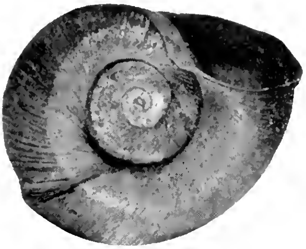
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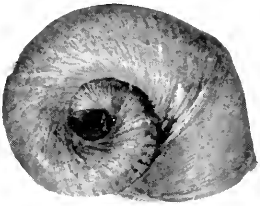
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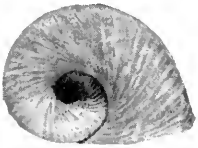
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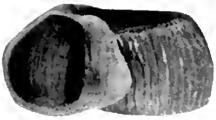
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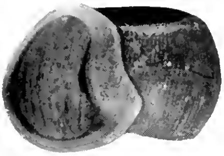
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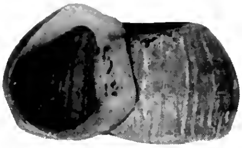
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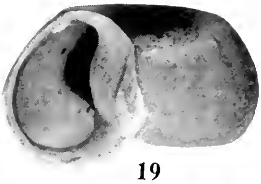
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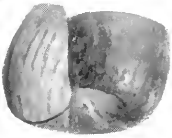
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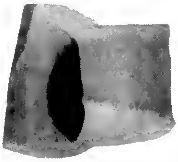
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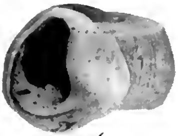
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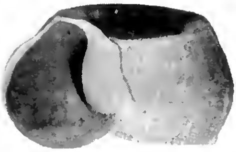
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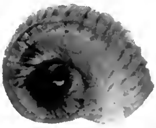
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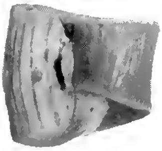
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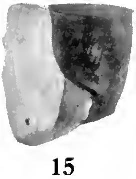
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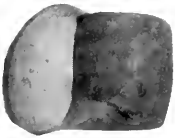
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PLATE 107

PLATE 108

Shells of Planorbidae

1–6. *Helisoma campanulatum* (Say). Cayuga Lake, New York. Type locality. U.S.N.M., 212700.

7–9. *Helisoma campanulatum* (Say). North end Cayuga Lake, New York. Probable type locality. B1043.

10, 11. *Helisoma campanulatum* (Say). Ottawa, Ontario, Canada. U.S.N.M., 120985.

12-14. *Helisoma campanulatum* (Say). North end Canandaigua Lake, New York. B3859.

15-17. *Helisoma campanulatum* (Say). Crooked Lake, Oden, Michigan. Variation in size. U.I., Z19877.

18. *Helisoma campanulatum ferrissi* F. C. Baker. Marl Lake, Fair Grounds, Joliet, Will Co., Illinois. Holotype. U.I., P1068a.

19. *Helisoma campanulatum ferrissi* F. C. Baker. Same locality as above. Paratype. U.I., P1068b.

20–25. *Helisoma campanulatum ferrissi* F. C. Baker. Same locality as above. Paratypes. U.I., P1068.

26–28. *Helisoma campanulatum ferrissi* F. C. Baker. White Lake, Oakland Co., Michigan. U.I., Z20908.

29–31. *Helisoma campanulatum ferrissi* F. C. Baker. Interior Charity Island, Michigan. B3860.

32–34. *Helisoma campanulatum ferrissi* F. C. Baker. Lermond, Bonne Bay, Newfoundland. B3858.

All figures are enlarged about two diameters

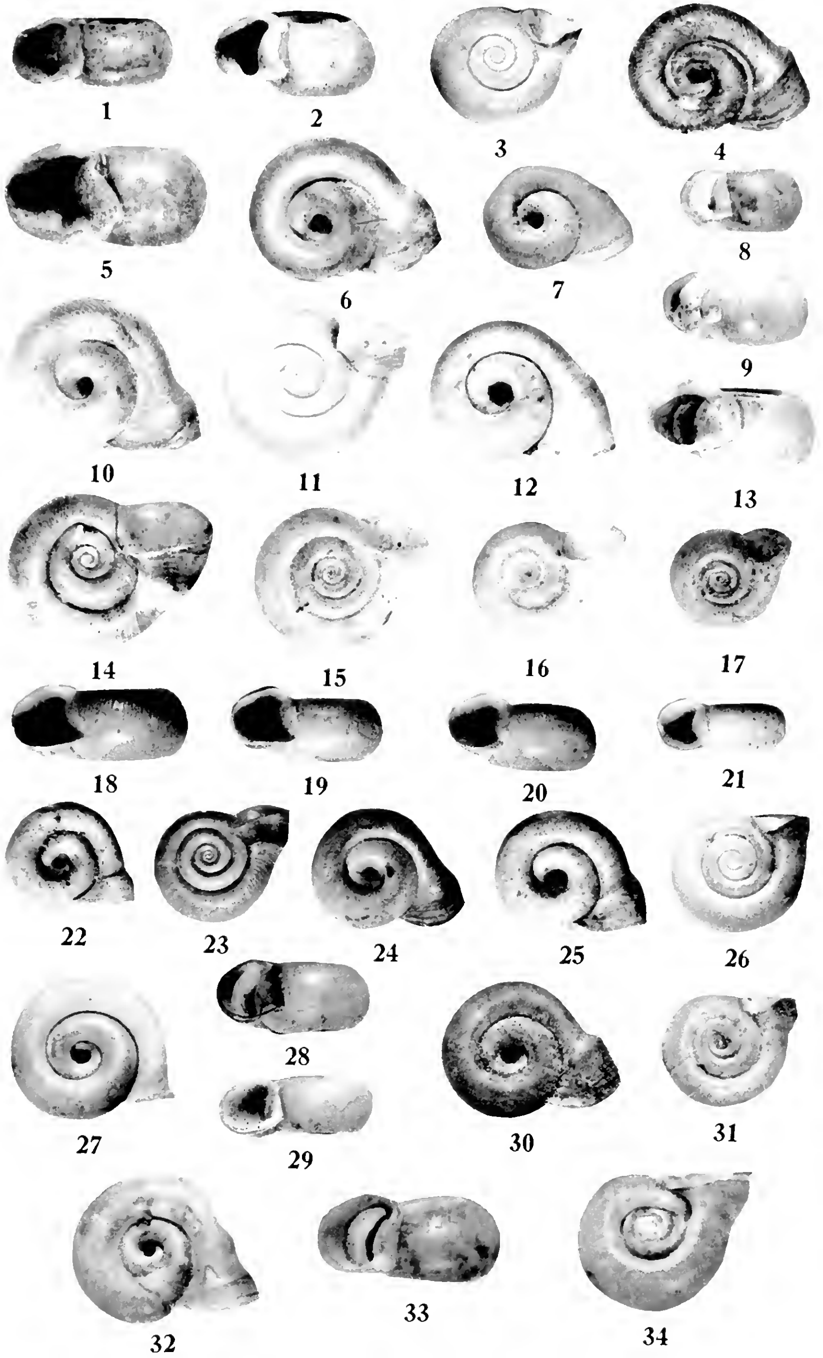
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PLATE 108

PLATE 109

Shells of Planorbidae

1–6. *Helisoma campanulatum* (Say). Pine Island Lake, Kent Co., Michigan. Exaggerated campanulate lip. B3922.

7. *Helisoma campanulatum wisconsinense* (Winslow). Little Arbor Vitae Lake, Vilas Co., Wisconsin. Type locality. U.I., Z18421.

8. *Helisoma campanulatum wisconsinense* (Winslow). Tomahawk Lake, Wisconsin. B1718.

9. *Helisoma campanulatum wisconsinense* (Winslow). Tomahawk Lake, Wisconsin. B1719.

10, 11. *Helisoma campanulatum wisconsinense* (Winslow). Tomahawk Lake, Wisconsin. B1725.

12, 13. *Helisoma campanulatum wisconsinense* (Winslow). Tomahawk Lake, Wisconsin. B3857.

14. *Helisoma campanulatum smithii* (F. C. Baker). Douglas Lake, Michigan. Holotype. B1054.

15,16. *Helisoma campanulatum smithii* (F. C. Baker). Douglas Lake, Michigan. Paratypes. B1728.

17–20. *Helisoma campanulatum smithii* (F. C. Baker). Douglas Lake, Michigan. Type locality. B3861.

21. *Helisoma campanulatum rideauense* F. C. Baker. Rideau River, Ottawa, Canada. Holotype. U.S.N.M., 346627.

22–24. *Helisoma campanulatum rideauense* F. C. Baker. Rideau River, Ottawa, Canada. Paratypes. U.S.N.M., 346627.

25. *Helisoma campanulatum smithii* (F. C. Baker). Douglas Lake, Michigan. Small form. B1056.

26–28. *Helisoma multivolvis* (Case). Howe Lake, Marquette Co., Michigan. U.I., Z23192.

29. *Helisoma multivolvis* (Case). Howe Lake, Marquette Co., Michigan. U.S.N.M., 272274.

All figures are enlarged about 1½ diameters

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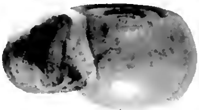

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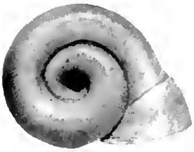

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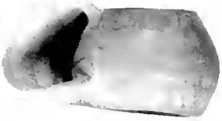

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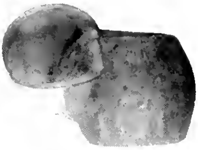

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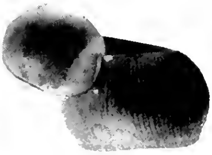

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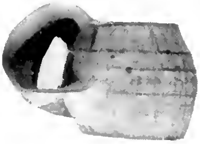

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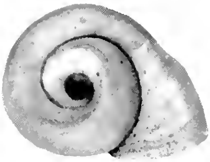

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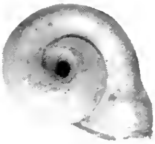

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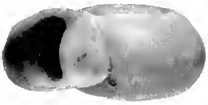

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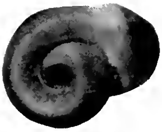

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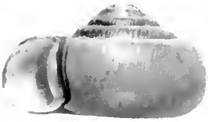

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PLATE 109

PLATE 110

Shells of Planorbidae

1–4. *Helisoma campanulatum wisconsinense* (Winslow). Tomahawk Lake, Wisconsin. 1, 2, Immature. 3, 4, Small form. U.I., Z29858.

5–7. *Helisoma campanulatum* near variety *smithii* (F. C. Baker). Douglas Lake, Michigan. U.I., Z13957.

8–10. *Helisoma campanulatum smithii* (F. C. Baker). Douglas Lake, Michigan. Small form. B1056.

11. *Helisoma campanulatum canadense* F. C. Baker. Bamiji Lake, Ontario, Canada. Holotype. U.I., Z30721.

12, 13. *Helisoma campanulatum canadense* F. C. Baker. Bamiji Lake, Ontario, Canada. Paratypes. U.I., Z30721.

14. *Helisoma campanulatum canadense* F. C. Baker. Brent Lake, Ontario, Canada. U.I., Z41303.

15–17. *Helisoma campanulatum canadense* F. C. Baker. Lake near Lake Mercutio, Ontario, Canada. Variation in size. U.I., Z40064.

18–20. *Helisoma campanulatum canadense* F. C. Baker. Sturgeon Lake, Ontario, Canada. Variation in size. U.I., Z32331.

21. *Helisoma campanulatum pleistocenicum* F. C. Baker. White Pond, Marlboro, New Jersey. Holotype. U.S.N.M., 121195.

22–26. *Helisoma campanulatum pleistocenicum* F. C. Baker. White Pond, Marlboro, New Jersey. Paratypes. U.S.N.M., 121195.

27–35. *Helisoma campanulatum collinsi* F. C. Baker. Cameron Lake, Lake of the Woods, Canada. Variation in size. U.I., Z41297.

All figures are enlarged about two diameters

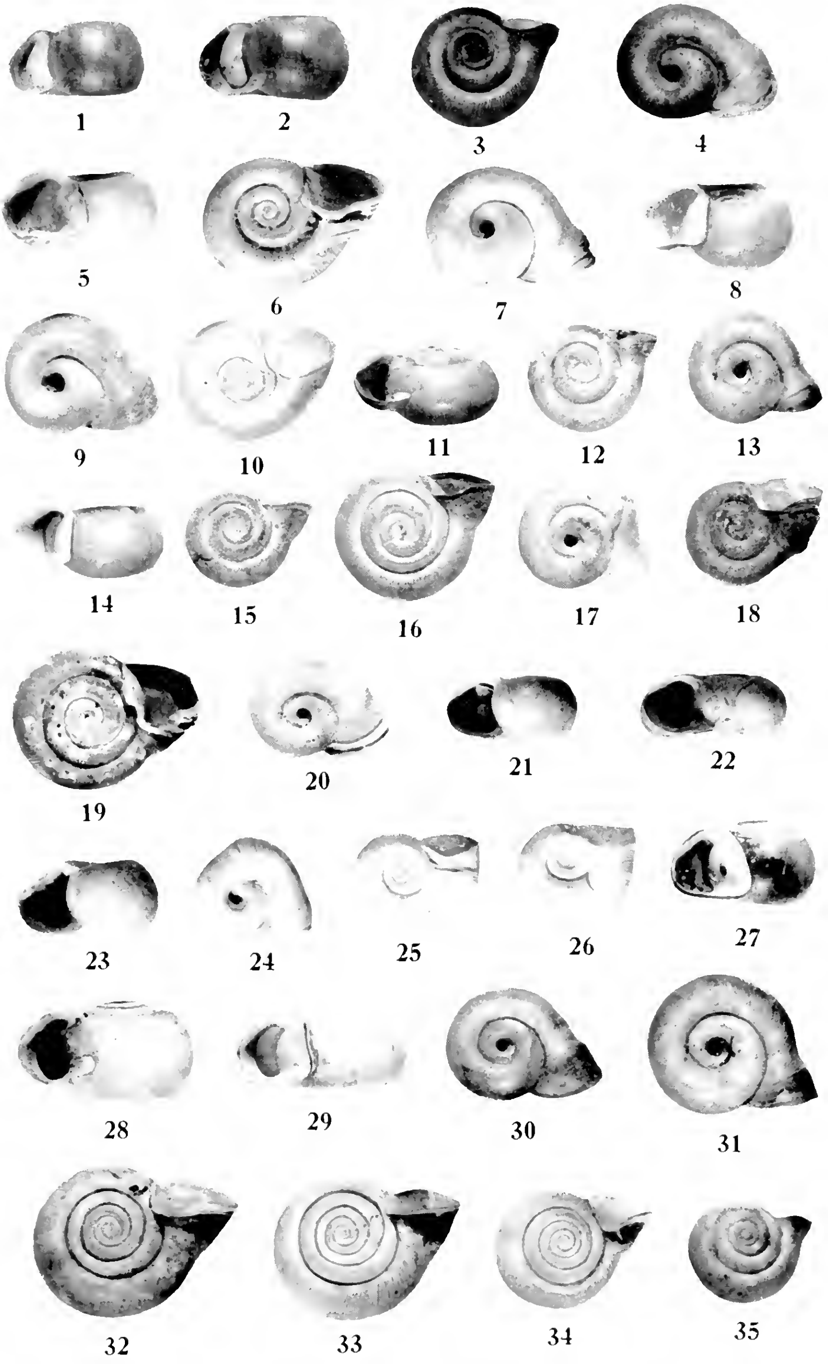
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PLATE 110

PLATE 111

Shells of Planorbidae

1–5. *Helisoma campanulatum rudentis* (Dall). Knee Lake, Manitoba, Canada. Paratypes. U.S.N.M., 365574.

6, 7. *Helisoma campanulatum michiganense* F. C. Baker. Marl Lake, Roscommon Co., Michigan. 6, holotype, B1809; 7, paratype, B1809a.

8, 9. *Helisoma campanulatum michiganense* F. C. Baker. Marl Lake, Roscommon Co., Michigan. U.S.N.M., 173102.

10, 11. *Helisoma campanulatum michiganense* F. C. Baker. Marl Lake, Michigan. U.S.N.M., 173102.

12, 13. *Helisoma campanulatum dalli* F. C. Baker. Anticosti Island, Canada. 12, holotype; 13, paratype. U.S.N.M., 162724.

14. *Helisoma campanulatum michiganense* F. C. Baker. Marl Lake, Michigan. Abnormal. U.S.N.M., 173102.

15, 16. *Helisoma campanulatum dalli* F. C. Baker. Anticosti Island, Canada. Paratypes. U.S.N.M., 162724.

17–19. *Helisoma campanulatum collinsi* F. C. Baker. Cameron Lake, Lake of the Woods, Ontario, Canada. 17, holotype; 18, 19, paratypes. U.I., Z41297.

20. *Helisoma campanulatum collinsi* F. C. Baker. Cameron Lake, Lake of the Woods, Canada. Paratype. A small specimen. U. I., Z41297.

21, 22. *Helisoma campanulatum* (Say). Crooked Lake, Emmet Co., Michigan. Young. B3868. ×3½.

23–31. *Helisoma scalare* (Jay). Everglades, Florida. Marl bed 10-15 ft. under peat. Variation toward *seminole* form. U.S.N.M., 348566.

32. *Helisoma duryi seminole* Pilsbry. Lake Apopka, Florida. Showing advanced lower part of aperture in contrast with the receding aperture of *scalare* (fig. 31). U.S.N.M., 566570.

All figures, excepting 21 and 22, are enlarged about 1¾ diameters


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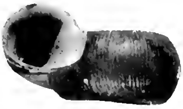
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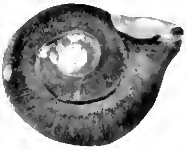
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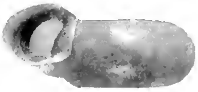
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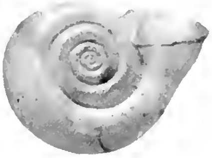
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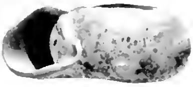
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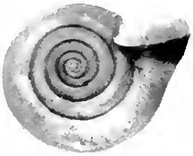
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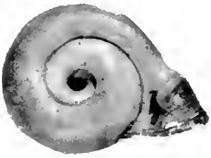
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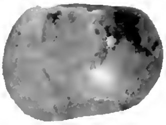
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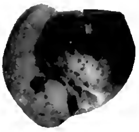
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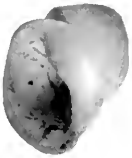
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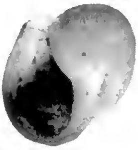
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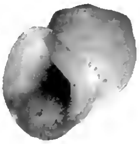
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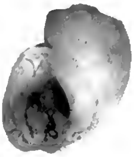
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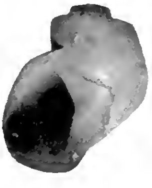
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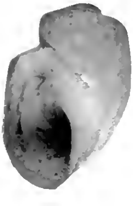
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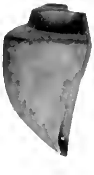
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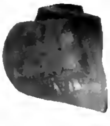
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PLATE 111

PLATE 112

Shells of Planorbidae

1-6. *Helisoma duryi seminole* Pilsbry. Lake Apopka, Florida. Range of variation. U.S.N.M., 506868.

