NORTH AMERICAN FRESHWATER SNAILS

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Distribution

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I. INTRODUCTION

North America is a vast area with abundant freshwater resources. Its lakes rank among the largest and its rivers among the most extensive in the world. The Great Lakes by themselves hold over 20% of the earth's freshwater reserves. The Mississippi River, with its major tributaries, the Missouri and Red Rock rivers, is 3,860 miles in length and drains an area of some 1,234,700 square miles. With such an extensive freshwater system, it is not surprising that a prominent freshwater snail fauna has developed on the continent. This fauna in North America (north of Mexico) comprises about 500 species.

The freshwater snails of North America are common, and most extant species are relatively easy to collect. But, in spite of this, their taxonomy, especially at the species level, has not been definitively established in most groups. This is unfortunate, because a number of Recent species, and even whole genera, are now extinct due to the biological destruction of their habitats, and many more species are threatened or endangered.

One reason for the lag in modern taxonomic studies of North American freshwater snails is that readily available comprehensive guides for identification are not available. Most of the previous publications are out-of-print, and now are available in only a few of the largest libraries. And, most such publications are now badly out-of-date.

Previous comprehensive accounts of the species of North American freshwater snails are those of Say (1830-34), Haldeman (1840-71; continued by Tryon, 1870-71), Binney (1865c,d) and Burch (1982a,b) [see Bibliography, pp. 293-337]. The first three are old publications, found only in a few specialized institutions and several private libraries. The latter publication, commissioned and published in one limited edition by the U.S. Environmental Protection Agency, was out-of-print only several months after it appeared. The present publication, an extension of the E.P.A. manual, is now presented to make more readily available a modern introduction to the North American freshwater snail fauna.

Binney's manual, which also included the land snails (W.G. Binney & T. Bland, 1869, *Land and fresh water shells of North America. Part I. Pulmonata Geophila*, Smithsonian Miscellaneous Collections, No. 194), was the only such reference available on North American non-marine mollusks for more than a century. But, during the years since Binney's book, various regional handbooks or monographs were published on, or included, North American freshwater snails. The more prominent of these publications, listed by geographic regions, are presented below.

Alaska

William H. Dall. 1905. *Land and fresh water mollusks of Alaska and adjoining regions.* Smithsonian Institution Harriman Alaska Expedition.

Canada

Arthur H. Clarke. 1973. *The freshwater mollusks of the Canadian Interior Basin.* Malacologia, Vol. 13.

Arthur H. Clarke. 1981. *The freshwater molluscs of Canada.* National Museum of Natural Sciences, National Museums of Canada.

United States (exclusive of Alaska)

George W. Tryon, Jr. 1870-71. *A monograph of the fresh-water univalve Mollusca of the United States.* Academy of Natural Sciences of Philadelphia.

Western United States (including Colorado)

Joseph C. Bequaert & Walter B. Miller. 1973. *The mollusks of the arid Southwest, with an Arizona check list.* The University of Arizona Press, Tucson.

R. Ellsworth Call. 1884. *On the Quaternary and Recent Mollusca of the Great Basin, with descriptions of new forms.* Bulletin of the U.S. Geological Survey, No. 11.

Ralph V. Chamberlain & David T. Jones. 1929. *A descriptive catalogue of the Mollusca of Utah.* Bulletin of the University of Utah, Vol. 19.

Harold Hannibal. 1912. *A synopsis of the Recent and Tertiary freshwater Mollusca of the California Province, based upon an ontogenetic classification.* Proceedings of the Malacological Society of London, Vol. 10.

Junius Henderson. 1907/1912. *The Mollusca of Colorado.* University of Colorado Studies, Vols. 4 (1907) and 9 (1912).

Junius Henderson. 1924. *Mollusca of Colorado, Utah, Montana, Idaho and Wyoming.* University of Colorado Studies, Vol. 13. (A supplement was published in 1936.)

Junius Henderson. 1929. *Non-marine Mollusca of Oregon and Washington.* University of Colorado Studies, Vol. 17. (A supplement was published in 1936.)

Josiah Keep. 1887. *West Coast shells.* Bancroft Brothers, San Francisco.

Josiah Keep. 1904. *West American shells.* Whitaker and Ray, San Francisco.

Josiah Keep. 1911 [1910]. *West Coast shells.* [Includes a chapter on "Shells of lakes and streams" by Harold Hannibal.] Whitaker and Ray-Wiggin, San Francisco.

Henry A. Pilsbry & J.H. Ferriss. 1905-1923. *Mollusca of the southwestern states.* Proceedings of the Academy of Natural Sciences of Philadelphia.

North Central United States

Frank Collins Baker. 1902. *The Mollusca of the Chicago area. Part 2, The Gastropoda.* Chicago Academy of Science.

Frank Collins Baker. 1928. *The fresh water Mollusca of Wisconsin.* Wisconsin Geological and Natural History Survey, Bull. 70.

R. Ellsworth Call. 1900. *A descriptive illustrated catalogue of the Mollusca of Indiana.* 24th Annual Report of the Department of Geology and Natural Resources of Indiana. (Revised [without figures] by Calvin Goodrich & Henry van der Schalie, 1944.)

Alan M. Cvancara. 1983. *Aquatic mollusks of North Dakota.* Report of Investigation No. 78, North Dakota Geological Survey.

Calvin Goodrich. 1932. *The Mollusca of Michigan.* Museum of Zoology, The University of Michigan.

Aurèle La Rocque. 1968. *Pleistocene Mollusca of Ohio.* Division of Geological Survey, Department of Natural Resources, State of Ohio, Bull. 62. (Includes Recent species.)

A. Byron Leonard. 1959. *Handbook of gastropods in Kansas.* University of Kansas Museum of Natural History Miscellaneous Publication, No. 20.

Eastern United States

William K. Emerson & Morris K. Jacobson. 1976. *Guide to shells, land, freshwater, and marine, from Nova Scotia to Florida.* Alfred A. Knopf, New York.

Northeastern United States

Augustus A. Gould. 1870. *Report on the Invertebrata of Massachusetts.* Edited by W.G. Binney. Wright and Potter, Boston.

Willard N. Harman & Clifford O. Berg. 1971. *The freshwater snails of central New York, with illustrated keys to the genera and species.* Search, Agriculture, Entomology (Ithaca) 2, Vol. 1.

Eileen H. Jokinen. 1983. *The freshwater snails of Connecticut.* State Geological and Natural History Survey of Connecticut, Department of Environmental Protection, Bulletin 109.