7, 8. *Helisoma duryi seminole* Pilsbry. Lake Apopka, Florida. *scalare*-like forms. U.S.N.M., 506870.

9-11. *Carinifex newberryi* (Lea). Owens Lake, California. U.S.N.M., 251516.

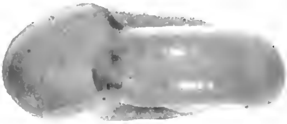
12-14. *Carinifex occidentalis* Hanna. Eagle Lake, Lasen Co., California. U.S.N.M., 120331.

15. *Carinifex occidentalis* Hanna. Eagle Lake, California. U.S.N.M., 120333.

16-21. *Carinifex occidentalis* Hanna. Eagle Lake, California. U.S.N.M., 120331.

Figures 12-21 show range of variation

All figures are enlarged about 1½ times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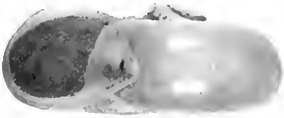
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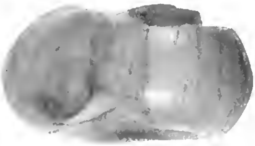
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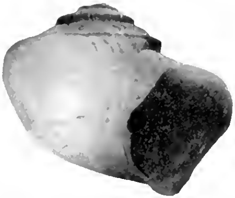
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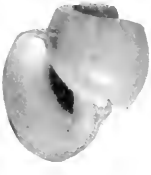
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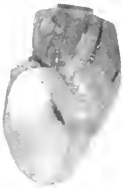
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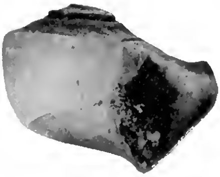
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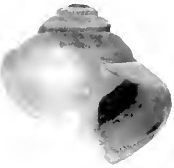
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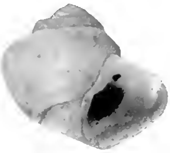
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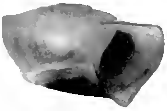
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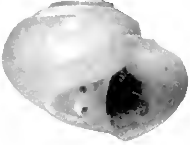
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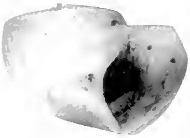
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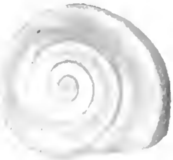
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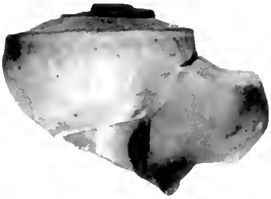
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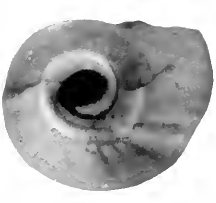
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PLATE 112

PLATE 113

Shells of Planorbidae

1–4. *Carinifex newberryi* (Lea). Canoe Creek, California. Type locality. U.S.N.M., 9254.

5, 6. *Carinifex newberryi* (Lea). Canoe Creek, California. Said to be types. See Binney, p. 75. U.S.N.M., 9256.

7, 8. *Carinifex newberryi* (Lea). Canoe Creek, California. Lea Collection, probably types. See Binney fig. 120. U.S.N.M., 120991.

9. *Carinifex newberryi* (Lea). Canoe Creek, California. Similar in form to *malleata*. U.S.N.M., 2954.

10, 11. *Carinifex newberryi* (Lea). Canoe Creek, California. U.S.N.M., 56405.

12-15. *Carinifex newberryi* (Lea). Walker Lake, Nevada. U.S.N.M., 349132.

16–23. *Carinifex newberryi* (Lea). Lakota Resort, Bear Lake, Utah. B3877.

24–28. *Carinifex newberryi malleata* Pilsbry. Pitt River, California. U.S.N.M., 9341.

29. *Carinifex newberryi malleata* Pilsbry. Pitt River, California. U.S.N.M., 170772.

30. *Carinifex newberryi malleata* Pilsbry. Pitt River, California. Binney's fig. 122. U.S.N.M., 9342.

All figures are enlarged about 1¾ diameters


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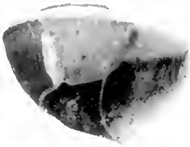
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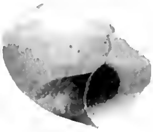
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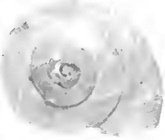
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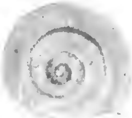
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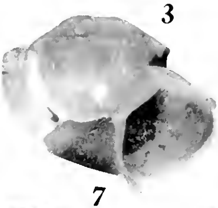
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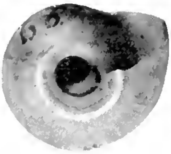
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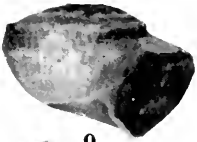
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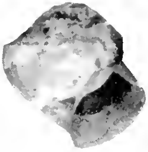
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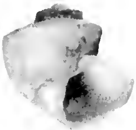
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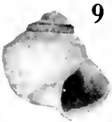
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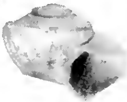
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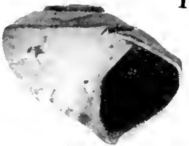
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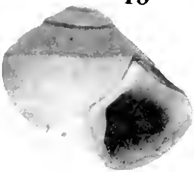
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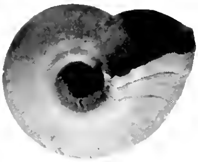
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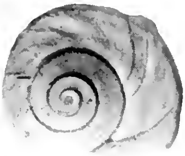
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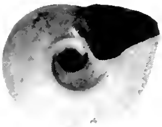
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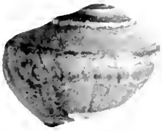
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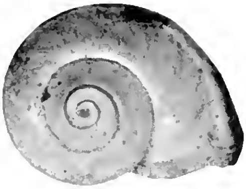
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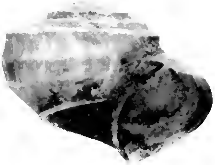
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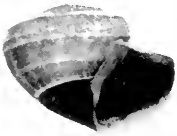
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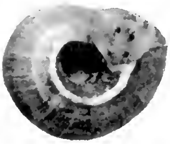
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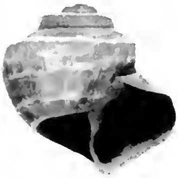
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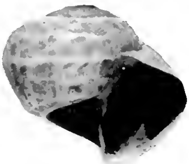
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PLATE 113

PLATE 114

Shells of Planorbidae

1. *Carinifex ponsonbyi* E. A. Smith. Lower Klamath Lake, Klamath Falls, Oregon. U.S.N.M., 334389.

2. *Carinifex ponsonbyi* E. A. Smith. Lower Klamath Lake, Klamath Falls, Oregon. U.S.N.M., 219749.

3, 4. *Carinifex ponsonbyi* E. A. Smith. South end Upper Klamath Lake, Oregon. B3924.

5, 6. *Carinifex ponsonbyi* E. A. Smith. South end Upper Klamath Lake, Oregon. 5, immature. B3924.

7–9. *Carinifex ponsonbyi* E. A. Smith. Lower Klamath Lake, Oregon. U.S.N.M., 337022.

10, 11. *Carinifex ponsonbyi* E. A. Smith. Upper Klamath Lake, Oregon. U.S.N.M., 380807.

12, 13. *Carinifex ponsonbyi* E. A. Smith. Lower Klamath Lake, Oregon. U.S.N.M., 334387.

14, 15. *Carinifex newberryi* (Lea). Canoe Creek, California. Immature. U.S.N.M., 9256.

16. *Carinifex newberryi* (Lea). Canoe Creek, California. Immature. U.S.N.M., 56405.

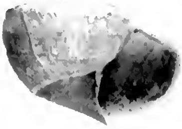
17. *Carinifex occidentalis* Hanna. Eagle Lake, California. Immature. U.S.N.M., 120333.

18. *Carinifex ponsonbyi* E. A. Smith. Klamath Falls, Lower Klamath Lake, Oregon. Immature. U.S.N.M., 510024.

19–24. *Carinifex newberryi minor* Cooper. Clear Lake, California. From Lea coll. U.S.N.M., 121025.

25-28. *Carinifex newberryi subrotunda* Pilsbry. Proc. Acad. Nat. Sci. Phil., 86, plate 11, figs. 2, 2a, 2b, type; 3, paratype.

Figures 1-13, 25-28 are enlarged about 1½ diameters; figs. 17-24 are enlarged 3 diameters.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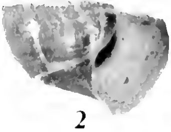
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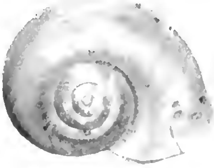
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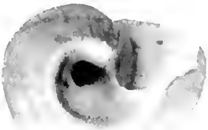
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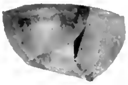
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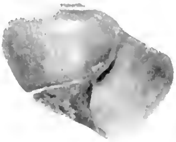
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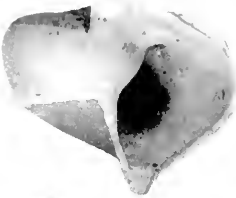
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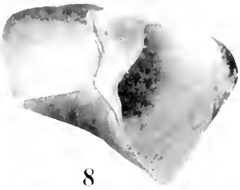
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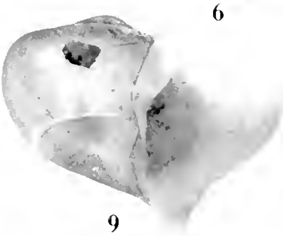
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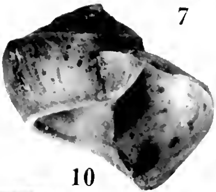
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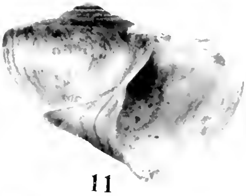
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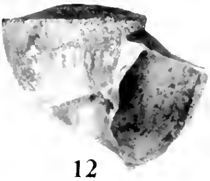
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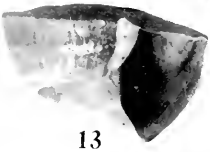
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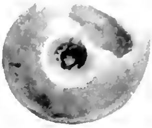
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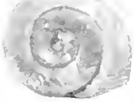
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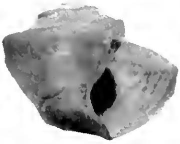
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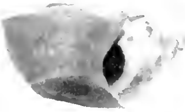
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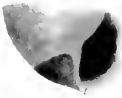
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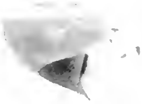
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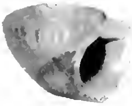
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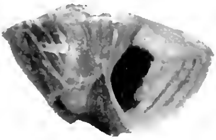
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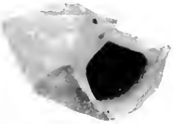
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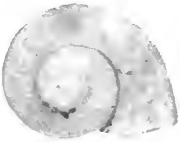
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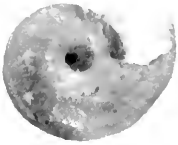
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PLATE 114

PLATE 115

Shells of Planorbidae

1. *Helisoma caribaeum* (Orb.). Jocolo, Guatemala. Immature. B3869.

2–4. *Helisoma caloderma* (Pilsbry). Esmeralda, Guatemala. Cotypes. U.I., Z28577.

5–7. *Helisoma eyerdami* Clench and Aguayo. Lake Miragoane, 2 miles southeast of Miragoane, Haiti. Paratypes. M.C.Z., 83888.

8, 9. *Carinifex jacksonensis* J. Henderson. Jackson's Lake, Wyoming. From type lot. B3925.

10–13. *Carinifex jacksonensis* J. Henderson. Jackson's Lake, Wyoming. From type lot. U.S.N.M., 510045.

14. *Parapholyx klamathensis* F. C. Baker. East side Upper Klamath Lake, 13 miles north of Klamath Falls, Oregon. Holotype. U.S.N.M., 406024.

15–17. *Parapholyx klamathensis* F. C. Baker. Same locality as above. Paratypes. U.S.N.M., 406024.

18. *Parapholyx klamathensis* F. C. Baker. Same locality as above. From type lot. U.S.N.M., 406024.

19. *Parapholyx klamathensis* F. C. Baker. Same locality as above. From type lot; slightly costate. U.S.N.M., 406024.

20. *Parapholyx klamathensis* F. C. Baker. Same locality as above. From type lot; with diagonal grooves. U.S.N.M., 406024.

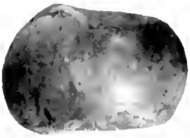
21–23. *Parapholyx klamathensis* F. C. Baker. Klamath Falls, Oregon. Small form. No. 23, costate. U.S.N.M., 219748.

24–26. *Parapholyx effusa costata* (Hemphill). Dalles of the Columbia River, Oregon. Type locality. U.S.N.M., 47520.

27. *Parapholyx effusa dalli* F. C. Baker. Klamath Falls, Oregon. Holotype. U.S.N.M., 219747.

28–30. *Parapholyx effusa dalli* F. C. Baker. Klamath Falls, Oregon. Paratypes. U.S.N.M., 219747.

Figures 1-7. 24-30 are enlarged about four diameters;
figs. 8-23 are enlarged about two diameters.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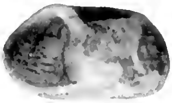
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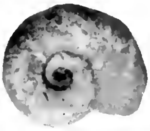
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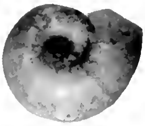
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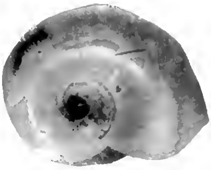
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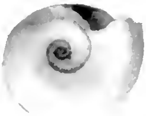
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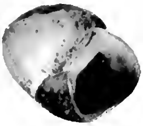
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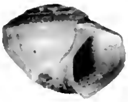
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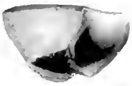
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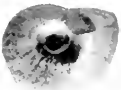
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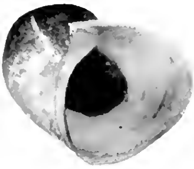
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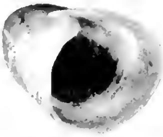
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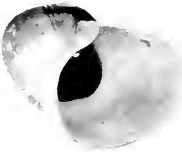
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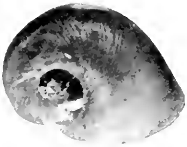
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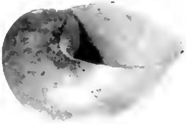
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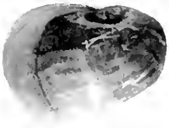
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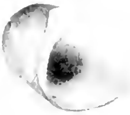
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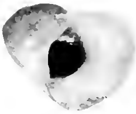
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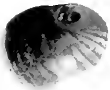
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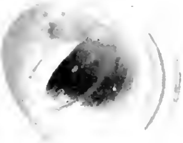
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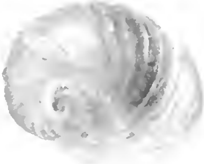
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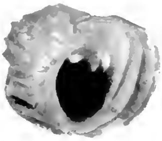
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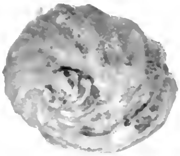
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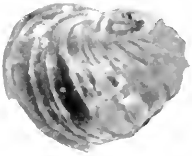
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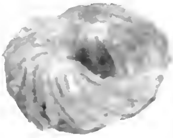
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PLATE 115

PLATE 116

Shells of Planorbidae

1, 2. *Parapholyx effusa* (Lea). Sacramento River, California. Type locality. Probably type lot. U.S.N.M., 121167.

3. *Parapholyx effusa* (Lea). Sacramento River, California. Type locality. U.S.N.M., 121133.

4–6. *Parapholyx effusa* (Lea). Oregon City, Oregon. U.S.N.M., 520085.

7, 8. *Parapholyx effusa neritoides* (Hemphill). Dalles of the Columbia River, Oregon. Type locality. U.S.N.M., 36615.

9–11. *Parapholyx effusa neritoides* (Hemphill). Dalles of the Columbia River, Oregon. Type locality. U.S.N.M., 37518.

12, 13. *Parapholyx effusa costata* (Hemphill). Dalles of the Columbia River, Oregon. Smooth form. U.S.N.M., 47519.

14. *Parapholyx effusa costata* (Hemphill). Dalles of the Columbia River, Oregon. Smooth form. U.S.N.M., 36617.

15–17. *Parapholyx effusa diagonalis* J. Henderson. Crater Lake, Oregon. Type locality. B3926.

18. *Parapholyx solida* (Dall). White Pine, Nevada. Lectotype. U.S.N.M., 56409.

19, 20. *Parapholyx solida* (Dall). White Pine, Nevada. Paratypes. U.S.N.M., 56409.

21. *Parapholyx solida* (Dall). White Pine, Nevada. U.S.N.M., 75438.

22, 25, 26. *Parapholyx solida* (Dall). White Pine, Nevada. U.S.N.M., 24839.

23, 24. *Parapholyx solida* (Dall). White Pine, Nevada. 24, slightly costate. U.S.N.M., 56410.

27–30. *Parapholyx mailliardi* Hanna. Eagle Lake, California. Type locality. U.S.N.M., 47652.