Imogene C.S. Robertson & Clifford L. Blakeslee. 1948. *The Mollusca of the Niagara Frontier region.* Bulletin of the Buffalo Society of Natural Science, Vol. 19.

Southeastern United States

William J. Clench & Ruth D. Turner. 1956. *Freshwater mollusks of Alabama, Georgia, and Florida from the Escambia to the Suwannee River.* Bulletin of the Florida State Museum (Biological Science), Vol. 1.

Fred G. Thompson. 1984. *Freshwater snails of Florida. A manual for identification.* University of Florida Press, Gainesville.

Also since Binney's (1865c,d) manual, various taxonomic groups of snails have been monographed, either regionally or totally. These are listed below.

Hydrobiidae

Elmer G. Berry. 1943. *The Amnicolidae of Michigan: distribution, ecology, and taxonomy.* Miscellaneous Publications of the Museum of Zoology, University of Michigan, No. 57.

Fred. G. Thompson. 1968. *The aquatic snails of the family Hydrobiidae of peninsular Florida.* University of Florida Press, Gainesville.

Fred G. Thompson. 1977. *The hydrobiid snail genus* Marstonia. Bulletin of the Florida State Museum (Biological Science), Vol. 21.

Pleuroceridae

Chas. C. Adams. 1915. *The variations and ecological distribution of the snails of the genus* Io. Memoirs of the National Academy of Science, Vol. 12.

Calvin Goodrich. 1917-44. [Numerous papers revising the large family Pleuroceridae, mostly published in the *Occasional Papers of the Museum of Zoology, University of Michigan* and the *Miscellaneous Publications of the Museum of Zoology, University of Michigan*.]

George W. Tryon, Jr. 1873. *Land and fresh-water shells of North America. Part IV. Strepomatidae (American melanians).* Smithsonian Miscellaneous Collections, Vol. 16.

Lymnaeidae

Frank Collins Baker. 1911. *The Lymnaeidae of North and Middle America, Recent and fossil.* Chicago Academy of Science.

Bengt Hubendick. 1951. *Recent Lymnaeidae. Their variation, morphology, taxonomy, nomenclature, and distribution.* Kungliga Svenska Vetenskapsakademiens Handlingar, Vol. 3.

Physidae

George A. Te. 1975. *Michigan Physidae, with systematic notes on* Physella *and* Physodon *(Basommatophora: Pulmonata).* Malacological Review, Vol. 8.

Planorbidae

Frank Collins Baker. 1945. *The molluscan family Planorbidae.* University of Illinois Press, Urbana.

Ancylidae

Paul F. Basch. 1963. *A review of the Recent freshwater limpet snails of North America (Mollusca: Pulmonata).* Bulletin of the Museum of Comparative Zoology at Harvard College, Vol. 129.

The taxonomic philosophies of the authors above have varied considerably, and the taxonomic treatments in the older publications especially need revision. But, the publications of the two lists above have been invaluable source material for the present manual, and may prove to be especially useful to current biologists who must deal with mollusks of the geographical areas or taxonomic groups covered.

In addition to the major publications listed above (and hundreds of more minor ones not listed here), an additional publication should be mentioned: Bryant Walker's (1918) *A synopsis of the classification of the freshwater Mollusca of North America, north of Mexico, and a catalogue of the more recently described species, with notes*, Miscellaneous Publications of the Museum of Zoology, University of Michigan, No. 6. Although this publication is now out-of-print and out-of-date, it has been one of the landmark publications on the classification of North American mollusks for the past 70 years.

II. SYSTEMATICS, NOMENCLATURE, IDENTIFICATION AND MORPHOLOGY

* * *

SYSTEMATICS

Interest in the systematics of North American freshwater snails began in the 17th century in Europe, but it was Thomas Say (1787-1834), an American, who made the most significant early advances in taxonomic malacology on this continent. Say recognized and described many new mollusks, most of which still stand today as valid species. A contemporary of Say's was C.F. Rafinesque, who added many more new taxa (and much confusion). Say and Rafinesque were followed by T.A. Conrad, A.A. Gould, S.S. Haldeman, James Lewis, Wm. G. Binney, G.W. Tryon, H.A. Pilsbry and scores of other authors who described hundreds of additional taxa.

This fauna in North America (north of Mexico), as currently recognized, comprises about 500 species, which are divided into 78 genera and 15 families. These snails are grouped into two large subclasses, the gill-breathing, operculated Prosobranchia and the lung-breathing, non-operculated Pulmonata (Order Lymnophila). The prosobranch snails are represented by 49 genera and about 350 species, and the pulmonate snails by 29 genera and about 150 species. Systematics are not well worked out in many groups of North American freshwater snails, and future studies undoubtedly will change these numbers. An outline of classification is presented below.

Subclass PROSOBRANCHIA

Order Neritacea (Neritopsina)

Superfamily Neritinoidea

NERITIDAE Rafinesque 1815

Neritina Lamarck 1816 (*Nerita pulligera* Linnaeus 1766)*

Vitta Mörch 1852 (*Nerita virginea* Linnaeus 1758)

*Type species are placed in parentheses after each generic-group name.

Order Mesogastropoda
Superfamily Valvatoidea

VALVATIDAE Gray 1840
Valvata Müller 1774 (*Valvata cristata* Müller 1774)

Superfamily Ampullarioidea

VIVIPARIDAE Gray 1847
Viviparinae
Tulotoma Haldeman 1840 (*Paludina magnifica* Conrad 1834)
Viviparus Montfort 1810 (*Helix vivipara* Linnaeus 1758)
Bellamyinae Röhrbach 1937
†*Cipangopaludina* Hannibal 1912 (*Paludina malleata* Reeve 1862)
Lioplacinae Gill 1863
Campeloma Rafinesque 1819 (*Campeloma crassula* Rafinesque 1819)
Lioplax Troschel 1857 (*Limnaea subcarinata* Say 1817)

AMPULLARIIDAE Guilding 1828
†*Marisa* Gray 1824 (*Helix cornuarietis* Linnaeus 1758)
Pomacea Perry 1810 (*Pomacea maculata* Perry 1810)

BITHYNIIDAE Troschel 1857
Bithynia Leach (in Abel) 1818 (*Helix tentaculata* Linnaeus 1758)

?MICROMELANIIDAE Thiele 1928
Antroselates Hubricht 1963 (*Antroselates spiralis* Hubricht 1963)

Superfamily Truncatelloidea

HYDROBIIDAE Troschel 1857
Hydrobiinae
Aphaostracon Thompson 1968 (*Aphaostracon rhadinus* Thompson 1968)

†Recent introduction to North America.