All figures are enlarged about three diameters

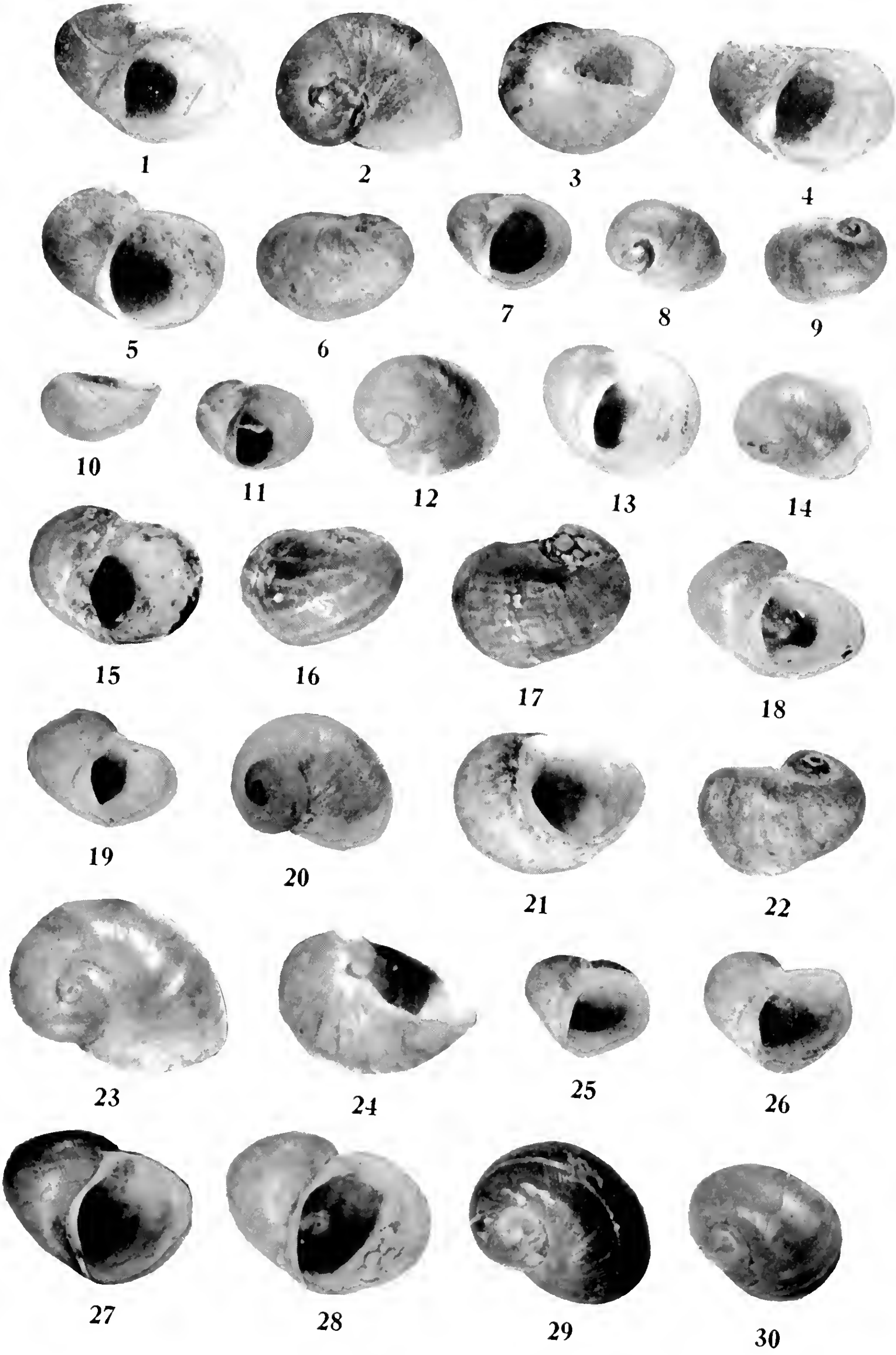
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PLATE 116

PLATE 117

Shells of Planorbidae

1–6. *Parapholyx pusilla* F. C. Baker. Six miles west of Pyramid Lake, Nevada. Figure 1, holotype; 2-5, paratypes; 6, costate specimen. U.S.N.M., 308925.

7–14. *Parapholyx nevadensis* J. Henderson. Pyramid Lake, Nevada. U.S.N.M., 75440.

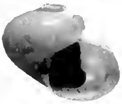
15. *Parapholyx nevadensis* J. Henderson. Pyramid Lake, Nevada. Scalariform specimen. U.S.N.M., 126765.

16. *Parapholyx nevadensis* J. Henderson. Pyramid Lake, Nevada. U.S.N.M., 75439.

17–26. *Parapholyx nevadensis* J. Henderson. Pyramid Lake, Nevada. Variation in form, neritoid to bulimoid. U.S.N.M., 63493.

27–30. *Parapholyx mailliardi* Hanna. Eagle Lake, California. From type lot. C.A.S., 23040.

All figures are enlarged about 3½ diameters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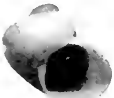
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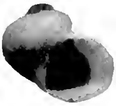
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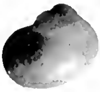
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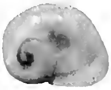
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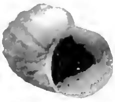
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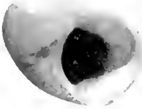
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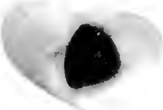
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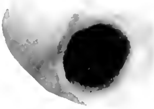
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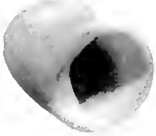
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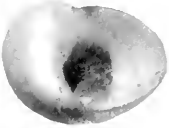
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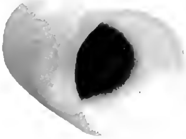
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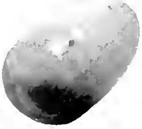
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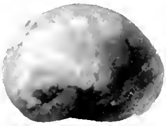
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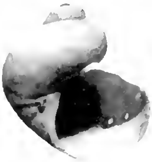
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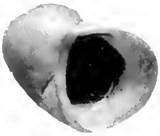
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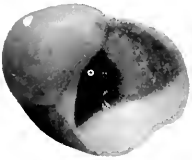
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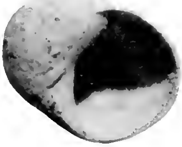
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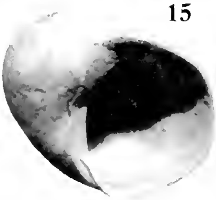
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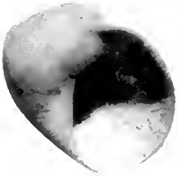
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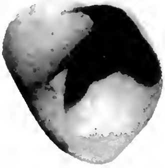
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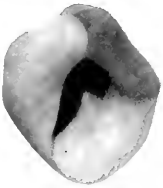
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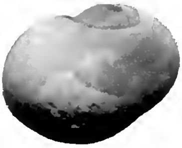
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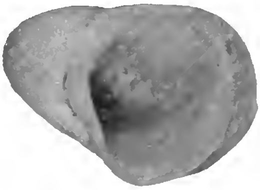
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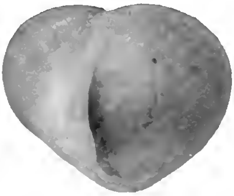
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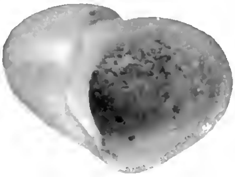
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PLATE 117

PLATE 118

Shells of Planorbidae

1. *Planorbula armigera* (Say). East Nebraska. U.S.N.M., 526054.
2. *Planorbula armigera palustris* F. C. Baker. Mason City, Iowa. U.S.N.M., 527656.
3. *Planorbula crassilabris* (Walker). Douglas Lake, Michigan. U.S.N.M., 251213.
4. *Planorbula armigera indianensis* F. C. Baker. Mt. Vernon, Indiana. U.I., Z2891.
5. *Planorbula jenksii* (H. F. Carpenter). Nayat, Rhode Island. B1195.
6. *Planorbula smithi* F. C. Baker. Stevenson, Alabama. U.S.N.M., 321196.
7. *Planorbula wheatleyi* (Lea). Boligee, Alabama. B1194.
8. *Planorbula campestris* (Dawson). High Bluff, Manitoba. U.S.N.M., 63393.

Figures 1-8 show the folds within the aperture of each species

9. *Planorbula armigera* (Say). East Nebraska. U.S.N.M., 526054.
10. *Planorbula jenksii* (H. F. Carpenter). Medford, Massachusetts. U.S.N.M., 41411.
11. *Planorbula smithi* F. C. Baker. Stevenson, Alabama. U.S.N.M., 321196.
12. *Planorbula smithi* F. C. Baker. Stevenson, Alabama. Specimen with double parietal lamella. U.S.N.M., 321196.

Figures 9-12 show the form of the parietal lamella in three species

13–15. *Planorbula armigera* (Say). East Nebraska. U.S.N.M., 526054.
16. *Planorbula armigera* variety? Camp Colfax, La Porte Co., Indiana. U.I., Z27094a.
17–19. *Planorbula armigera* variety? Camp Colfax, Indiana. U.I., Z27094b.
20–22. *Planorbula crassilabris* (Walker). Hamtramck, Wayne Co., Michigan. Type locality. B1200.
23-25. *Planorbula crassilabris* (Walker). Carr's Slough, Brookston, White Co., Indiana. U.I., Z27086.
26. *Planorbula armigera* variety? Big slough near Mason City, Iowa. Pathologic. U.S.N.M., 527656.
27–30. *Planorbula jenksii* (H. F. Carpenter). Nayat, Rhode Island. B1195.
31. *Planorbula armigera* (Say). East Nebraska. U.S.N.M., 526054.
32. *Planorbula crassilabris* (Walker). Brookston, Indiana. U.I., Z27086.
33. *Planorbula wheatleyi* (Lea). Boligee, Alabama. B1194.

Figures 31-33 show condition of crest behind aperture

All figures are enlarged about four diameters

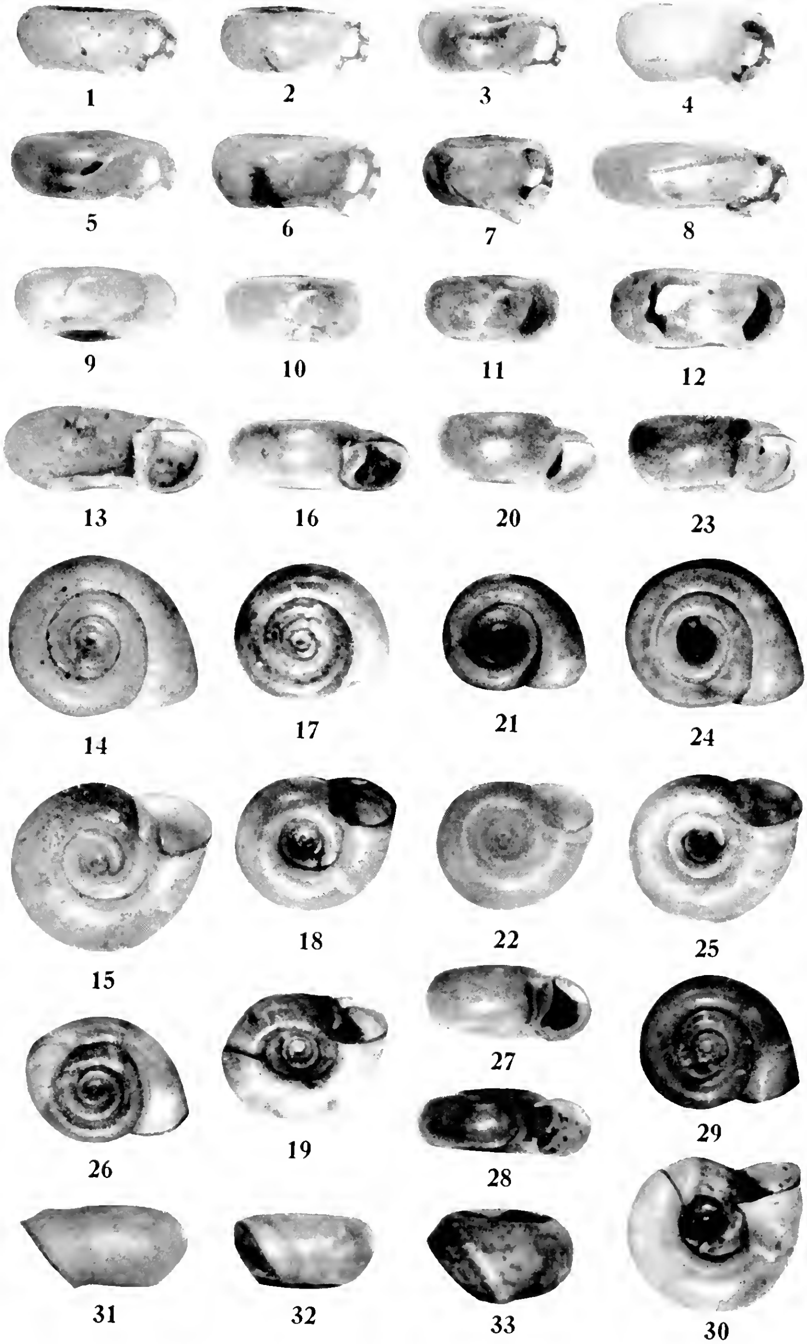
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PLATE 118

PLATE 119

Shells of Planorbidae

1-3. *Planorbula armigera indianensis* F. C. Baker. Uniontown Road, 2 miles southwest of Mt. Vernon, Indiana. 1, holotype; 2, 3, paratypes. U.I., P2833.

4-6. *Planorbula jenksii* (H. F. Carpenter). Medford, Massachusetts. U.S.N.M., 41411.

7, 8. *Planorbula wheatleyi* (Lea). Catoma, Montgomery Co., Alabama. Type. U.S.N.M., 29292.

9. *Planorbula wheatleyi* (Lea). Catoma Creek, Montgomery Co., Alabama. U.S.N.M., 120929.

10. *Planorbula smithi* F. C. Baker. Stevenson, Alabama. Holotype. U.S.N.M., 321196.

11, 12. *Planorbula smithi* F. C. Baker. Stevenson, Alabama. Paratypes. U.S.N.M., 321196.

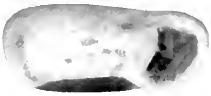
13. *Planorbula christyi* (Dall) (= *campestris* Dawson). High Bluff, Manitoba. Figured type, Alaska Moll., plate ii, figs. 10, 11. U.S.N.M., 63393.

14, 15. *Planorbula christyi* (Dall). High Bluff, Manitoba. Paratypes. U.S.N.M., 63393.

16-21. *Helisoma columbiense* F. C. Baker. Lake La Hache, Caribou Dist., British Columbia. 16, holotype; 17-21, paratypes. M.C.Z., 93710.

22-25. *Helisoma caribaeum cubense* F. C. Baker. Zapata Swamp, Cuba. Marl between layers of peat. 22, holotype; 23-25, paratypes. U.S.N.M., 404719.

Figures 1-15 are enlarged about 3½ diameters; figs. 16-25 are enlarged about 1¾ diameters.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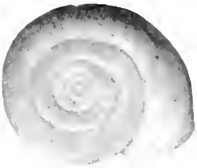
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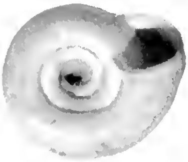
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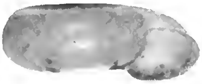
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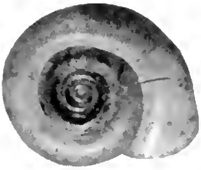
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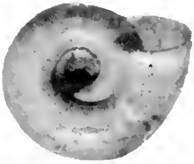
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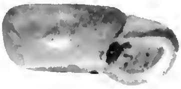
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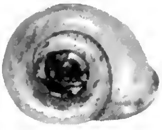
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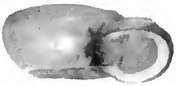
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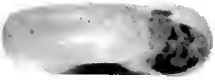
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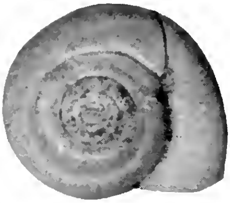
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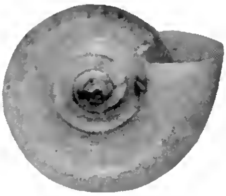
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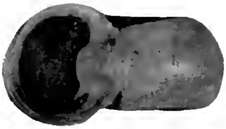
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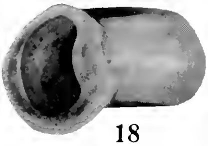
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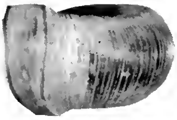
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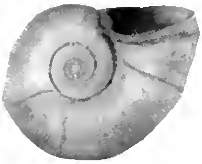
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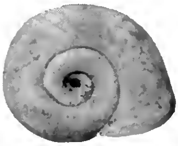
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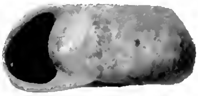
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PLATE 119

PLATE 120

Shells of Planorbidae

1–10. *Menetus opercularis* (Gould). Mountain Lake, San Francisco, California. U.S.N.M., 47627.

11, 12. *Menetus cooperi* F. C. Baker (= *planulatus* Cooper). Whidby's Island, Puget Sound, Washington. Type locality. U.S.N.M., 152185.

13. *Menetus cooperi* F. C. Baker. Whidby's Island, Puget Sound, Washington. Holotype of *M. planulatus*. Binney's fig. 209 (No. 9118). U.S.N.M., 29280a.

14. *Menetus cooperi* F. C. Baker. Whidby's Island, Puget Sound, Washington. Cotype of *M. planulatus*. U.S.N.M., 29280.

15–18. *Menetus cooperi* F. C. Baker. Lake Union, Washington. U.S.N.M., 253617.

19–21. *Menetus cooperi callioglyptus* (Vanatta). Freeport, Washington. Cotypes. Hemphill coll. U.S.N.M., 47630.

22. *Menetus cooperi* F. C. Baker. Olga, Washington. U.S.N.M., 216936.

23–26. *Menetus cooperi multilineatus* (Vanatta). Pass Lake, Fidalgo Island, Washington. U.S.N.M., 346742.

27. *Menetus cooperi* F. C. Baker. Bellingham, Washington. Very flat spire. U.S.N.M., 525100.

28. *Menetus cooperi* F. C. Baker. Lake Washington, Seattle, Washington. U.S.N.M., 169070.

29–31. *Menetus cooperi multilineatus* (Vanatta). Salem, Oregon. Type locality. B3927.

32. *Parapholyx solida optima* (Pilsbry). Lake Bigler, Nevada. Paratype. A.N.S.P., 125363.

Figures 1-31 are enlarged about four diameters; fig. 32 is enlarged two diameters.