Hoyia F. C. Baker 1926 (*Amnicola sheldoni* Pilsbry 1890)
Hyalopyrgus Thompson 1968 (*Bythinella aequicostata* Pilsbry 1889)
Littoridinops Pilsbry 1952 (*Amnicola tenuipes* Couper (in Haldeman) 1844)
Probythinella Thiele 1928 (*Paludina emarginata* Küster 1852 = *Probythinella lacustris limafodens* Morrison 1947)
Pyrgophorus Ancey 1888 (*Pyrgulopsis spinosus* Call & Pilsbry 1886)
Tryonia Stimpson 1865 (*Tryonia clathrata* Stimpson 1865)

Lithoglyphinae Troschel 1857
Antrobia Hubricht 1971 (*Antrobia culveri* Hubricht 1971)
Clappia Walker 1909 (*Clappia clappi* Walker 1909 = *Somatogyrus umbilicatus* Walker 1904)
Cochliopina Morrison 1946 (*Cochliopa riograndensis* Pilsbry & Ferriss 1906)**
Fluminicola Stimpson 1865 (*Paludina nuttalliana* Lea 1838)
Gillia Stimpson 1865 (*Melania altilis* Lea 1842)
Lepyrium Dall 1896 (*Neritina showalteri* Lea 1861)
Somatogyrus Gill 1863
Somatogyrus s.s. (*Amnicola depressa* Tryon 1862)
Walkerilla Thiele 1928 (*Somatogyrus coosaensis* Walker 1904)

Nymphophilinae Taylor 1966
Birgella F. C. Baker 1926 (*Paludina subglobosa* Say 1825)
Cincinnatia Pilsbry 1891 (*Paludina cincinnatiensis* Anthony 1840)
Fontelicella Gregg & Taylor 1965
Fontelicella s.s. (*Fontelicella californiensis* Gregg & Taylor 1965)
Microamnicola Gregg & Taylor 1965 (*Amnicola micrococcus* Pilsbry (in Stearns) 1893)
Natricola Gregg & Taylor 1965 (*Pomatiopsis robusta* Walker 1908)
Marstonia F. C. Baker 1926 (*Amnicola lustrica* Pilsbry 1890)
Notogillia Pilsbry 1953 (*Hydrobia wetherbyi* Dall 1885)
Orygoceras Brusina 1882 (*Orygoceras cornucopiae* Brusina 1882)

**See Thompson (1984, p. 109) for subfamilial placement of *Cochliopina*.

Pyrgulopsis Call & Pilsbry 1886 (*Pyrgula nevadensis* Stearns 1883)
Rhapinema Thompson 1969 (*Rhapinema dacryon* Thompson 1969)
Spilochlamys Thompson 1968 (*Spilochlamys conica* Thompson 1968)
Stiobia Thompson 1978 (*Stiobia nana* Thompson 1978)
Amnicolinae Tryon 1862
Amnicola Gould & Haldeman 1840
Amnicola s.s. (*Paludina porata* Say 1821 = *Paludina limosa* Say 1817)
Lyogyrus Gill 1863 (*Valvata pupoidea* Gould 1841)
?*Hauffenia* Pollonera 1898 (*Horatia tellini* Pollonera 1898)
?*Horatia* Bourguignat 1887 (*Horatia klecakiana* Bourguignat 1887)
Fontigentinae Taylor 1966
Fontigens Pilsbry 1933 (*Paludina nickliniana* Lea 1838)

POMATIOPSIDAE Stimpson 1865
Pomatiopsis Tryon 1862 (*Cyclostoma lapidaria* Say 1817)

Superfamily Cerithioidea

THIARIDAE Troschel 1857
†*Melanoides* Olivier 1804 (*Nerita tuberculata* Müller 1774)
†*Thiara* Röding 1798 (*Helix amarula* Linnaeus 1758)

PLEUROCERIDAE Fischer 1885 (Strepomatidae Haldeman 1863, ?Paludomidae Gill 1871)
Elimia H. & A. Adams 1854 (*Melania acutocarinata* Lea 1841 = *Melania clavaeformis* Lea 1841) [synonyms: *Goniobasis, Macrolimen, Melasma*]
Gyrotoma Shuttleworth 1845 (*Gyrotoma ovoidea* Shuttleworth 1845 = *Melania excisa* Lea 1843) [synonyms: *Apella*; *Schizostoma* Lea 1843, non Bronn 1835; *Schizocheilus* Lea 1852]
Io Lea 1831 (*Fusus fluvialis* Say 1825) [synonym: *Melafusus*]

†Recent introduction to North America.

Juga H. & A. Adams 1854
Juga s.s. (*Melania silicula* Gould 1847)
Calibasis Taylor 1966 (*Melania* (?*Goniobasis*) *acutifilosa* Stearns 1890)
Oreobasis Taylor 1966 (*Melania newberryi* Lea 1860 = ?*Melania bulbosa* Gould 1847)
Leptoxis Rafinesque 1819 (*Melania praerosa* Say 1821) [synonyms: *Anaplocamus, Anculosa*]
Mudalia Haldeman 1840 (*Paludina dissimilis* Say 1819 = *Bulimus carinatus* Bruguière 1792) [synonyms: *Alleghenya, Nitocris, Spirodon*]
Lithasia Haldeman 1840 (*Anculosa (Lithasia) geniculata* Haldeman 1840) [synonyms: *Angitrema, Athearnia, Eurycaelon, Glottella, Megara, Meseschiza*]
Pleurocera Rafinesque 1818 (*Pleurocera acuta* Rafinesque (in Blainville) 1824) [synonyms: *Ceriphasia, Oxytrema, Strepoma, Telescopella, Trypanostoma*]
Strephobasis Lea 1861 (*Strephobasis cornea* Lea 1861 = *Melania plena* Anthony 1854)

Subclass PULMONATA
Order Lymnophila
Suborder Archaeopulmonata
Superfamily Acroloxoidea

ACROLOXIDAE Thiele 1931
Acroloxus Beck 1837 (*Patella lacustris* Linnaeus 1758)

Suborder Branchiopulmonata
Superfamily Lymnaeoidea

LYMNAEIDAE Rafinesque 1815
Lymnaeinae
Acella Haldeman 1841 (*Lymnaea gracilis* Jay 1839, preocc. = *Limnaea haldemani* "Deshayes" W.G. Binney 1867)
Bulimnea Haldeman 1841 (*Lymnaeus megasomus* Say 1824)
Fossaria Westerlund 1885
Fossaria s.s. (*Buccinum truncatulum* Müller 1774)

Bakerilymnaea Weyrauch 1964 (*Limnaea cubensis* Pfeiffer 1839)
Lymnaea Lamarck 1799 (*Helix stagnalis* Linnaeus 1758)
Pseudosuccinea F. C. Baker 1908 (*Lymnaea columella* Say 1817)
†*Radix* Montfort 1810 (*Radix auriculatus* Montfort 1810 = *Helix auricularia* Linnaeus 1758)
Stagnicola Leach (in Jeffreys) 1830
Stagnicola s.s. (*Buccinum palustre* Müller 1774)
Hinkleyia F. C. Baker 1928 (*Lymnaeus caperatus* Say 1829)
Lancinae Hannibal 1914
Fisherola Hannibal 1912 (*Fisherola lancides* Hannibal 1912)
Lanx Clessin 1882
Lanx s.s. (*Ancylus newberryi* Lea 1858 = *Ancylus patelloides* Lea 1856)
Walkerola Hannibal 1912 (*Lanx (Walkerola) klamathensis* Hannibal 1912)

Superfamily Ancyloidea

PHYSIDAE Fitzinger 1833
Physinae
Physa Draparnaud 1801 (*Bulla fontinalis* Linnaeus 1758)
Physella Haldeman 1843
Physella s.s. (*Physa globosa* Haldeman 1841)
Costatella Dall 1870 (*Physa costata* Newcomb 1861)
Petrophysa Pilsbry 1926 (*Physa (Petrophysa) zionis* Pilsbry 1926)
Aplexinae Starobogatov 1967
Aplexa Fleming 1820 (*Bulla hypnorum* Linnaeus 1758)
Stenophysa Martens 1898 (*Physa sowerbyana* d'Orbigny 1853)

PLANORBIDAE Rafinesque 1815
Planorbinae
Planorbini
Gyraulus "Agassiz" Charpentier 1837
Gyraulus s.s. (*Planorbis hispidus* Draparnaud 1805 = *Planorbis albus* Müller 1774)

†Recent introduction to North America.

Armiger Hartmann 1840 (*Planorbis cristatus* Draparnaud 1805 = *Nautilus crista* Linnaeus 1758)
Torquis Dall 1905 (*Planorbis parvus* Say 1817)
Drepanotremini Zilch 1959 (?Acrorbini Starobogatov 1958)
Drepanotrema Fischer & Crosse 1880 (*Planorbis yzabalensis* Crosse & Fischer 1879 = *Planorbis anatinus* d'Orbigny 1835)
Antillorbis Harry & Hubendick 1964 (*Planorbis circumlineatus* Shuttleworth 1854 = *Planorbis aeruginosus* Morelet 1851)
Fossulorbis Pilsbry 1934 (*Planorbis cultratus* d'Orbigny 1841 = *Planorbis kermatoides* d'Orbigny 1835)
Biomphalariini Watson 1954
Biomphalaria Preston 1910 (*Biomphalaria smithi* Preston 1910)
Helisomini F. C. Baker 1928
Helisoma Swainson 1840
Helisoma s.s. (*Planorbis bicarinatus* Say 1817, preocc. = *Planorbis anceps* Menke 1830)
Carinifex W.G. Binney 1865 (*Planorbis newberryi* Lea 1858)
Menetus H. & A. Adams 1855
Menetus s.s. (*Planorbis opercularis* Gould 1847)
Micromenetus F. C. Baker 1945 (*Planorbis dilatatus* Gould 1841)
Planorbella Haldeman 1842
Planorbella s.s. (*Planorbis campanulatus* Say 1821)
Pierosoma Dall 1905 (*Planorbis trivolvis* Say 1817)
Seminolina Pilsbry 1934 (*Paludina scalaris* Jay 1839)
Planorbula Haldeman 1840 (*Planorbis armigerus* Say 1821)
Promenetus F. C. Baker 1935 (*Planorbis exacuous* Say 1821)
Vorticifex Meek (in Dall) 1870
Vorticifex s.s. (*Carinifex (Vorticifex) tryoni* Meek (in Dall) 1870)
Parapholyx Hanna 1922 (*Pompholyx effusa* Lea 1856)
Neoplanorbinae Hannibal 1912
Amphigyra Pilsbry 1906 (*Amphigyra alabamensis* Pilsbry 1906)
Neoplanorbis Pilsbry 1906 (*Neoplanorbis tantillus* Pilsbry 1906)

ANCYLIDAE Rafinesque 1815
Ancylinae
Rhodacmea Walker 1917

Rhodacmea s.s. (*Ancylus filosus* Conrad 1834)
Rhodocephala Walker 1917 (*Rhodacmea (Rhodocephala) rhodacme* Walker 1917)
Ferrissinae Walker 1917
Ferrissia Walker 1903 (*Ancylus rivularis* Say 1817)
Laevapecinae Hannibal 1912
Hebetancylus Pilsbry 1914 (*Ancylus moricandi* d'Orbigny 1836)
Laevapex Walker 1903 (*Ancylus fuscus* C.B. Adams 1841)

The sizes of the various genera vary enormously, a variation which in some cases undoubtedly reflects real numbers of valid species, but perhaps more often simply indicates the disparate quality of current taxonomy. Below is a taxonomic list of North American freshwater snail genera showing the number of species and subspecies presently recognized for each.

	Number of North American (north of Mexico) Species	Number of Subspecies [and recognized "morphs" or "forms"] *
Subclass Prosobranchia		
Order Neritacea		
Superfamily **Neritinoidea**		
Family NERITIDAE		
Genus *Neritina*		
Subgenus *Vitta*	1	3
Order Mesogastropoda		
Superfamily **Valvatoidea**		
Family VALVATIDAE		
Genus *Valvata*	11	2 [+ 18 "morphs" or "forms"]
Superfamily **Ampullarioidea**		
Family VIVIPARIDAE		
Subfamily Viviparinae		
Genus *Tulotoma*	1	
Genus *Viviparus*	3	

*The numbers in this column are the subspecies [or "morphs" or "forms"] listed in this manual for the various species of each genus. Singly listed subspecies of species in which all other subspecies occur extralimitally are not enumerated.