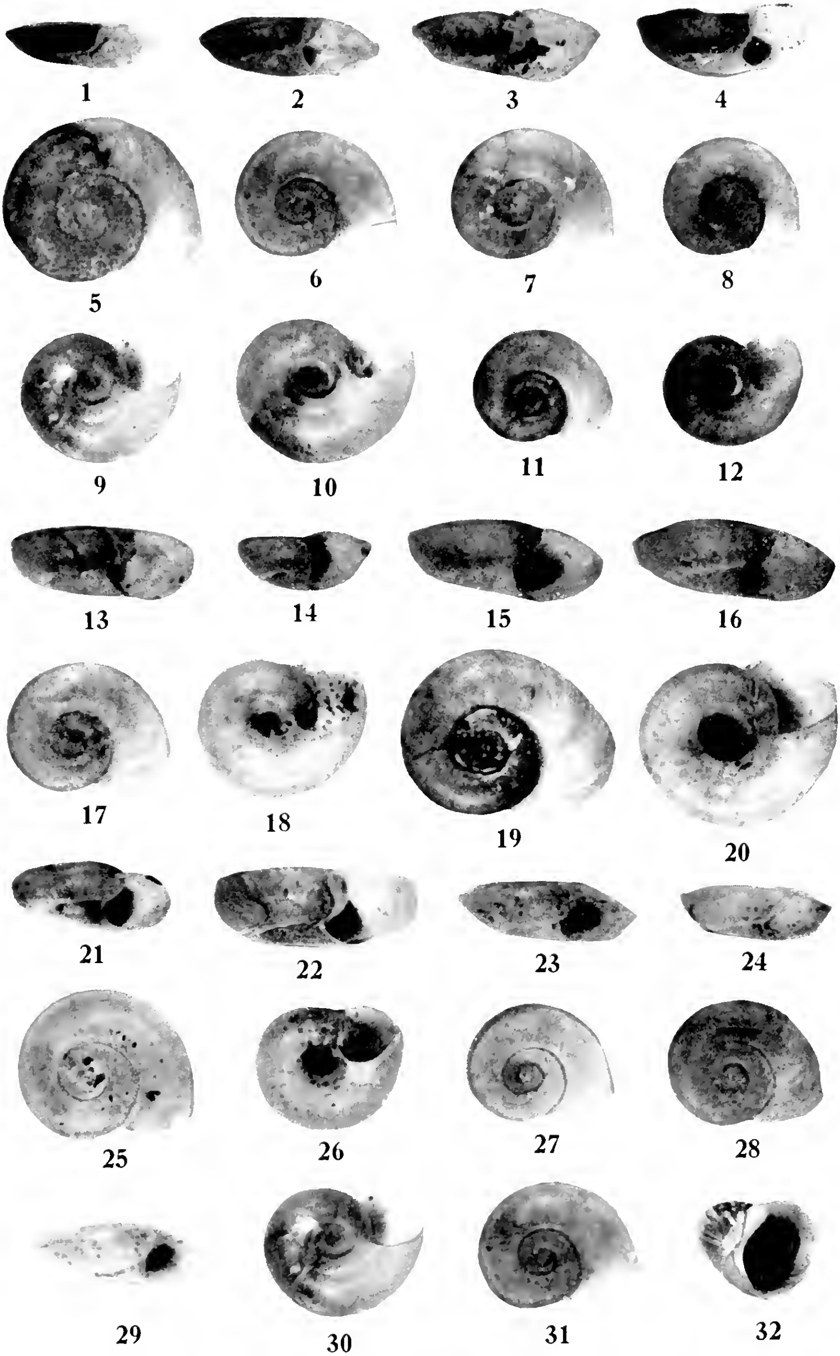
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PLATE 120

PLATE 121

Shells of Planorbidae

1–5. *Menetus centervillensis* (Tryon). Noyo, California. U.S.N.M., 47639.

6–8. *Menetus centervillensis* (Tryon). Bear Lake, San Bernardino Mts., California. U.S.N.M., 175089.

9, 10. *Menetus labiatus* F. C. Baker. Terminal Island, Los Angeles Co., California. Paratypes. U.S.N.M., 190021.

11. *Menetus labiatus* F. C. Baker. Terminal Island, Los Angeles Co., California. Holotype. U.S.N.M., 190021.

12–18. *Menetus portlandensis* F. C. Baker. Tanner Creek, Portland, Oregon. 12, holotype; 13-18, paratypes. U.S.N.M., 184182.

19, 20. *Menetus cooperi crassilabris* F. C. Baker. Seattle, Washington. 20, holotype; 19, paratype. U.S.N.M., 214590.

21. *Menetus cooperi crassilabris* F. C. Baker. Portland, Oregon. U.S.N.M., 99302.

22, 25. *Menetus dilatatus* (Gould). Hingham, Massachusetts. Lea coll. Type locality. U.S.N.M., 121002.

23, 27, 28. *Menetus dilatatus buchanensis* (Lea). Cincinnati, Ohio. Lea coll. Types. U.S.N.M., 120948.

24, 30. *Menetus dilatatus buchanensis* (Lea). Half mile west of Luray, Virginia. Variation toward *dilatatus*. U.S.N.M., 473961.

26. *Menetus dilatatus* (Gould). Medford, Massachusetts. U.S.N.M., 41725.

29. *Menetus dilatatus buchanensis* (Lea). Near Luray, Virginia. Pathologic. U.S.N.M., 473961.

31. *Menetus dilatatus buchanensis* (Lea). Mt. Pleasant, District of Columbia. U.S.N.M., 227832.

32, 35, 36. *Menetus dilatatus pennsylvanicus* Pilsbry. Three and one-half miles southwest of Cambridge, Maryland. B168.

33. *Menetus dilatatus buchanensis* (Lea). Harbert, Berrien Co., Michigan. U.M., 88030.

34. *Menetus alabamensis* (Pilsbry). Woodville, Jackson Co., Alabama. Type locality. U.M., 85913.

37. *Menetus alabamensis* (Pilsbry). Woodville, Alabama. Part of type lot. B3928.

38. *Menetus alabamensis* (Pilsbry). Woodville, Alabama. Type locality. U.M., 85913.

39. *Menetus alabamensis* (Pilsbry). Woodville, Alabama. Paratype. U.S.N.M., 129005.

40, 41. *Menetus alabamensis avus* (Pilsbry). Hammock near St. Johns River, Florida. U.S.N.M., 101698.

42–44. *Menetus brogniartianus* (Lea). Cincinnati, Ohio. Lea coll. 42, lectotype; 43-44, paratypes. U.S.N.M., 120981.

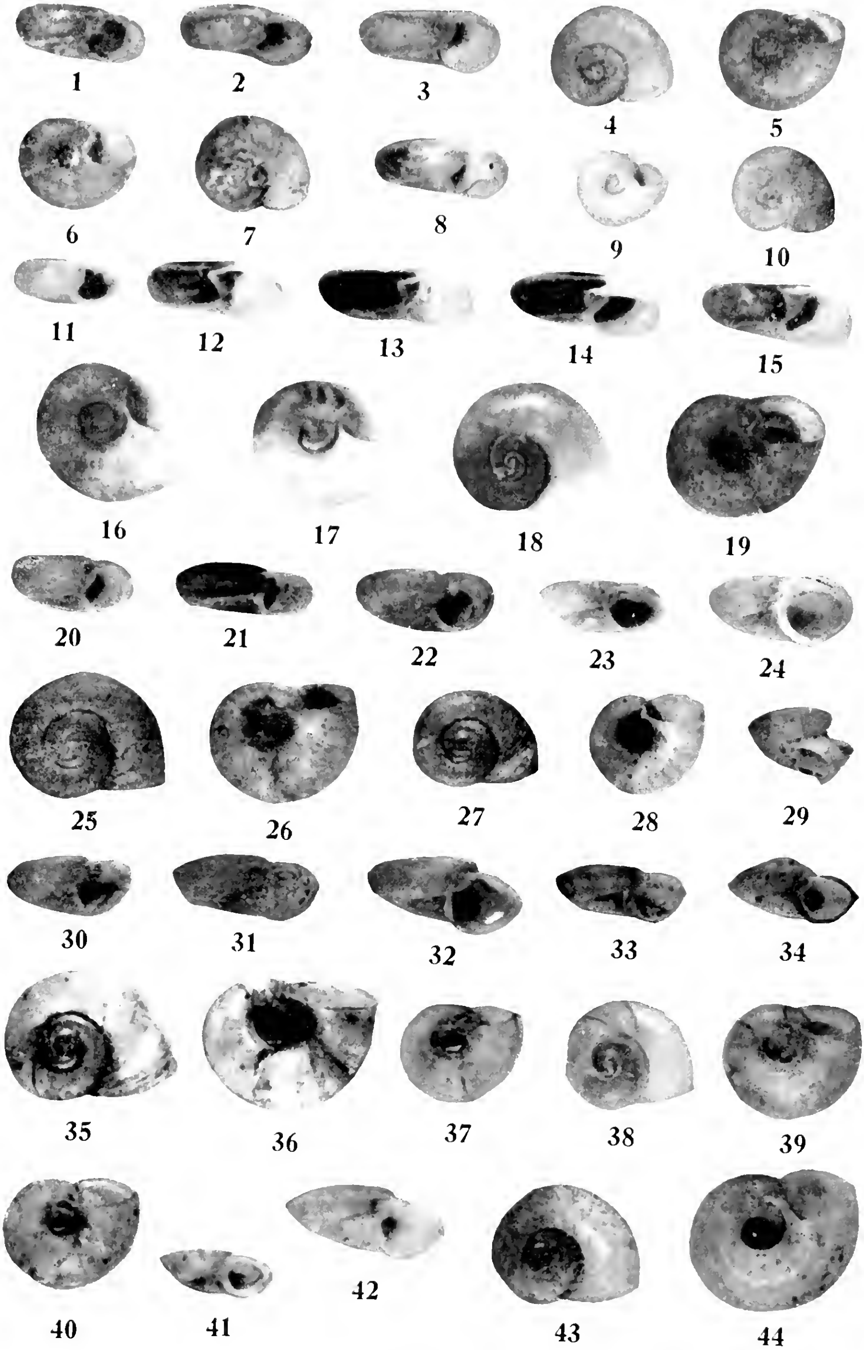
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PLATE 121

PLATE 122

Shells of Planorbidae

1, 2. *Menetus cooperi* F. C. Baker. Blue Lake, Grand Coulee, Washington. B3935.

3–6. *Menetus cooperi planospirus* F. C. Baker. Orcas Island, Puget Sound, Washington. Figure 5, holotype; 3, 4, 6, paratypes. Figure 5 shows well the very flat spire. M.C.Z., 31583.

7. *Menetus cooperi* F. C. Baker. Two miles north of Petaluma, California. U.S.N.M., 531171.

8. *Menetus cooperi callioglyptus* (Vanatta). Quamichan Lake, British Columbia. B2030.

9–12. *Menetus cooperi multilineatus* (Vanatta). Salem, Oregon. Type locality. B3929.

13. *Menetus cooperi crassilabris* F. C. Baker. Colma, San Mateo Co., California. U.S.N.M., 525095.

14. *Promenetus exacuous* (Say). Chimney Point, Hospital Creek, Lake Champlain, Vermont. U.S.N.M., 336591.

15–18. *Promenetus exacuous* (Say). New York, New York. B3930.

19. *Promenetus exacuous* (Say). West Lake Okoboji, Iowa. U.S.N.M., 475975.

20–22. *Promenetus exacuous megas* (Dall). Birtle, Manitoba. Types. U.S.N.M., 63391.

23-25. *Menetus coloradoensis* F. C. Baker. Swamp, head of Eldora Lake, near Eldora, Colorado. Figure 25, holotype; 23, 24, paratypes. U.C., 10114.

26–28. *Promenetus exacuous* variety? Gresham Lake, between Gresham and Ward, Boulder Co., Colorado. U.C., 526.

All figures are enlarged about four diameters

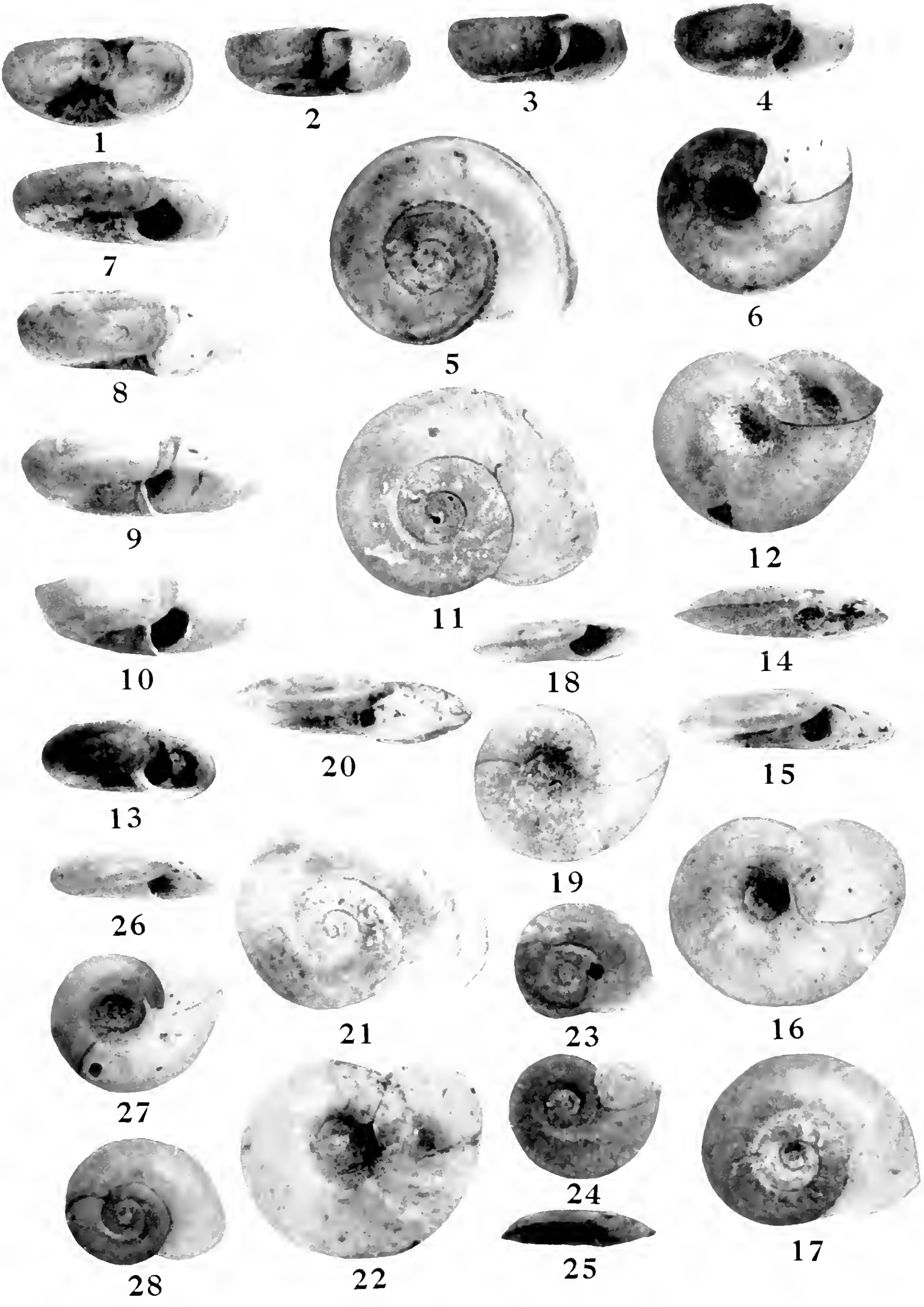

PLATE 122

PLATE 123

Shells of Planorbidae

1. *Menetus alabamensis avus* (Pilsbry). South end Lake Panasoffkee, Sumter Co., Florida. U.S.N.M., 211002.

2–10. *Parapholyx klamathensis sinitsini* F. C. Baker. Bercley Spring, 14 miles north of Klamath Falls, Oregon. Figure 2, holotype; 3, 4, paratypes; U.S.N.M., 531029. Figures 5-10, locotypes; U.S.N.M., 531064.

11. *Menetus sampsoni* (Ancey). Pond in Flat Creek bottom, near Sedalia, Missouri. Part of type lot. B166.

12, 13. *Menetus alabamensis* (Pilsbry). Temporary pond half mile south of Fountain, Illinois. B3923.

14–16. *Menetus sampsoni* (Ancey). Pond in Flat Creek bottom, near Sedalia, Missouri. Type locality. M.C.Z., 4900.

17–19. *Promenetus hudsonicus* (Pilsbry). Four miles southeast of Canandaigua, in beach pond, east side Canandaigua Lake, New York. B2904.

20–22. *Menetus dilatatus floridensis* F. C. Baker. St. Johns River, Palatka, Florida. Figure 20, holotype; 21, 22, paratypes. U.S.N.M., 37585.

23–25. *Menetus uliginosus* (Vanatta). Devonshire Swamp, near Hamilton, Bermuda. M.C.Z., 108996.

26. *Menetus cooperi crassilabris* F. C. Baker. Colma, San Mateo Co., California. U.S.N.M., 525095.

27, 28. *Menetus uliginosus* (Vanatta). Proc. Phil. Acad. Sci., Vol. 62, p. 669, fig. 2. Pembroke Marsh, near Hamilton, Bermuda. Types.

29, 30. *Promenetus imus* (Vanatta). Proc. Phil. Acad. Sci., Vol. 62, p. 669, fig. 3. Bermuda. Types.

31–33. *Menetus sampsoni* (Ancey). Meredosia, Illinois. B2018.

34, 35. *Promenetus umbilicatellus* (Ckll.). Plummers Point, Lake Butte des Morts, Wisconsin. B2101.

36. *Promenetus umbilicatellus* (Ckll.). Upper Dells, Kilbourn, Wisconsin. B2102.

37–39. *Promenetus rubellus* (Sterki). Ditch south of New Philadelphia, Ohio. Cotypes. B160.

Figures 2 to 10 are enlarged about two diameters; figs. 1, 11 to 26, 31 to 33, 37 to 39, six diameters; figs. 34 to 36, four diameters; figs. 27 to 30, one-half size of original figures, but enlargement of shells is about five diameters.