Subfamily Bellamyinae		
Genus *Cipangopaludina*	2	
Subfamily Lioplacinae		
Genus *Campeloma*	8	[9 "forms"]
Genus *Lioplax*	5	2
Family AMPULLARIIDAE (PILIDAE)		
Genus *Marisa*	1	
Genus *Pomacea*	2	
Family BITHYNIIDAE		
Genus *Bithynia*	1	2
Superfamily **Truncatelloidea**		
Family MICROMELANIIDAE		
Genus *Antroselates*	1	
Family HYDROBIIDAE		
Subfamily Hydrobiinae		
Genus *Aphaostracon*	9	
Genus *Hoyia*	1	
Genus *Hyalopyrgus*	2	
Genus *Littoridinops*	2	
Genus *Probythinella*	1	
Genus *Pyrgophorus*	2	
Genus *Tryonia*	5	
Subfamily Lithoglyphinae		
Genus *Antrobia*	1	
Genus *Clappia*	2	
Genus *Cochliopina*	1	
Genus *Fluminicola*	12	
Genus *Gillia*	1	
Genus *Lepyrium*	1	
Genus *Somatogyrus*		
Subgenus *Somatogyrus* s.s.	32	
Subgenus *Walkerilla*	3	
Subfamily Nymphophilinae		
Genus *Birgella*	1	
Genus *Cincinnatia*	14	
Genus *Fontelicella*		
Subgenus *Fontelicella* s.s.	6	
Subgenus *Microamnicola*	1	
Subgenus *Natricola*	3	
Genus *Marstonia*	8	
Genus *Notogillia*	2	
Genus *Orygoceras*	1	
Genus *Pyrgulopsis*	5	2
Genus *Rhapinema*	1	
Genus *Spilochlamys*	3	
Genus *Stiobia*	1	
Subfamily Amnicolinae		
Genus *Amnicola*		
Subgenus *Amnicola* s.s.	11	7
Subgenus *Lyogyrus*	7	
Genus *Hauffenia*	1	
Genus *Horatia*	1	
Subfamily Fontigentinae		
Genus *Fontigens*	8	

Incertae Sedis	3	
Family POMATIOPSIDAE		
Genus *Pomatiopsis*	6	
Superfamily **Vermetoidea**		
Family THIARIDAE		
Genus *Melanoides*	1	
Genus *Thiara*	1	
Family PLEUROCERIDAE		
Genus *Elimia*	83	41
Genus *Gyrotoma*	6	
Genus *Io*	1	
Genus *Juga*		
Subgenus *Juga* s.s.	3	2
Subgenus *Calibasis*	2	3
Subgenus *Oreobasis*	4	
Genus *Leptoxis*		
Subgenus *Leptoxis* s.s.	16	
Subgenus *Athearnia*	1	2
Subgenus *Mudalia*	6	2
Genus *Lithasia*		
Subgenus *Lithasia* s.s.	3	6
Subgenus *Angitrema*	7	
Genus *Pleurocera*		
Subgenus *Pleurocera* s.s.	18	13
Subgenus *Strephobasis*	3	2
Subclass Pulmonata		
Order Lymnophila		
Superfamily **Acroloxoidea**		
Family ACROLOXIDAE		
Genus *Acroloxus*	1	
Superfamily **Lymnaeoidea**		
Family LYMNAEIDAE		
Subfamily Lymnaeinae		
Genus *Acella*	1	
Genus *Bulimnea*	1	
Genus *Fossaria*		
Subgenus *Fossaria* s.s.	11	
Subgenus *Bakerilymnaea*	11	
Genus *Lymnaea*	2	2
Genus *Pseudosuccinea*	1	
Genus *Radix*	1	
Genus *Stagnicola*		
Subgenus *Stagnicola* s.s.	21	
Subgenus *Hinkleyia*	3	
Subfamily Lancinae		
Genus *Fisherola*	1	3
Genus *Lanx*		
Subgenus *Lanx* s.s.	3	
Subgenus *Walkerola*	1	
Superfamily **Ancyloidea**		
Family PHYSIDAE		
Subfamily Physinae		
Genus *Physa*	2	

Genus *Physella*		
Subgenus *Physella* s.s.	16	16 [+ 5 "morphs"]
Subgenus *Costatella*	14	14 [+ 4 "morphs"]
Subgenus *Petrophysa*	1	
Subfamily Aplexinae		
Genus *Aplexa*	2	[1 "morph"]
Genus *Stenophysa*	2	
Family PLANORBIDAE		
Subfamily Planorbinae		
Tribe Planorbini		
Genus *Gyraulus*		
Subgenus *Gyraulus* s.s.	1	
Subgenus *Armiger*	1	
Subgenus *Torquis*	3	
Tribe Drepanotremini		
Genus *Drepanotrema*		
Subgenus *Antillorbis*	1	
Subgenus *Fossulorbis*	2	
Tribe Biomphalariini		
Genus *Biomphalaria*	2	
Tribe Helisomini		
Genus *Helisoma*		
Subgenus *Helisoma* s.s.	2	2
Subgenus *Carinifex*	1	3
Genus *Menetus*		
Subgenus *Menetus* s.s.	1	
Subgenus *Micromenetus*	3	
Genus *Planorbella*		
Subgenus *Planorbella* s.s.	2	2
Subgenus *Pierosoma*	12	7
Subgenus *Seminolina*	2	[6 "races" or "forms"]
Genus *Planorbula*	2	2
Genus *Promenetus*	2	
Genus *Vorticifex*		
Subgenus *Parapholyx*	2	
Subfamily Neoplanorbinae		
Genus *Amphigyra*	1	
Genus *Neoplanorbis*	4	
Family ANCYLIDAE		
Subfamily Ancylinae		
Genus *Rhodacmea*	3	
Subfamily Ferrissinae		
Genus *Ferrissia*	5	
Subfamily Laevapecinae		
Genus *Hebetancylus*	1	
Genus *Laevapex*	2	

NOMENCLATURE

Nomenclature in the North American freshwater snails has been the subject of considerable controversy and seemingly continuing change. Part of this changing nomenclature has been the discovery from time to time of older names for currently used taxa. Another factor that has caused some nomenclatural instability has been the changing of the rules of nomenclature over the years. Hopefully, the nomenclature is now reasonably stable, but it will no doubt still be subject to some change in the several groups for which there is not yet enough information from which to provide a reasonably definitive classification. Also, probably there will still be some differences in the names used for several taxa because of differing attitudes among individual malacologists regarding application of nomenclature, and about how much difference between taxa is significant enough to warrant the recognition of particular grades of taxa.