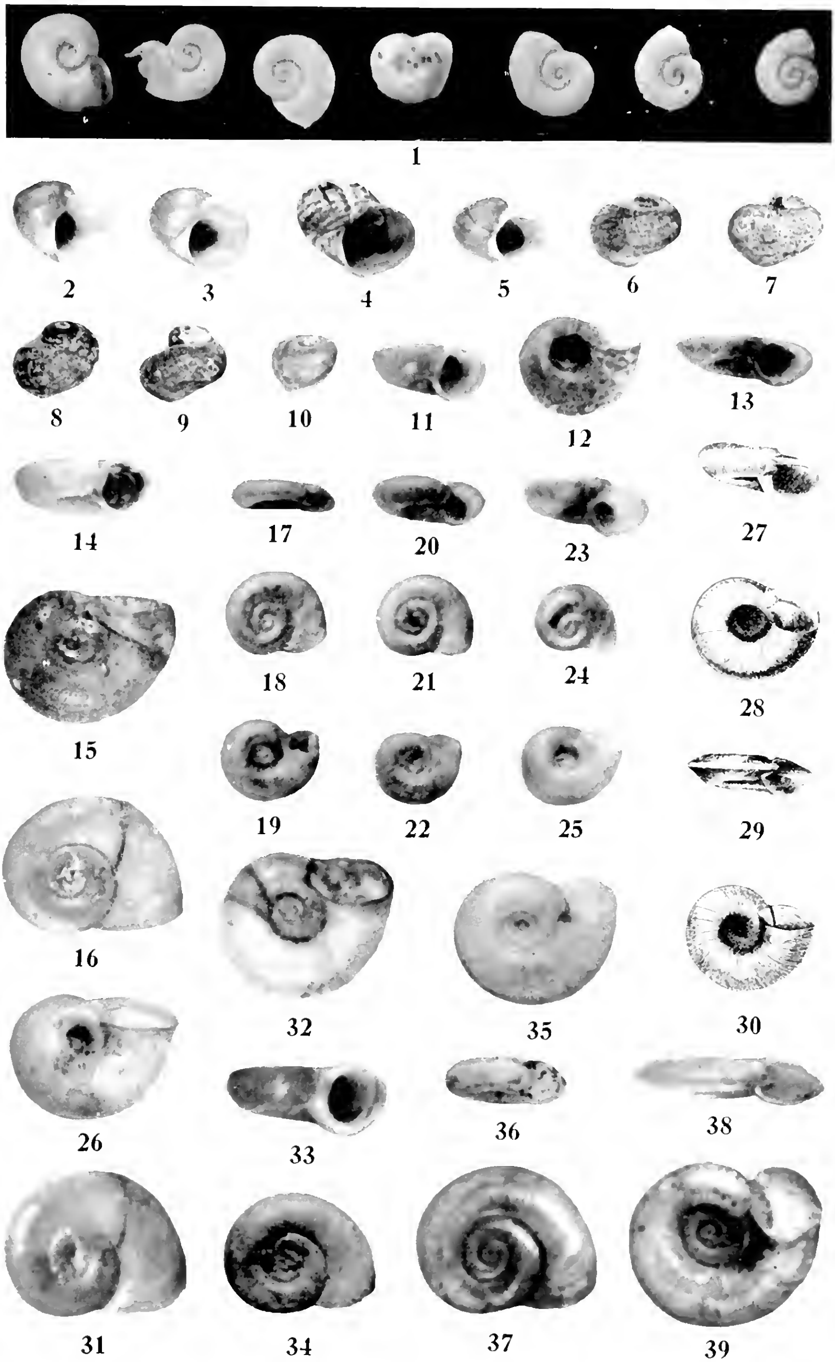
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PLATE 123

PLATE 124

Shells of Planorbidae

1, 2. *Drepanotrema anatinum* (Orb.). Para, Brazil. U.S.N.M., 348535.

3. *Drepanotrema anatinum* (Orb.). Para, Brazil. M.C.Z., 72832.

4–6. *Drepanotrema anatinum* (Orb.). Lake Miragoane, two miles SE of Miragoane, Haiti. M.C.Z., 83729.

7. *Drepanotrema anatinum* (Orb.). Jamaica. (= *Planorbis haldemani* C. B. Adams.) Lea Collection, probably part of original lot of *haldemani*. U.S.N.M., 94758.

8–10. *Drepanotrema anatinum* (Orb.). Esperanza, Cuba. Type locality of *Planorbis esperanzensis* Tryon. M.C.Z., 85875.

11–13. *Drepanotrema anatinum* (Orb.). Baron Hills, Trelawny, Jamaica. (= *Planorbis haldemani* C. B. Adams.) M.C.Z., 65839.

14–20. *Drepanotrema parapseide* (Orb.). Buena Vista, Santa Cruz, Bolivia. U.M., 87196.

21–28. *Drepanotrema ahenum* H. B. Baker. Tuccas, Venezuela. Type lot, showing age variation in shell. U.M., 87164.

29, 31, 32. *Drepanotrema lucidum* (Pfr.). Juninaguas, Dept. Loreto, Peru. U.S.N.M., 381510.

30. *Drepanotrema anatinum* (Orb.). Juninaguas, Dept. Loreto, Peru. U.S.N.M., with 381510.

All figures are enlarged about four diameters

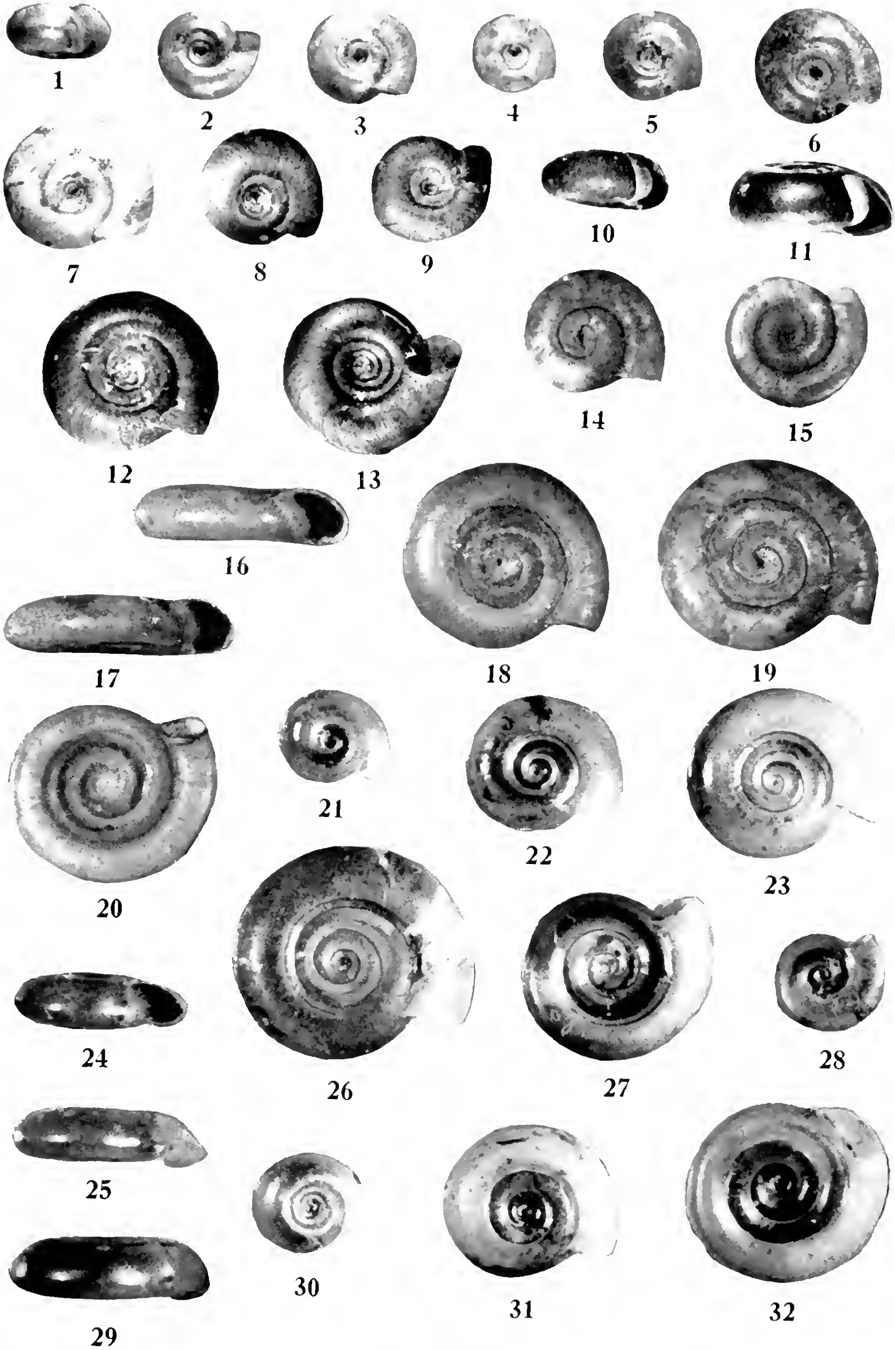
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PLATE 124

PLATE 125

Shells of Planorbidae

1, 4, 6, 7. *Drepanotrema lucidum* (Pfeiffer). Laguna del Bili, Alacranes Mts., Cuba. M.C.Z., 129991.

2, 3. *Drepanotrema lucidum* (Pfeiffer). St. Louis, Dept. du Sud, Haiti. Immature shells. U.S.N.M., 402809.

5. *Drepanotrema lucidum* (Pfeiffer). Maggoty, St. Elizabeth, Jamaica. U.S.N.M., 376088.

8. *Drepanotrema lucidum* (Pfeiffer). Jamaica. (= *Planorbis redfieldi* C. B. Adams.) Lea Collection. Possibly part of original lot of *redfieldi*. U.S.N.M., 94757.

9, 10. *Drepanotrema lucidum* (Pfeiffer). Jealousy Stream, St. Croix. U.S.N.M., 423966.

11–17. *Drepanotrema lucidum* (Pfeiffer). Large variety with closely coiled whorls. Half mile NE of Orange Creek, Cat Island, Bahamas. M.C.Z., 107179.

18–21. *Drepanotrema melleum* (Lutz). Rio de Janeiro, Brazil. U.S.N.M., 535918.

All figures are enlarged about four diameters


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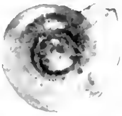
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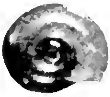
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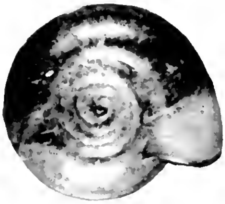
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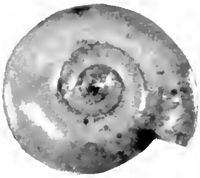
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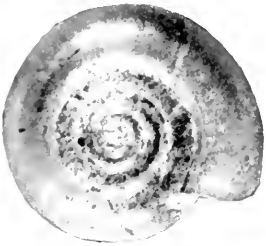
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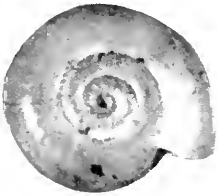
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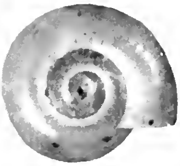
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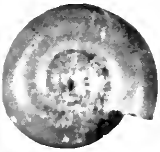
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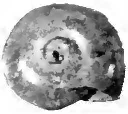
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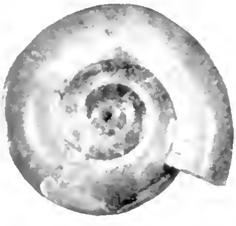
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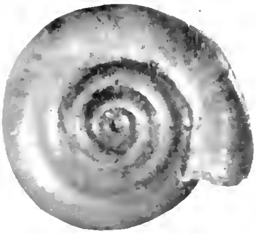
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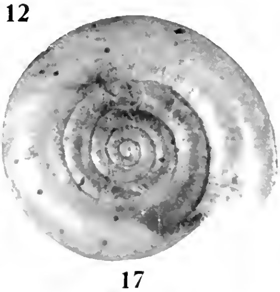
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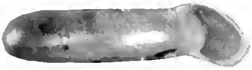
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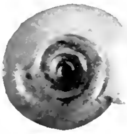
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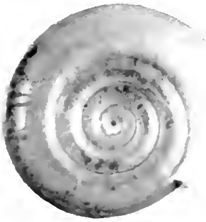
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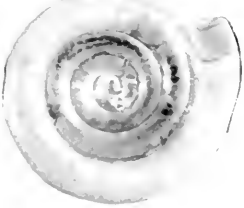
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PLATE 125

PLATE 126

Shells of Planorbidae

1–5. *Drepanotrema castaneonitens* (Pils. and Van.). Near Maldonado, Uruguay. Type locality. U.S.N.M., 151668.

6. *Drepanotrema hoffmanni* F. C. Baker. Isabela, Puerto Rico. Holotype. B3952.

7–9. *Drepanotrema hoffmanni* F. C. Baker. Isabela, Puerto Rico. Paratypes. B3953.

10–12. *Drepanotrema hoffmanni* F. C. Baker. Near San Juan, Puerto Rico. Age variation. U.S.N.M., 420573.

13. *Drepanotrema kermatoides* (Orb.). Puerto Haberton, Argentina. U.S.N.M., 362857.

14–16. *Drepanotrema kermatoides* (Orb.). Lima, Peru. Type locality. Figure 14 shows an immature specimen. U.S.N.M., 20705.

17–19. *Drepanotrema cultratum anitense* (Cooper). Laguna, Santa Rita, Lower California. U.S.N.M., 129292.

All figures are enlarged about four diameters


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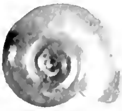
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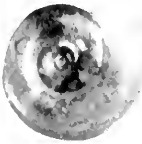
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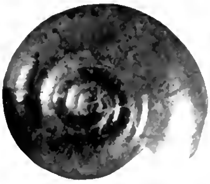
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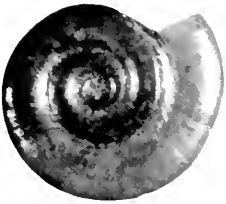
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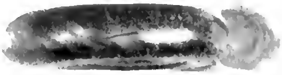
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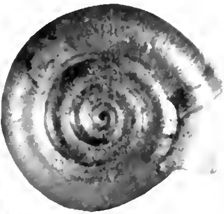
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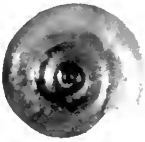
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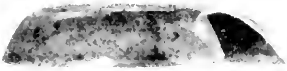
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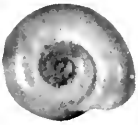
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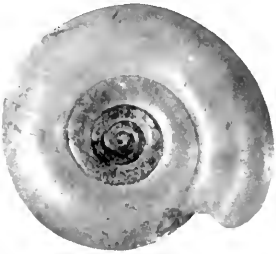
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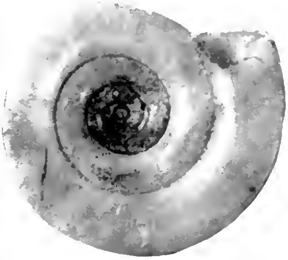
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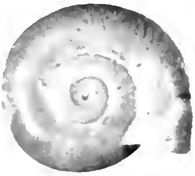
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PLATE 126

PLATE 127

Shells of Planorbidae

1-3. *Drepanotrema cimex* (Moricand). Valle de Yumuri, Matanzas, Cuba. M.C.Z., 129995.

4-6. *Drepanotrema cultratum* (Orb.). Painters Pond, Painters, Antigua. U.S.N.M., 272282.

7, 8. *Drepanotrema cimex* (Moricand). Hunts Bay, St. Andrew, Jamaica. U.S.N.M., 378054.

9-12. *Drepanotrema cultratum duenasianum* (Tristram). Pools along railway near Lake Amatitlan, Guatemala. B1258.

13-15. *Drepanotrema cimex pistiae* H. B. Baker. Rincon del Valle, near Caracas, Venezuela. U.S.N.M., 362133.

16. *Drepanotrema cimex* (Moricand). Jamaica. (= *Planorbis macnabianus* C. B. Adams.) Lea Collection, probably part of original lot. U.S.N.M., 94756.

17-19. *Drepanotrema depressissimum* (Moricand). Bahia, Brazil. Paratypes. M.C.Z., 31432.

All figures are enlarged about four diameters


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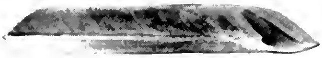
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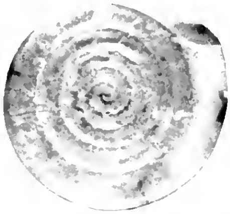
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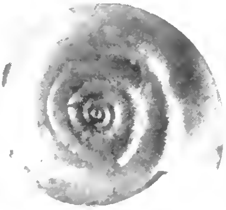
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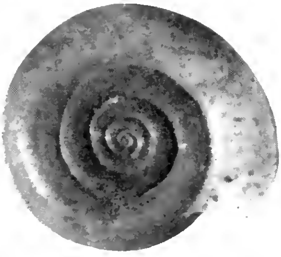
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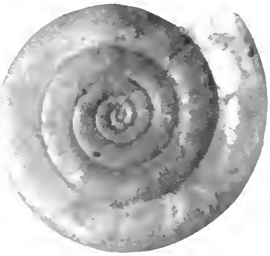
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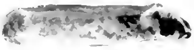
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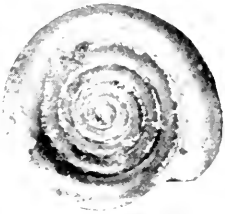
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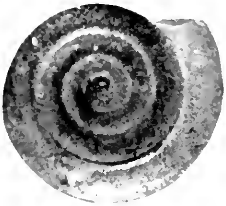
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PLATE 127

PLATE 128

Shells of Planorbidae

1, 2. *Drepanotrema cultratum panuco* Pilsbry. Tampico, Mexico. B1183.

3–5. *Drepanotrema cultratum panuco* Pilsbry. Pasture west of San Dieguito, San Luis Potosi Co., Mexico. Locotypes. B2124.

6. *Drepanotrema cultratum labrosum* Pilsbry. Brownsville, Texas. U.S.N.M., 273933.

7–10. *Drepanotrema cultratum labrosum* Pilsbry. Brownsville, Texas. Locotypes. B1192.

11–16. *Drepanotrema sumichrasti* (Crosse and Fischer). Barbour Lathrop Trail, Barro Colorado Island, Gatun Lake, Canal Zone. B3967.

17-19. *Drepanotrema cimex* (Moricand). Brazil. U.S.N.M., 121018.

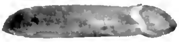
20–22. *Drepanotrema cimex* (Moricand). Anapolis, Guyoz, Brazil. M.C.Z., 65716.

23-25. *Drepanotrema peninsularis* (Cooper). (=*Drepanotrema anatinum*). Santa Anita, Lower California. U.S.N.M., 129291.

26-30. *Tropicorbis obstructus* (Morelet). Tampico, Mexico. U.I., Z28550.

31–33. *Tropicorbis obstructus* (Morelet). Lake Amatitlan, Guatemala. B2125.

Figures 1 to 30 are enlarged about five diameters; figs. 31 to 33 are enlarged about four diameters.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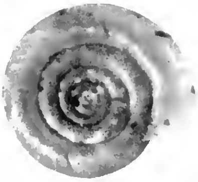
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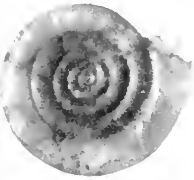
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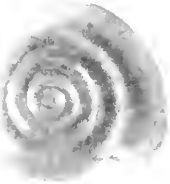
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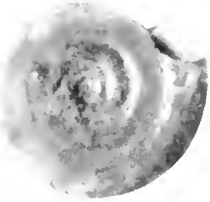
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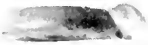
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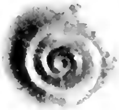
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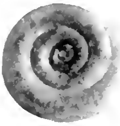
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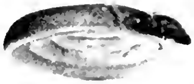
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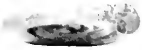
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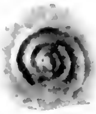
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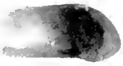
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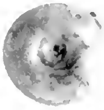
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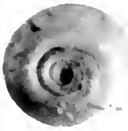
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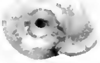
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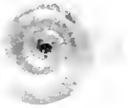
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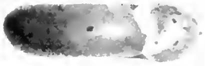
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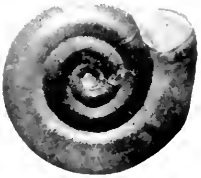
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PLATE 128

PLATE 129

Shells of Planorbidae

1–3. *Tropicorbis orbiculus* (Morelet). Near San Miguel, Cozumel Island, Quintana Roo, Mexico. M.C.Z., 75102.

4. *Tropicorbis obstructus* (Morelet). Same as above. M.C.Z., 75102.

5–7. *Tropicorbis orbiculus* (Morelet). (= *Planorbis liebmanni* Dunker). Vera Cruz, Mexico. U.S.N.M., 210881.

8, 9. *Tropicorbis obstructus* (Morelet). Same locality as above. U.S.N.M., 210881.

10–15. *Tropicorbis orbiculus* (Morelet). Chamiai Creek, below Valles, Mexico. U.I., Z28528.

16. *Tropicorbis orbiculus* (Morelet). Catanas Lake, El Abra, Mexico. B1191.

17–22. *Tropicorbis obstructus donbilli* (Tristram). Edentate. Guadalupe River, Victoria Co., Texas. U.S.N.M., 464970.

23–25. *Tropicorbis obstructus donbilli* (Tristram). Edentate. Brownsville, Texas. B1187.

26–31. *Tropicorbis orbiculus dunkeri* F. C. Baker. New name. Dry pool near Tampico, Mexico. B1184.

32–36. *Tropicorbis orbiculus dunkeri* F. C. Baker. Los Canoas, Mexico. B2113.

37–42. *Drepanotrema heteropleurus* Pilsbry and Vanatta. Lake Titicaca, Peru. Topotypes. Agassiz Expedition.

All figures are enlarged about two diameters

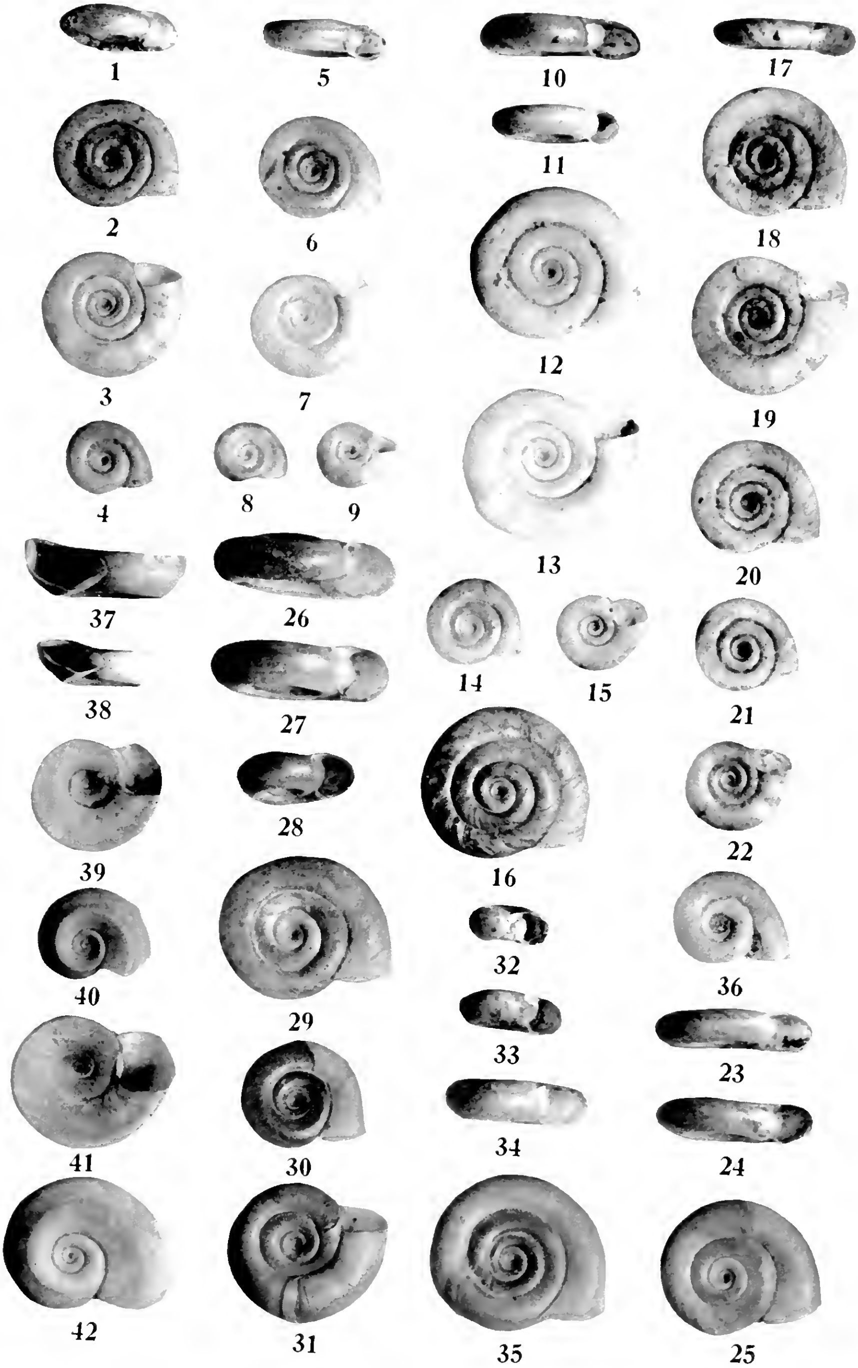
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PLATE 129

PLATE 130

Shells of Planorbidae

1–3. *Tropicorbis gracilentus* (Gould). Colorado Desert. Binney's fig. 183, p. 108. Holotype. U.S.N.M., 26477.

4–12. *Tropicorbis gracilentus* (Gould). San Marcos, Texas, in drift adjoining fish hatchery. Figure 10 shows closely coiled whorls like those of *Tropicorbis orbiculus*. B3298.

13–17. *Tropicorbis maya* (Morelet). Merida, Yucatan. M.C.Z., 59646.

18–20. *Tropicorbis havanensis* (Pfeiffer). Havana, Cuba. Type locality. U.M., 84039.

21-25. *Tropicorbis havanensis* (Pfeiffer). New Orleans, Louisiana. A small variety. B3954.

26. *Tropicorbis havanensis* (Pfeiffer). Guayos, Santa Clara Prov., Cuba. U.M., 84038.

27–28. *Tropicorbis havanensis* (Pfeiffer). New Braunfels, Texas. M.C.Z., 13622.

29–32. *Tropicorbis philippianus* (Dunker). Asuncion, Paraguay. Figure 31, loosely coiled. M.C.Z., 62490.

33, 34. *Tropicorbis philippianus* (Dunker). Esperanza de Santa Fe, Argentina. M.C.Z., 64963.

35–37. *Tropicorbis centimetralis* (Lutz). Ceará Mirim, Rio Grande do Norte, Brazil. Type locality. M.C.Z., 92825.

38–41. *Tropicorbis peregrinus* (Orbigny). Rio Grande de Sul, Brazil. M.C.Z., 75376.

All figures are enlarged about two diameters

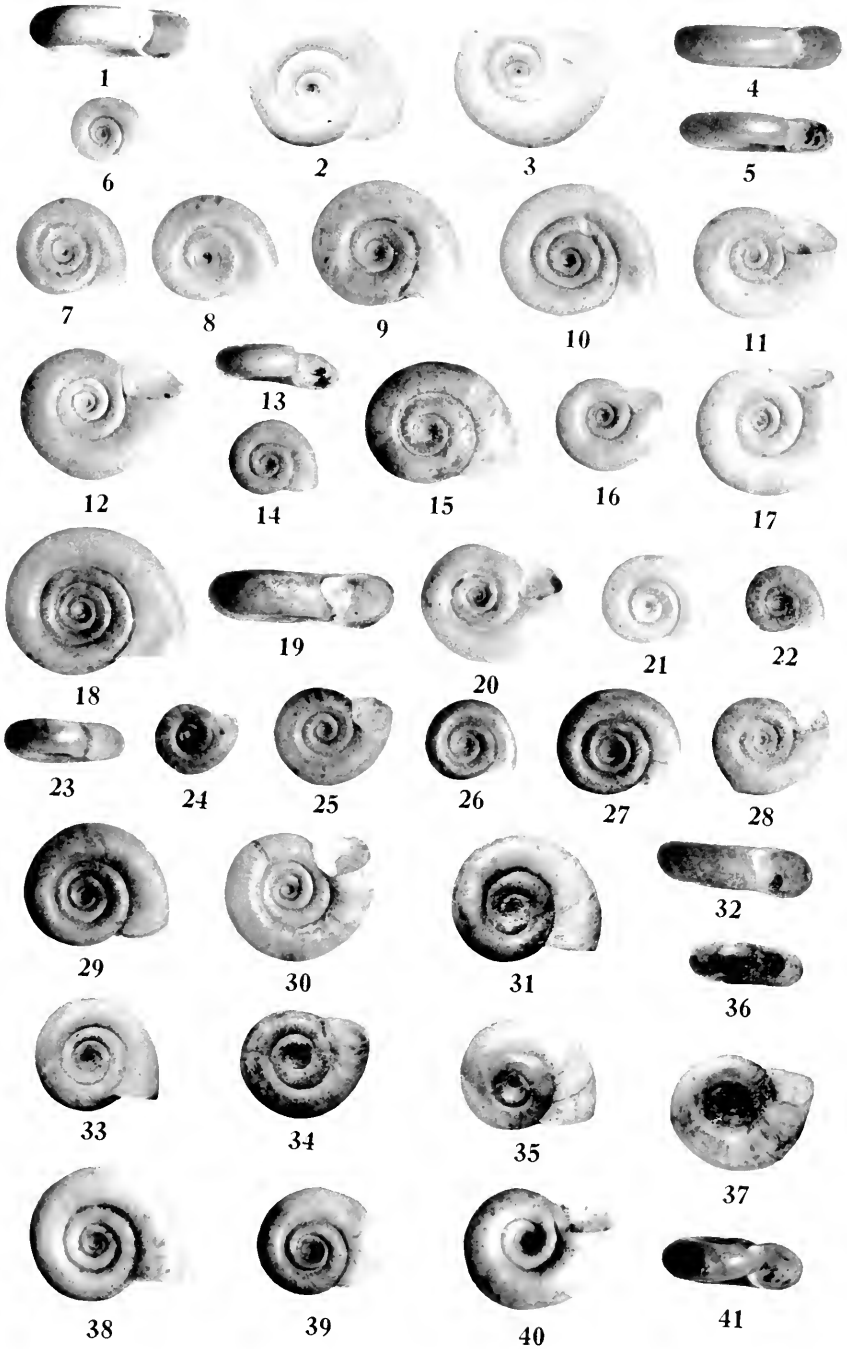
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PLATE 130

PLATE 131

Shells of Planorbidae

1–4. *Tropicorbis isthmicus* (Pilsbry). Panama City, Panama. Type locality. U.M., 88180.

5–7. *Tropicorbis isthmicus* (Pilsbry). Miraflores Lake, Panama. U.M., 88181.

8–10. *Tropicorbis decipiens* (C. B. Adams). Rockport, Jamaica. B3966.

11. *Tropicorbis decipiens* (C. B. Adams). Puerto Rico. U.I., Z40460.

12–14. *Tropicorbis chilensis* (Clessin). Valparaiso, Chile. M.C.Z., 74655.

15–24. *Tropicorbis obstructus donbilli* (Tristram). Dry pool in Tampico, Mexico. B1189.

25, 26. *Tropicorbis obstructus donbilli* (Tristram). Brownsville, Texas. B127.

27–31. *Taphius andecolus montanus* (Orbigny). Tanja (Oroya), Peru. M.C.Z., 36702.

32–35. *Taphius andecolus* (Orbigny). Puoa, Peru. U.I., Z40575.

36–40. *Taphius subpronus* (von Martens). Terrialba, Costa Rica. U.S.N.M., 162827.

Figures 1 to 35 are enlarged about two diameters; figs. 36 to 40, four diameters.

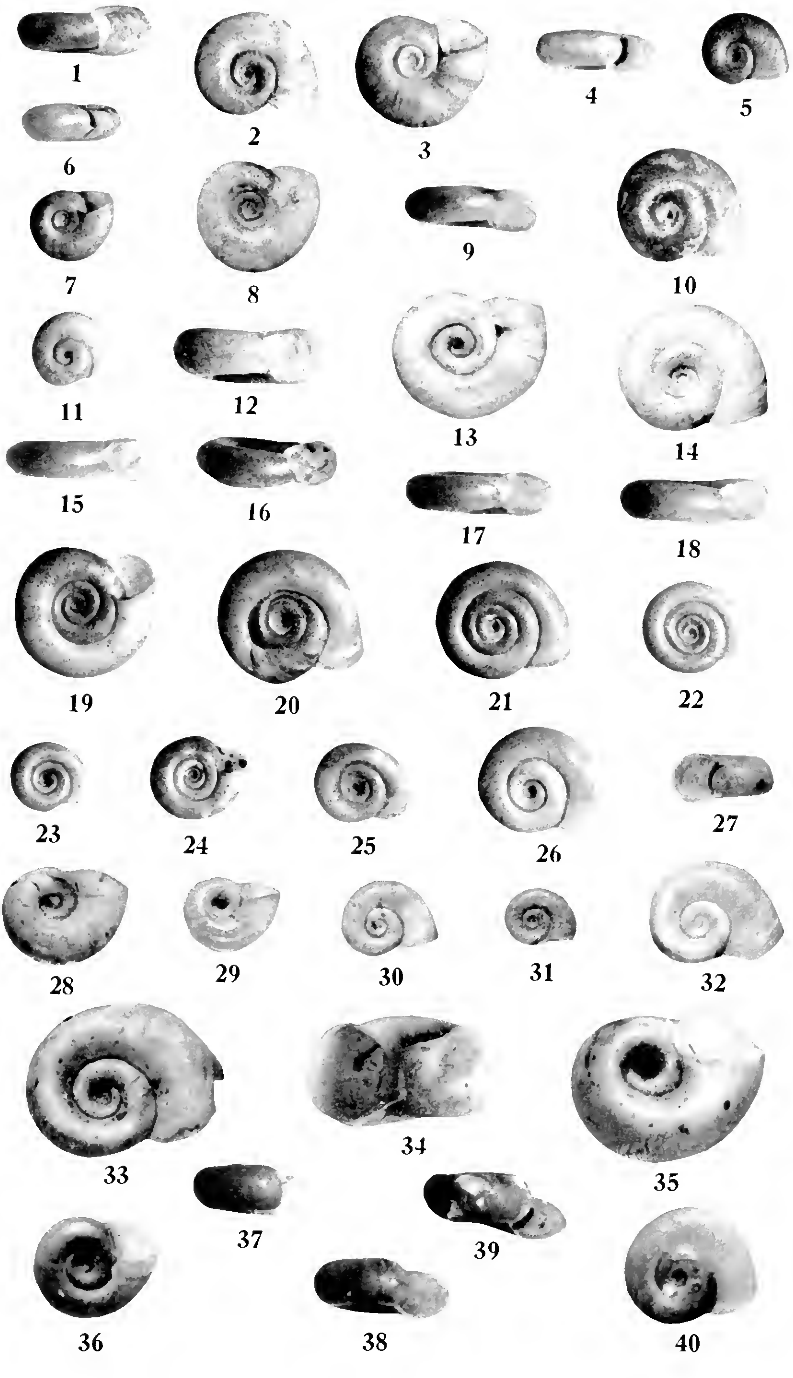
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PLATE 131

PLATE 132

Shells of Planorbidae

1–3. *Tropicorbis pallidus* (C. B. Adams). Kingston, Jamaica. U.I., Z40466.

4, 5. *Tropicorbis pallidus* (C. B. Adams). Tucaras, Venezuela. U.M., 89990.

6–9. *Tropicorbis kuhnianus* (Dunker). Bejuma, Venezuela. U.M., 89991.

10–12. *Tropicorbis stramineus* (Dunker). Venezuela. Paratypes. Ex Dunker. M.C.Z., 74654.

13, 14. *Tropicorbis stramineus* (Dunker). Lagoa Giboia, Municipio de Aquraz, Ceara, Brazil. M.C.Z., 65720.

15–21. *Tropicorbis riisei* (Dunker). Lares, Puerto Rico. B3955.

22, 23. *Tropicorbis meridaensis* (Preston). Merida, Venezuela. U.I., Z40463.

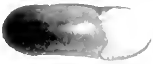
24–28. *Tropicorbis fieldi* (Tryon). Gatun, Panama Canal. Type locality. M.C.Z., 21187.

29, 30. *Tropicorbis fieldi* (Tryon). Near Granada, Nicaragua. M.C.Z., 4534.

31, 32. *Tropicorbis bourcardianus* (Preston). Mexico. U.S.N.M., 202523.

33–35. *Tropicorbis gundlachi* (Dunker) (= *stramineus*). Trinidad. U.I., Z40461.

All figures are enlarged about three diameters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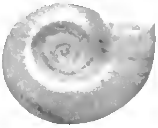
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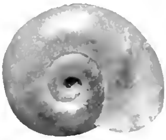
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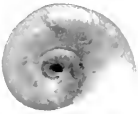
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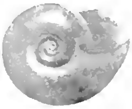
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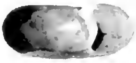
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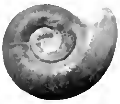
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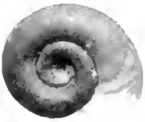
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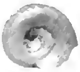
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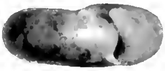
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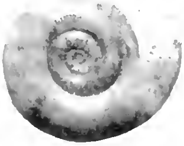
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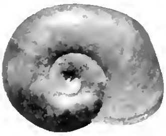
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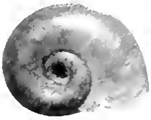
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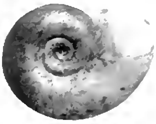
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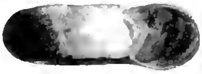
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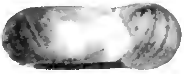
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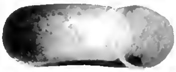
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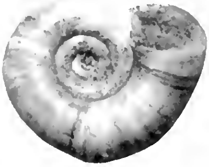
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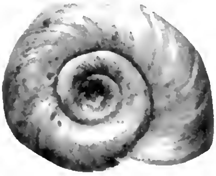
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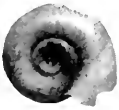
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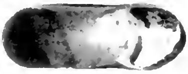
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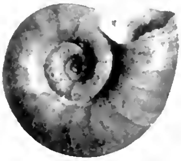
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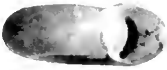
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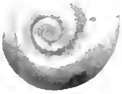
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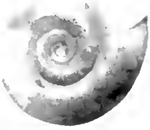
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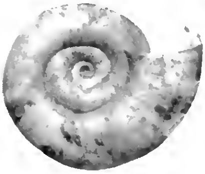
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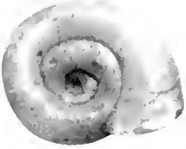
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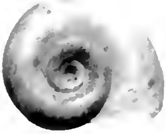
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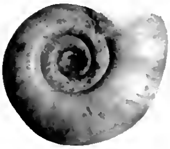
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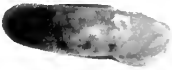
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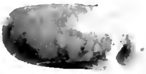
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PLATE 132

PLATE 133

Shells of Planorbidae

1–3. *Tropicorbis petenensis* Morelet. Tehauntepec, Mexico. M.C.Z., 64995.