Perhaps the greatest subjects of controversy in the past have been the application of some of the ill-defined names of C.S. Rafinesque. These debates are still going on, although one of the longest running disputes was recently settled by a 1981 ruling (Opinion 1195) of the International Commission on Zoological Nomenclature in designating for *Pleurocera* Rafinesque 1818 the type species *P. acuta* Rafinesque (in Blainville) 1824 (see p. 24).

During various periods in the history of North American freshwater malacology, certain familial and generic names were in common use, only to be changed later. Also, there was some confusion as to the authorship of familial names. For example, Rafinesque (1815) is credited now as the first to use formally the family-group names Neritidae*, Lymnaeidae, Planorbidae and Ancylidae, but since his authorship of these families was not generally recognized until relatively recently, most workers credited these names to other authors. In fact, North American authors succeeding Rafinesque, and foreign authors as well, did not divide the freshwater gastropods into the basic groups that we recognize today. Haldeman (1840-71) included all the freshwater pulmonates in the family "Physadae." Tryon (1870-71), who continued Haldeman's monograph, used this

*Rehder (1980) credited the introduction of the family name Neritidae to the vernacular form ["Neritacées" (sic)] used by Lamarck (1812, p. 117). However, there are even earlier vernacular versions of this name (e.g., see Férussac, 1807). Incidentally, Lamarck's "Néritaces" contained only four names as included taxa, all in the vernacular.

same family name, but divided the family into subfamilies, several of which are no longer recognized as family-group assemblages (Pompholiginae Dall 1866; Megasistrophinae Tryon 1870). For the North American freshwater prosobranchs, Haldeman (1845, see pp. 1-3) placed them all in the families Turbidae (based on the marine genus *Turbo*) and Melaniadae* [Pleuroceridae], although he acknowledged other familial arrangements made by Europeans, including that of J.E. Gray (1821), who split the freshwater operculates into several families, represented by the genera *Ampullaria, Paludina* and *Valvata*. [For these latter three groups, modern usage has not changed: these families are Ampullariidae [= Pilidae], Viviparidae (*Paludina*†) and Valvatidae (*Valvata*). Tryon (1870-71) used Turbidae on the cover page of his monograph for the freshwater prosobranchs, but in the text he recognized as families the Ampulariidae, Amnicolidae§ [= Hydrobiidae], Valvatidae and Strepomatidae [= Pleuroceridae].

The nomenclature followed here (pp. 7-14 and Section IV) adheres to the Rules, Recommendations, Opinions and Directions set forth by the International Commission on Zoological Nomenclature. In following the Law of Priority, one well-known generic name now regrettably falls by the wayside: *Goniobasis* Lea 1862 (type species *Goniobasis osculata* Lea 1862 by subsequent designation (Hannibal, 1912)) (= *Elimia* H. & A. Adams 1854, type species *Melania acutocarinata* Lea 1841 by subsequent designation (Pilsbry & Rhodes, 1896)). Getting a ruling by the Commission to conserve the name *Goniobasis* would seem to be virtually impossible, if the case of fixing the type species of *Pleurocera* is taken as an example. It took more than 56 years (from January 20, 1925, until November 1981) to get a ruling on a case less

*Excluding the pleurocerid *Anculosa*, which Haldeman included in the Turbidae.

†*Paludina* Lamarck (in Férussac) 1812, a synonym of *Viviparus* Montfort 1810, was the name given to all members of the Viviparidae in the early literature, to be replaced by *Melantho* Bowdich 1822 for the *P. decisa* Say 1817 group. *Melantho* was later replaced in the literature by *Campeloma* Rafinesque 1819, and this is the name still in use today.

§ In the Hydrobiidae (also referred in past literature to Rissoidae, a family name now restricted to a group of marine prosobranch snails related to the Hydrobiidae, and included with them and several other families in the superfamily Rissoacea [= Truncatelloidea]) and Amnicolidae [a synonym for, or subfamily of, the Hydrobiidae] was *Amnicola* Gould & Haldeman 1840, but today that generic name is used in a much more restricted sense. Many of the species once included in "*Amnicola*" are now placed in various other hydrobiid genera.

clearcut in nature, but of more serious consequence in regard to nomenclatural stability.

Opinions and Directions of the International Commission on Zoological Nomenclature that specifically affect the nomenclature of freshwater snails in North America are listed below and on the several pages following (pp. 20-24).

The Status of Proof Sheets in Nomenclature. This topic brought to question whether *Megasystropha* Lea 1864 (type species *Planorbis newberryi* Lea 1858) should be used rather than *Carinifex* W.G. Binney 1865 (same type species), since the latter was introduced two years earlier (1863) in publically distributed proof-sheets. OPINION 87, December 16, 1925: Printer's proof-sheets do not constitute publication and, therefore, have no status under the International Rules of Zoological Nomenclature. [However, in Opinion 432 (see below), the Commission ruled in favor of *Carinifex* Binney 1865, suppressing *Megasystropha*.]

Twenty-two Mollusk and Tunicate Names Placed in the Official List of Generic Names. These names have priority and therefore do not have to be adopted as *"nomina conservanda"* under "Suspension of the Rules." OPINION 94, October 8, 1926: The following names are hereby placed in the Official List of Generic Names: MOLLUSCA: *Anodonta, Argonauta, Buccinum, Calyptraea, Columbella, Dentalium, Helix, Limax, Mactra, Mya, Mytilus, Ostrea, Physa, Sepia, Sphaerium, Succinea, Teredo.* TUNICATA: *Botryllus, Clavelina, Diazona, Distaplia, Molgula.* [Of interest here to North American freshwater gastropod malacology is the name *Physa*.]

Bulimus Scopoli, 1777, vs. *Bulinus* Mueller, 1781, vs. *Bulimus* Bruguière, 1792. Of importance to North American freshwater malacology is whether or not the name *Bulimus* Scopoli would replace the generic name *Bithynia*. OPINION 116, January 10, 1931: The Commission does not interpret *Bulimus* Scopoli, 1777, as an obvious typographical error; the premises do not show that the genotype (which must be selected from the four originally included species) has been definitely and properly designated. *Bulinus* Mueller, 1781, has for its type *Bulinus senegalensis*, and is not invalidated by *Bulimus*, 1777. *Bulimus* Bruguière, 1792, type *haemastomus* seu *oblonga* is a dead homonym of *Bulimus*, 1777. [In Opinion 475 (see below), the Commission suppressed the name *Bulimus* Scopoli 1777 in favor of *Bithynia* Leach (in Abel) 1818.]