4–9. *Tropicorbis tepicensis* (Martens). Tepic, Guadalajara, Mexico. U.S.N.M., 102211.

10–13. *Tropicorbis heloicus* (Orbigny). In small creek back of the Cerro, Montevideo, Uruguay. Type locality. U.S.N.M., 535720.

14–17. *Tropicorbis nigrilabris* (Lutz). Rio de Janeiro, Brazil. Type locality. U.S.N.M., 535713.

18–21. *Tropicorbis janeirensis* (Clessin). Bahia, Brazil. U.S.N.M., 152677.

22. *Tropicorbis schrammi* (Crosse). Martinique. M.C.Z., 113883.

23, 24. *Tropicorbis schrammi* (Crosse). Antigua. U.I., Z40465.

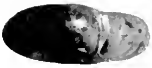
25–27. *Tropicorbis declivis* (Tate). Nicaragua. U.S.N.M., 24006.

28–33. *Tropicorbis obstructus* (Morelet). Pool at Piste, Yucatan. M.C.Z., 59754.

34, 35. *Tropicorbis obstructus* (Morelet). Falls of the Valles River, Valles, Mexico. B2117.

36–40. *Tropicorbis obstructus anodontus* (Pilsbry). Reservoir north of Guatemala City, Guatemala. Type locality. B2061.

All figures are enlarged about three diameters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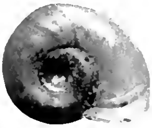
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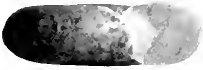
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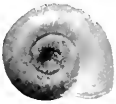
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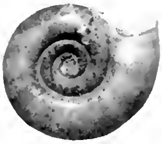
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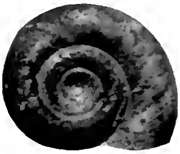
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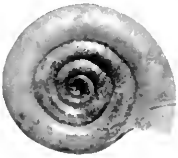
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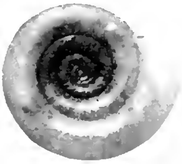
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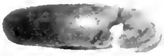
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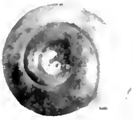
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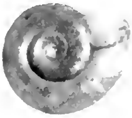
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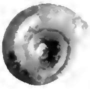
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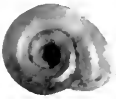
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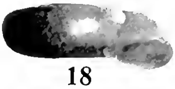
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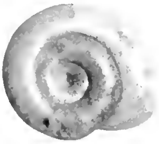
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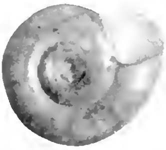
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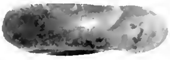
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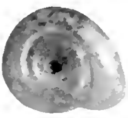
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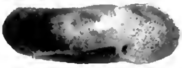
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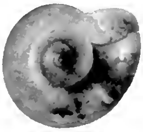
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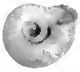
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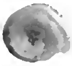
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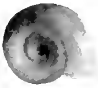
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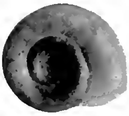
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PLATE 133

PLATE 134

Shells of Planorbidae

1–3. *Tropicorbis paparyensis* (F. Baker). Anapolis, Goyaz, Brazil. M.C.Z., 65717.

4–6. *Tropicorbis albicans* (Pfr.). Cuba. U.I., Z40459.

7. *Tropicorbis schrammi* (Crosse). Antigua. U.I., Z40465.

8, 9. *Tropicorbis dentiferus* (C. B. Adams). Bog Walk, St. Catherine, Jamaica. M.C.Z., 65838.

10, 11. *Tropicorbis obstructus* (Morelet). Catamas Lake, El Abra, Mexico. B1218.

12. *Tropicorbis shimeki* F. C. Baker. Ometope, Nicaragua. Holotype. U.S.N.M., 534290.

13, 14. *Tropicorbis shimeki* F. C. Baker. Ometope, Nicaragua. Paratypes. U.S.N.M., 534290.

15–18. *Tropicorbis albicans* (Pfr.). Mangrove Cay, along Kings Road, Lisbon Point, Andros Island, Bahamas. U.S.N.M., 270084.

19. *Tropicorbis albicans* (Pfr.). Cuba. U.I., Z40459.

20. *Tropicorbis paparyensis* (F. Baker). Anapolis, Brazil. M.C.Z., 65717.

21. *Tropicorbis obstructus donbilli* (Tristram). Tamosopo, Mexico. U.I., Z28545.

Figures 18 to 21 illustrate form of lamellae in aperture

22. *Tropicorbis obstructus* (Morelet). Pistae, Yucatan. M.C.Z., 59754.

23. *Tropicorbis obstructus donbilli* (Tristram). Tamosopo, Mexico. U.I., Z28545.

24. *Tropicorbis janeirensis* (Clessin). Bahia, Brazil. U.S.N.M., 152677.

25. *Tropicorbis nigrilabris* (Lutz). Brazil. U.S.N.M., 535713.

26. *Tropicorbis paparyensis* (F. Baker). Anapolis, Brazil. M.C.Z., 65717.

27. *Tropicorbis schrammi* (Crosse). Martinique. U.I., Z40464.

28. *Tropicorbis shimeki* F. C. Baker. Coatzocoalcos, Mexico. U.S.N.M., 219696.

29. *Tropicorbis albicans* (Pfr.). Mangrove Cay, Andros, Bahamas. U.S.N.M., 270084.

Figures 22 to 29 illustrate lamellae on parietal wall

Figures 1 to 11 are enlarged about four diameters; figs. 12 to 29, six diameters.


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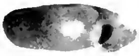
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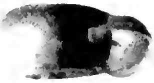
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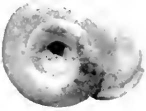
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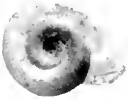
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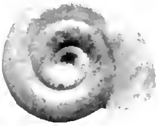
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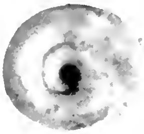
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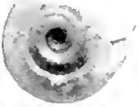
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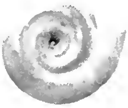
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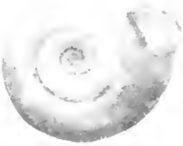
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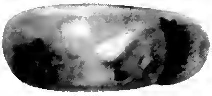
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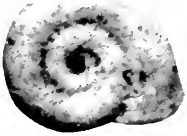
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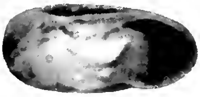
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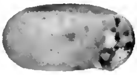
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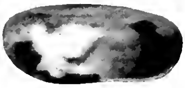
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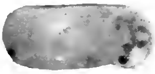
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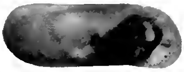
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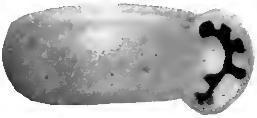
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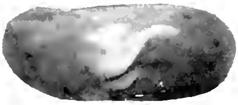
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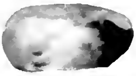
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PLATE 134

PLATE 135

Shells of Planorbidae

1–3. *Tropicorbis peregrinus* (Orbigny). Montevideo, Uruguay. U.S.N.M., 535952.

4. *Tropicorbis peregrinus* (Orbigny). Arroyo de Solon, Uruguay. U.S.N.M., 380999.

5–8. *Tropicorbis centimetralis* (Lutz). From Lutz. U.S.N.M., 535956.

9–11. *Tropicorbis chilensis* (Clessin). Peru. Lea Coll. from Paris Museum. U.S.N.M., 126412.

12, 13. *Tropicorbis philippianus* (Dunker). Lake near Coma de Ipaguaza, Bolivia (15 mi. N.E. of Yacuiba). U.S.N.M., 341049.

14–16. *Tropicorbis meridaensis* (Preston). Ruicon de Valle, near Caracas, Venezuela. U.S.N.M., 362132.

17–19. *Tropicorbis bourcardianus* (Preston). Manzanello, Mexico. U.S.N.M., 219755.

20, 21. *Tropicorbis canonicus* (Cousin). Soacha, near Bogata, Colombia. M.C.Z.

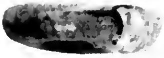
22, 23. *Tropicorbis canonicus* (Cousin). 'La Picata' near Bogata, Colombia. M.C.Z.

24–27. *Tropicorbis canonicus* (Cousin). Ibarra, Ecuador. M.C.Z., 64967.

28–31. *Tropicorbis triggrus* (Philippi). Small lake near Titicaca, Peru. (14,000 feet elevation). U.S.N.M., 271591.

32–35. *Tropicorbis gracilentus* (Gould). 30 miles S.W. of Santiago, Mexico. U.S.N.M., 28384.

All figures are enlarged about 2½ diameters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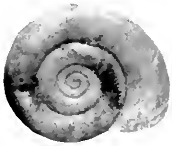
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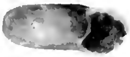
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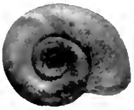
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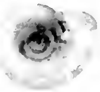
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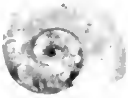
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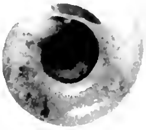
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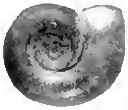
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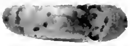
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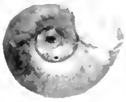
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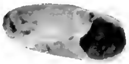
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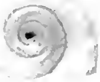
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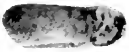
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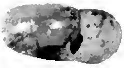
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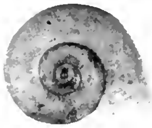
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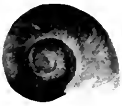
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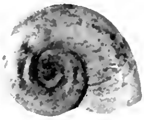
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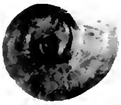
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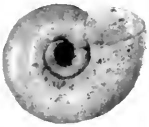
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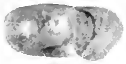
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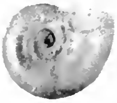
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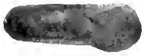
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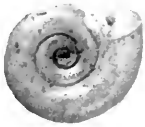
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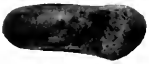
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PLATE 135

PLATE 136

Shells of Planorbidae

1–3. *Gyraulus albus* (Müller). Sealy Beck, near Scarborough, England. No. 3 shows fine spiral sculpture. Baker coll., 2768.

4–7. *Gyraulus hirsutus* (Gould). Lynnfield, Massachusetts. M.C.Z., 34915.

8–10. *Gyraulus hirsutus* (Gould). Lynnfield, Massachusetts. M.C.Z., 34915.

11. *Gyraulus hirsutus* (Gould). Lynnfield, Massachusetts. Base of shell showing rounded whorls. M.C.Z., 34915.

12. *Gyraulus hirsutus* (Gould). Lynnfield, Massachusetts. Hirsute shell showing larger and less numerous rows than in *albus*, fig. 3.

13–15. *Gyraulus deflectus* (Say). Miller Bay, Lake Winnebago, Wisconsin. Baker Coll., 2036.

16, 17. *Gyraulus deflectus* (Say). Lake Maxinkuckee, Indiana. Baker Coll., 127.

18–20. *Gyraulus deflectus* (Say). Miller Bay, Lake Winnebago, Wisconsin. Baker Coll. 2036.

21. *Gyraulus deflectus* (Say). Harbor Island, Lake George, New York. U.S.N.M., 426560. Showing hirsute periostracum.

22. *Gyraulus deflectus obliquus* (DeKay). Okoboji Lake, Iowa. Showing hirsute epidermis. U.S.N.M., 525319.

23. *Gyraulus deflectus* (Say). Lake Maxinkuckee, Indiana. Immature specimen with hairy periostracum. Baker Coll., 127.

24. *Gyraulus deflectus* (Say). Harbor Island, Lake George, New York. Specimen with very acute periphery and hairy periostracum. U.S.N.M., 426560.

25, 26. *Gyraulus deflectus* (Say). Lake Maxinkuckee, Indiana. Immature. Baker Coll., 127.

27–31. *Gyraulus deflectus obliquus* (DeKay). Round Pond, Charlotte, near Rochester, New York. Baker Coll., 1120.

32–37. *Gyraulus borealis* (Westerlund). Tanana River, Chena, Alaska. U.S.N.M., 193289.

38. *Gyraulus borealis* (Westerlund). Popoff Island, Shumigins Group, Alaska. U.S.N.M., 180292.

39. *Gyraulus borealis* (Westerlund). Saigan, Siberia. From Zool. Mus. Russia. Named by Westerlund. U.S.N.M., 15248.

All specimens are enlarged four diameters


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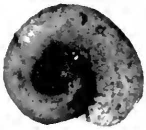
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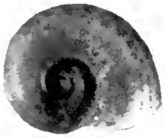
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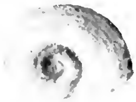
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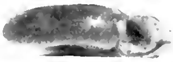
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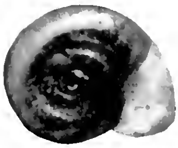
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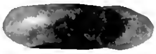
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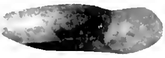
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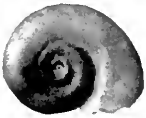
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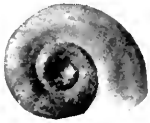
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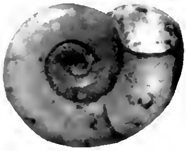
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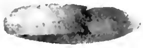
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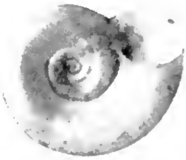
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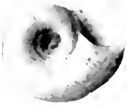
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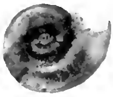
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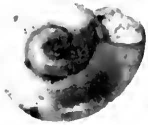
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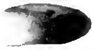
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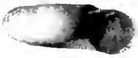
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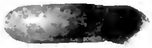
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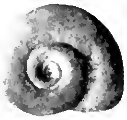
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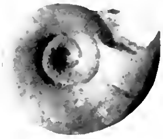
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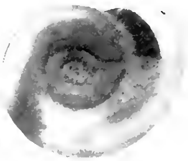
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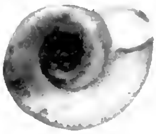
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PLATE 136

PLATE 137

Shells of Planorbidae

1–13. *Taphius andecolus* (Orb.). Duli, Lake Titicaca, Peru. U.S.N.M., 251596.

14, 15. *Taphius pronus* (Martens). From Lutz. U.S.N.M., 535957.

16, 17; 19–21. *Taphius pronus* (Martens). Penninsula de Cobrera, Lake Valencia, Venezuela. M.C.Z., 111649.

18, 22–24. *Taphius pronus* (Martens). (Fossil, 110 ft.). Lake Valencia, Venezuela. B3382.

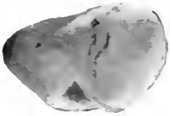
25–27. *Taphius montanus* (Orb.). Duli, Lake Titicaca, Peru. C. Brües. U.S.N.M., 271598.

28. *Australorbis immunis* (Lutz). Immature. Rio de Janeiro, Brazil. M.C.Z., 74578.

29, 30. *Australorbis immunis* (Lutz). Rio de Janeiro, Brazil. M.C.Z., 74578.

31–34. *Australorbis immunis* (Lutz). (From Lutz) Rio de Janeiro, Brazil. U.S.N.M., 535953.

35, 36. *Australorbis guadeloupensis* (Sowb.). Guadeloupe. Salle Coll. U.S.N.M., 151238.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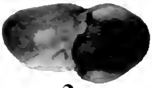
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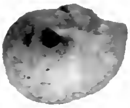
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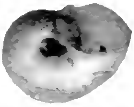
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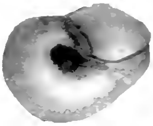
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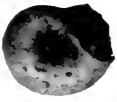
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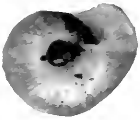
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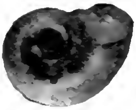
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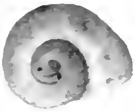
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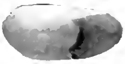
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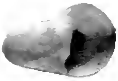
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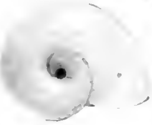
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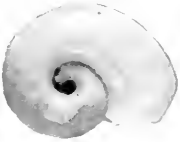
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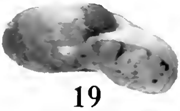
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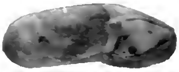
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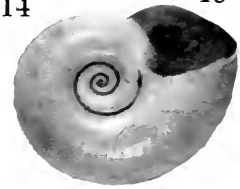
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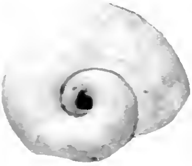
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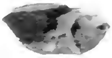
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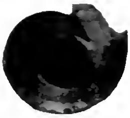
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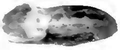
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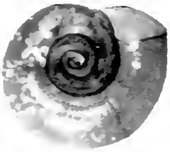
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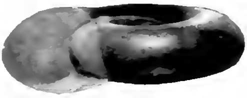
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PLATE 137

PLATE 138

Shells of Planorbidae

1, 2. *Australorbis lugubris* (Wagner). Caracas, Venezuela. Lea Coll. U.S.N.M., 126406.

3, 4. *Australorbis lugubris* (Wagner). Between Caracas and Puerto Cabello, Venezuela. Salle Coll. U.S.N.M., 336132.

5–7. *Australorbis lugubris* (Wagner). San Domingo, Brazil. M.C.Z., 74588.

8, 9. *Australorbis lugubris* (Wagner). Near Caracas, Venezuela. U.S.N.M., 426247.

10. *Australorbis lugubris* (Wagner). Brazil. Lea Coll. U.S.N.M., 121006.

11, 12. *Australorbis blauneri* (Germain). Isle Vieques, Puerto Rico. Webb Coll. U.I., Z40479.

13–15, 19. *Australorbis bahiensis* (Dunker). Montevideo, Uruguay. U.S.N.M., 124592.

16, 18. *Australorbis bahiensis* (Dunker). Campos, Brazil. M.C.Z., 74584.