Six Molluscan Generic Names Placed in the Official List of Generic Names. These names have priority and therefore do not have to be adopted as *"nomina conservanda"* under "Suspension of the Rules." OPINION 119, January 10, 1931: The following six generic names of *MOLLUSCA* are hereby placed in the Official List of Generic Names, with types as stated: *Cerion* (*uva*), *Oleacina* (*voluta*), *Neritina* (*pulligera*), *Clausilia* (*rugosa*), *Vitrina* (*pellucida*), *Tornatellina* (*clausa*). [Of interest here to North American freshwater malacology is the name *Neritina*.]

Addition to the "Official List of Generic Names in Zoology" of the names of thirty-four non-marine genera of the Phylum Mollusca. OPINION 335, March 17, 1955:- ... (2) The under-mentioned names of non-marine genera of the Class Gastropoda are hereby placed on the *Official List of Generic Names in Zoology* with the Name Nos. 810 to 841 respectively:- ... (iii) *Aplexa* Fleming, 1820 (gender of name: feminine) (type species by monotypy: *Bulla hypnorum* Linnaeus, 1758). ... (xxix) *Valvata* Müller (O.F.), 1774 (gender of name: feminine) (type species, by monotypy: *Valvata cristata* Müller (O.F.), 1774). ... (5) The under-mentioned specific names, being the names of type species of genera of the Class Gastropoda placed on the *Official List of Generic Names in Zoology* under (2) above, are hereby placed on the *Official List of Specific Names in Zoology* with the Name Nos. 292 to 315 respectively:- ... (vii) *cristata* Müller (O.F.), 1774, as published in the combination *Valvata cristata* (specific name of the type species of *Valvata* Müller (O.F.), 1774). ... (xii) *hypnorum* Linnaeus, 1758, as published in the combination *Bulla hypnorum* (specific name of type species of *Aplexa* Fleming, 1820) ... .

Addition to the "Official List of Specific Names in Zoology" of the Specific names of one hundred and twenty-two non-marine species of the Phylum Mollusca. OPINION 336, March 17, 1955: (1) the under-mentioned specific names of non-marine species of the Class Gastropoda are placed on the *Official List of Generic Names in Zoology* with the Name Nos. 324 to 425 respectively:- (i) *acuta* Draparnaud, [1805], as published in the combination *Physa acuta;* (ii) *albus* Müller (O.F.), 1774, as published in the combination *Planorbis albus;* ... (x) *auricularia* Linnaeus 1758, as published in the combination *Helix auricularia;* ... (xx) *crista* Linnaeus, 1758, as published in the combination *Nautilus crista;* ... (xxiv) *dilatatus* Gould, 1841, as published in the combination *Planorbis dilatatus;* ... (xxxii) *fontinalis* Linnaeus, 1758, as published in the combination *Bulla fontinalis;* ... (lxxxvii) *stagnalis* Linnaeus, 1758, as published in the combination *Helix stagnalis;* ... (xcv) *truncatulum* Müller (O.F.), 1774, as published in the combination *Buccinum truncatulum;* ...

Addition to the "Official List of Family-Group Names in Zoology" of Family-Group Names Based on the Names of Certain Genera of Non-marine Mollusca Placed on the *Official List of Generic Names in Zoology* by the Ruling Given in "Opinion" 335. "DIRECTION 27, August 5, 1955:- (1) The under-mentioned family-group names, each of which is the name of a family-group taxon, the type genus of which was placed on the *Official List of Generic Names in Zoology* by the Ruling given in Opinion 335, are hereby placed on the *Official List of Family-Group Names in Zoology* with the Name Nos. severally specified below:- ... (xi) PLANORBIDAE Gray (J.E.), 1840 (type genus: *Planorbis* Müller (O.F.), 1774 (Name No. 47) [Planorbia Rafinesque 1815, subfamily, = Planorbinae (now Planorbidae), has priority]; ... (xviii) VALVATIDAE Gray (J.E.), 1840 (Type genus: *Valvata* Müller (O.F.), 1774) (Name No. 54); ... .

Designation, Under the Plenary Powers, of a Type Species in Harmony with Accustomed Usage for the Nominal Genus "*Ancylus*" Müller (O.F.), 1774 (Class Gastropoda). OPINION 363, November 4, 1955:- (1) Under the Plenary Powers (a) selections of type species for the nominal genus *Ancylus* Müller (O.F.), 1774 (Class Gastropoda) made prior to the present Ruling are hereby set aside, and (b) the nominal species *Ancylus fluviatilis* Müller (O.F.), 1774, is hereby designated to be the type species of the foregoing genus. (2) The under-mentioned generic names are hereby placed on the *Official List of Generic Names in Zoology* with the Name Nos. 884 and 885 respectively:- (a) *Ancylus* Müller (O.F.), 1774 (gender: masculine) (type species, by designation under the Plenary Powers under (1)(b) above: *Ancylus fluviatilis* Müller (O.F.), 1774: 199-200); (b) *Acroloxus* Beck, 1837 (gender: masculine) (type species, by selection by Herrmannsen (1846): *Patella lacustris* Linnaeus, 1758, as interpreted by Müller (O.F.), 1774: 199-200); (3) The under-named specific names are hereby placed on the *Official List of Specific Names in Zoology* with the Name Nos. 502 and 503 respectively:- (a) *fluviatilis* Müller (O.F.), 1774, as published in the combination *Ancylus fluviatilis* (specific name, by designation under the Plenary Powers under (1)(b) above, of type species of *Ancylus* Müller (O.F.), 1773; (b) *lacustris* Linnaeus, 1758, as published in the combination *Patella lacustris*, as interpreted in the manner specified in (2)(b) above (specific name of type species of *Acroloxus* Beck, 1837). .... .