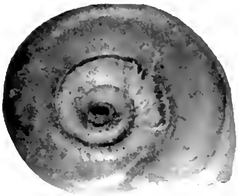
17. *Australorbis bahiensis* (Dunker). Campos, Brazil. M.C.Z., 74585.

20. *Australorbis bahiensis* (Dunker). (*nigricans*, from Lutz). U.S.N.M., 535955.

21–23. *Australorbis bahiensis* (Dunker). Victoria, Brazil. M.C.Z., 74586.

24, 25. *Australorbis bahiensis* (Dunker). San Domingo, Brazil. M.C.Z., 74588.

26, 27. *Australorbis bahiensis* (Dunker). Bahia, Brazil. M.C.Z., 74587.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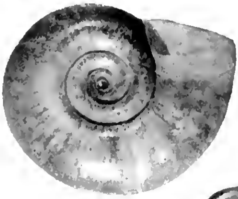
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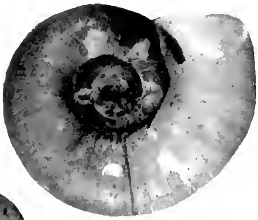
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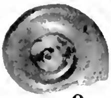
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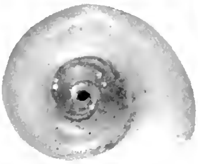
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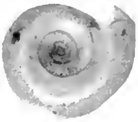
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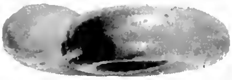
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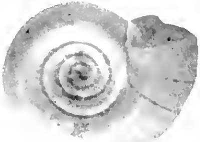
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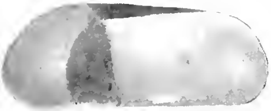
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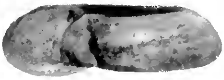
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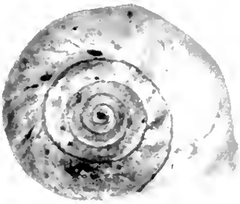
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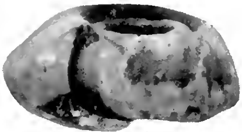
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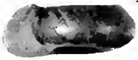
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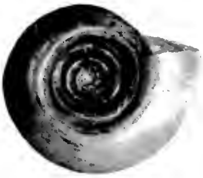
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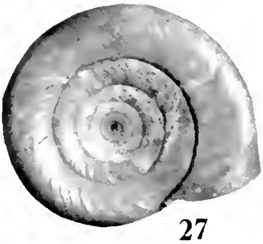
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PLATE 138

PLATE 139

Shells of Planorbidae

1, 2. *Australorbis paysanduensis* (Marshall). (Figured type). Paysandu, Uruguay. U.S.N.M., 380693.

3, 4. *Australorbis paysanduensis* (Marshall). (Paratype). Paysandu, Uruguay. U.S.N.M., 380694.

5. *Australorbis paysanduensis* (Marshall). Paysandu, Uruguay. F. Felippo Coll. U.S.N.M., 322385.

6, 7. *Australorbis tenagophilus* (Orb.). Corrientes, Brazil. M.C.Z., 104573.

8–10. *Australorbis tenagophilus* (Orb.). Montevideo, Uruguay. U.S.N.M., 380522.

11, 12. *Australorbis tenagophilus* (Orb.). Young. Arroyo Jurical, Dept. San Jose, Uruguay. U.S.N.M., 380746.

13, 14. *Australorbis tenagophilus* (Orb.). Arroyo Jurical, Dept. San Jose, Uruguay. U.S.N.M., 346818.

15, 16. *Australorbis tenagophilus* (Orb.). Arroyo de Solon, Dept. Duragno, Uruguay. U.S.N.M., 380997.

17, 18. *Australorbis tenagophilus* (Orb.). Rio Couraguam, Brazil. Von Ihering Coll. U.S.N.M., 122309.

19–25. *Australorbis glabratus christopherensis* Pilsbry. St. Kitts. West Indies.

26–28. *Australorbis antiguensis* (Sowb.). Near Quebradillas, Puerto Rico. Pilsbry Coll. M.C.Z., 103302.

29, 30. *Australorbis antiguensis* (Sowb.). St. Kitts. M.C.Z., 74651.

31. *Australorbis glabratus refulgens* (Dunker). Cotype. Santo Domingo. M.C.Z., 83890.

32. *Australorbis glabratus olivaceus* (Spix and Wagner). Immature. Januaria, Brazil. M.C.Z., 74577.

33. *Australorbis glabratus olivaceus* (Spix and Wagner) Immature. Brazil. M.C.Z., no number.

34, 35. *Australorbis glabratus olivaceus* (Spix and Wagner). Januaria, Brazil. M.C.Z., 74577.

36. *Australorbis glabratus olivaceus* (Spix and Wagner). St. Laurent du Maroni, French Guiana. Bequaert Coll. M.C.Z., 102281.

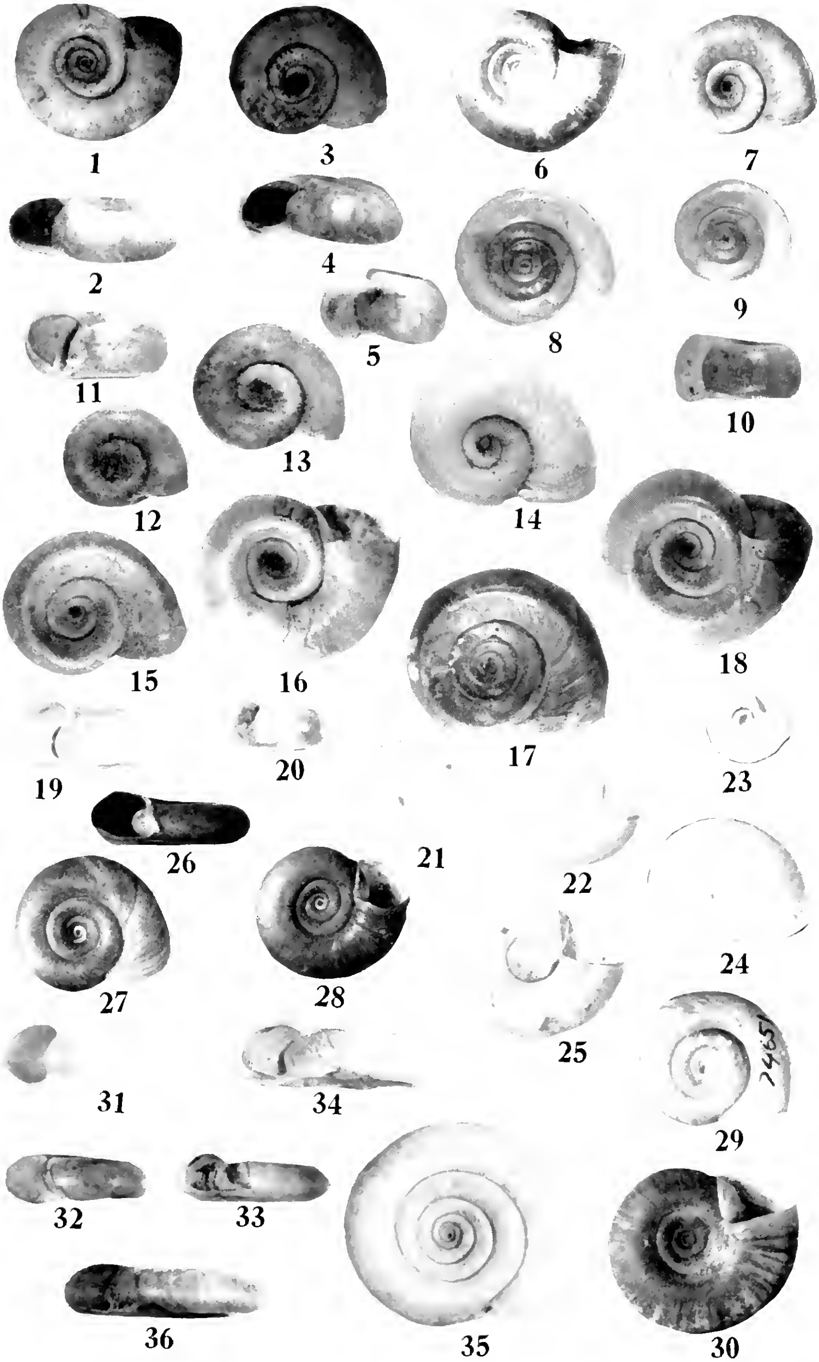
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PLATE 139

PLATE 140

Shells of Planorbidae

1–3. *Australorbis glabratus olivaceus* (Spix and Wagner). Brazil. Lea Coll. U.S.N.M., 121204.

4. *Australorbis glabratus olivaceus* (Spix and Wagner). Near Maracay, Arugua State, Venezuela. U.S.N.M., 349069.

5, 6. *Australorbis glabratus* (Say). San Juan, Puerto Rico. Bequaert. M.C.Z., 65218.

7, 8. *Australorbis glabratus* (Say). Guadeloupe Island. Bequaert. M.C.Z., 64969.

9. *Australorbis glabratus* (Say). Immature. Guadeloupe Island. Bequaert. M.C.Z., no number.

10–12. *Australorbis glabratus* (Say). Immature. Castres, St. Lucia, W.I. M.C.Z., 72552.

13, 14. *Australorbis glabratus* (Say). Young. La Juria, Tortuoguera, Puerto Rico. Henderson Coll. U.S.N.M., 535961.

15–17. *Australorbis glabratus* (Say). Antigua. Th. Gill Coll. U.S.N.M., 454061.

18. *Australorbis glabratus* (Say). Immature. Puerto Rico. U.S.N.M., 535961.

19, 20. *Australorbis glabratus christopherensis* Pilsbry. Marie Galante. U.S.N.M., 390137.

21. *Australorbis glabratus christopherensis* Pilsbry. Franklin Estate. St. Christopher. U.S.N.M., 390136.

22. *Menetus dalli* F. C. Baker. Holotype. Pliocene. Caloosahatchie River, Florida. W. H. Dall Coll. U.S.N.M., 112556.

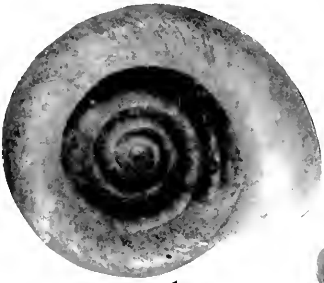
23, 24. *Menetus dalli* F. C. Baker. Paratypes. Pliocene. Caloosahatchie River, Florida. W. H. Dall Coll. U.S.N.M., 112556.

25. *Menetus alabamensis avus* (Pilsbry). Caloosahatchie River, Florida. W. H. Dall Coll. U.S.N.M., 112556.

26. *Menetus kansasensis* F. C. Baker. Paratype. (90 feet deep in clay). Meade County, Kansas. U.I., P6778.

27. *Menetus kansasensis* F. C. Baker. Holotype. (90 feet deep in clay). Meade County, Kansas. U.I., P6778.

28, 29. *Menetus kansasensis* F. C. Baker. Paratypes. U.I., P6778.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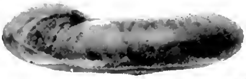
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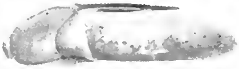
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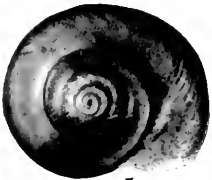
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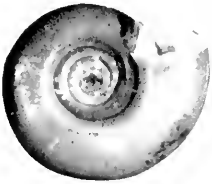
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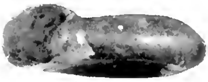
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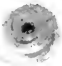
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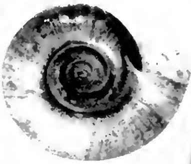
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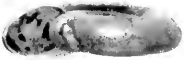
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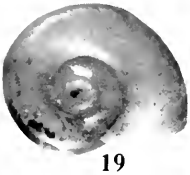
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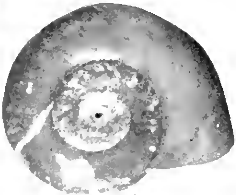
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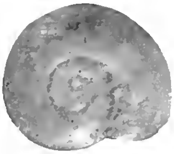
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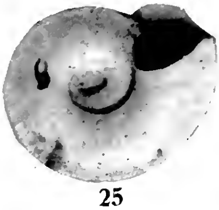
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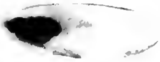
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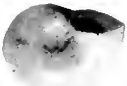
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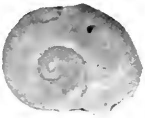
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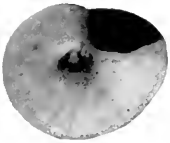
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PLATE 140

PLATE 141

Shells of Planorbidae

1. *Tropicorbis pedrinus* (Miller). Rio Lope Castro, Parana, Brazil. W. L. Schmidt Coll. U.S.N.M., 365157.

2–4. *Tropicorbis petenensis* Morelet. Laguna de Peten. Remate, Guatemala. U.S.N.M., 382775.

5–7. *Tropicorbis dentiens* (Morelet). Belize, Honduras. A.N.S.P., 123897.

8–11. *Helisoma affine*. Young. Hents Bay, St. Andrew, Jamaica. U.S.N.M., 378049.

12. *Helisoma foveale* (Menke). U.S.N.M., 378040.

13–18. *Helisoma foveale* (Menke). Frankfield, Clarendon, Jamaica. U.S.N.M., 400632.

19. *Helisoma equatorium* (Cousin). (Beach) Eben, Peru. U.S.N.M., 347900.

20, 21. *Helisoma equatorium* (Cousin). Milagis, Ecuador. U.I., Z40572.

22, 23. *Helisoma equatorium* (Cousin). (Labelled *bahiensis*). Ecuador. Lea Coll. U.S.N.M., 126411.

24, 25. *Helisoma equatorium* (Cousin). Quito, Ecuador. Bequaert. M.C.Z., 64965.

26–28. *Planorbis turgidus* Jeffr. Type. 'Georgia.' (Britain in error). U.S.N.M., 65265.

29, 30. *Helisoma peruvianum* (Brod.). Callao, Peru. (Like Clessin's figures). U.I., Z40593.

31, 32. *Helisoma peruvianum* (Brod.) (= *moricandi* Beck.). Brazil. U.S.N.M., 20702.

33, 34. *Planorbis pedrinus* Miller (= *Tropicorbis*). Moll. Blatt. n.s. 1. Plate 7.

35. *Planorbis boetzkesi* Miller (= *Gyraulus*). Moll. Blatt. n.s. 1. Plate 7.

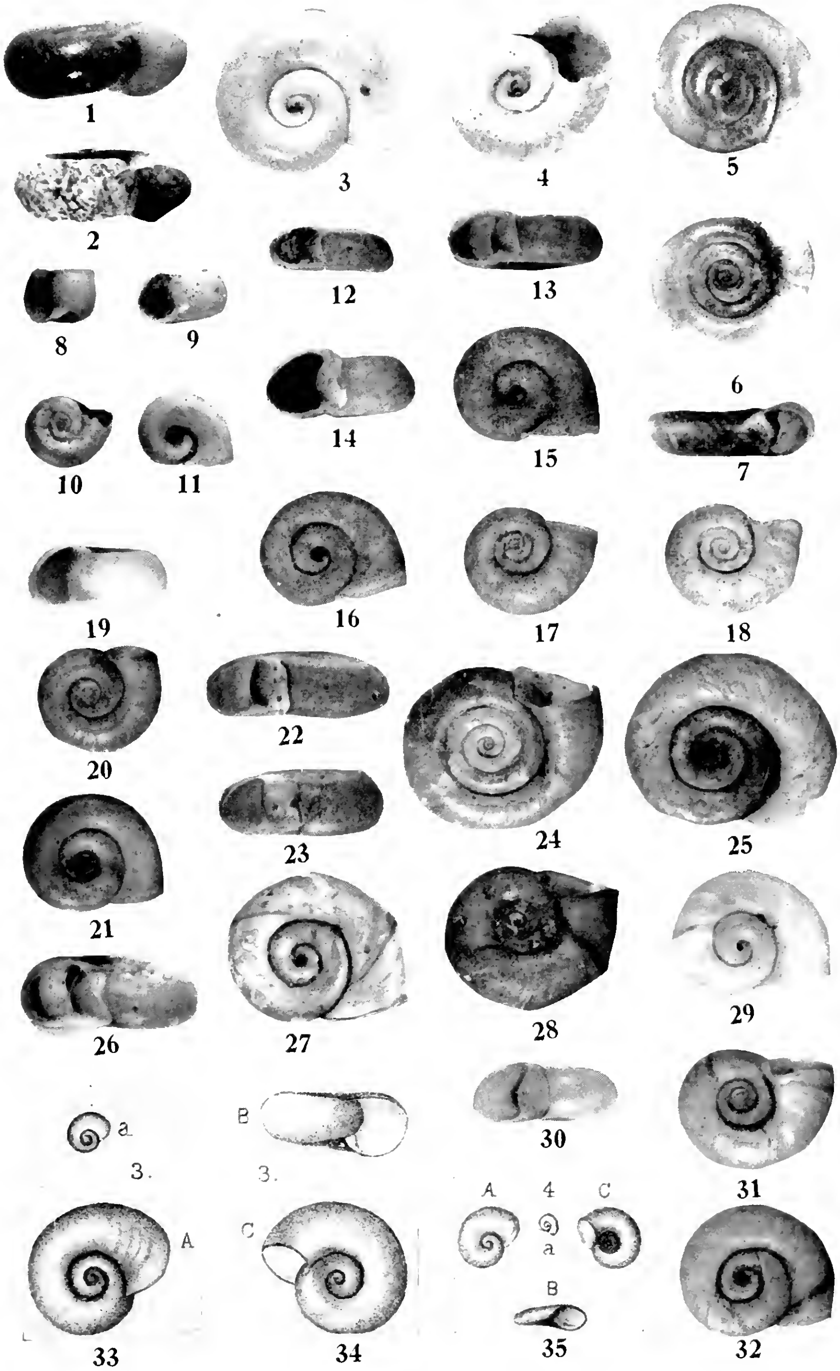
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PLATE 141

INDEXES

INDEX TO TEXT

Since in the text of this volume all anatomical features, synonymy, distribution, and lists of valid species are treated in full for each genus and subgenus, references to these details are not cited in the index. Similarly, the inclusion of all taxonomic names, morphological terms, and names of authorities where these appear in descriptions and comparisons would extend the size of the index unreasonably without adding value to the reader, hence these items are likewise omitted. A list of the more important synonyms is conveniently available in the text in a chronological list following the heading for each group; consequently these names are not repeated in the index.

For each scientific name the chief reference to the full taxonomic and morphological treatment is cited in boldface type.

To avoid confusion of numerals for page, plate, and figure numbers, a separate index to the illustrations has been prepared wherein all figures are listed under the respective generic and specific names used in the explanation of the plates.

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