Addition to the "Official List of Family-Group Names in Zoology" ... of the Family-Group Names Involved in Volume 11 of the "Opinions and Declarations Rendered by the International Commission on Zoological Nomenclature", Other Than Family-Group Names Already Dealt With in Those "Opinions". DIRECTION 41, February 24, 1956:- (1) The under-mentioned family-group names involved in the cases dealth with in the *Opinions* included in volume 11 of the *Opinions and Declarations Rendered by the International Commission on Zoological Nomenclature* are hereby placed on the *Official List of Family-Group Names in Zoollogy* with the Name Numbers severally specified below:- ... (c) ANCYLINAE (correction of ANCYLIDIA) Rafinesque (C.S.), 1815 (type genus: *Ancylus* Müller (O.F.), 1774) (name proposed by Rafinesque as the name for a "sous-famille"; first published with an approved termination (as ANCYLINAE) by Fischer (P.), [1883]) (Class Gastropoda) (*Opinion* 363) (Name No, 78); (d) ACROLOXINAE Thiele (J.), 1931 (type genus: *Acroloxus* Beck, 1837) (Class Gastropoda) (*Opinion* 363) (Name No. 79); .... .

Proposed Use of the Plenary Powers to Validate the Generic Name *"Carinifex"* Binney, 1865 (Class Gastropoda). Joshua L. Bailey, Jr., reopened the case of *Megasystropha* Lea vs. *Carinifex* Binney, giving additional relevant information and pointing out the almost universal use of *Carinifex* over *Megasystropha*. OPINION 432, November 14, 1956: Rejection, as an unpublished proof, of the paper by Binney (W. G.) dated "9th December 1863" and entitled *Synopsis of the Species of Air-breathing Mollusks of North America* (confirmation of Ruling given in *Opinion* 87) and validation under the Plenary Powers of the generic name *Carinifex* Binney, 1865 (Class Gastropoda).

Proposed Validation under the Plenary Powers of the Generic Name *"Bithynia"* Leach, 1818 (Class Gastropoda). The purpose of this application was to prevent "the appalling confusion and disturbance which would result from the disappearance of this long-established name as a junior synonym of *Bulimus* Scopoli, 1777." OPINION 475, July 31, 1957: Under the Plenary Powers the undermentioned generic name is hereby suppressed for the purposes of the Law of Priority but not for those of the Law of Homonymy: *Bulimus* Scopoli, 1777. (2) The under-mentioned generic names are hereby placed on the *Official List of Generic Names in Zoology* with the Name Numbers severally specified below:- (a) *Bithynia* Leach, 1818, as validated under the Plenary Powers in (1) above (gender: feminine) (type species, by original designation: *Helix tentaculata* Linneaus, 1758) (Name Number 1195); .... (3) the under-mentioned specific names are hereby placed on the *Official List of Specific Names in Zoology* with the Name Numbers severally specified below:- (a) *tentaculata* Linnaeus, 1758, as published in the combination *Helix tentaculata* (specific name of type species of *Bithynia* Leach, 1818) (Name No. 1301). ... (5) The under-mentioned family-group name is hereby placed on the *Official List of Family-Group Names in Zoology* with the Name Number 181:- BITHYNIIDAE (correction of BITHINIADAE) Gray (J.E.), 1857 (type genus: *Bithynia* Leach, 1818) for use by specialists who on taxonomic grounds consider that the genus *Bithynia*

Leach is not referable to any nominal family-group taxon having an older name). ... .

Proposed use of the Plenary Powers to give precedence to the generic name *Biomphalaria* Preston. OPINION 735, May, 1965: (1) Under the plenary powers it is hereby ruled that the generic name *Biomphalaria* Preston, 1910, is to be given precedence over the generic names *Planorbina* Haldeman, 1842, *Taphius* H. & A. Adams, 1855, and *Armigerus*, Clessin, 1884, by any zoologist who considers that any or all of these names apply to the same taxonomic genus. (2) The following names are hereby placed on the Official List of Generic Names in Zoology with the Name Numbers specified: (a) *Biomphalaria smithi* Preston, 1910 (Name No. 1675); (b) *Planorbina* Haldeman, 1842, (gender: feminine), type-species, by designation by Dall, 1905, *Planorbis olivaceus* Spix, 1827 (by direction under the plenary powers, not available for use in preference to *Biomphalaria* Preston, 1910, by any zoologist who considers the type-species of these two nominal genera to be congeneric) (Name No. 1676); (c) *Taphius* H. & A. Adams, 1855 (gender: masculine), type-species, by original designation, *Planorbis andecolus* d'Orbigny, 1835 (by direction under the plenary powers, not available for use in preference to *Biomphalaria* Preston, 1910, by any zoologist who considers the type-species of these two nominal genera to be congeneric) (Name No. 1677); (c) *Armigerus* Clessin, 1884, (gender: masculine), type-species, by designation by Morrison, 1947, *Planorbis albicans* Pfeiffer, 1839) (by direction under the plenary powers, not available for use in preference to *Biomphalaria* Preston, 1910, by any zoologist who considers the type-species of these two nominal genera to be congeneric) (Name No. 1678). (3) The following specific names are hereby placed on the *Official List of Specific Names in Zoology* with the Name Numbers specified: (a) *smithi* Preston, 1910, as published in the binomen *Biomphalaria smithi* (type-species of *Biomphalaria* Preston, 1910) (Name No. 2079); (b) *olivaceus* Spix, 1827, as published in the binomen *Planorbis olivaceus* (type-species of *Planorbina* Haldeman, 1842) (Name No. 2080); (c) *andecolus* d'Orbigny, 1835, as published in the binomen *Planorbis andecolus* (type-species of *Taphius* H. & A. Adams, 1855) (Name No. 2081); (d) *albicans* Pfeiffer, 1839, as published in the binomen *Planorbis albicans* (type-species of *Armigerus* Clessin, 1884) (Name No. 2082).

Completion and in certain cases correction of entries relating to the names of genera of the phyla Mollusca, Brachiopoda, Echinoderma and Chordata made on the "Official List of Generic Names in Zoology" by rulings given in "Opinions" rendered in the period up to the end of 1936. DIRECTION 72, September 20, 1957. Ruling: - ... (2) In the case of the names of each of the undermentioned genera belonging to the Classes severally noted below the entry made on the *Official List of Generic Names in Zoology* by the Ruling given in *Opinion 94* is hereby completed by the insertion of the particulars as to the manner in which the type species was determined under Article 30 specified below. (i) Class Gastropoda, ... (d) *Physa* Draparnaud, [1801]: by selection by Children (J.G.) (1823). ... (16) The under-mentioned generic names or reputed generic names are hereby placed on the *Official Index of Rejected and Invalid Generic Names in Zoology* with the Name Numbers severally specified below: - ... (xix) *Physa* Raffray, 1890 (a junior homonym of *Physa* Draparnaud, [1801]; (name No. 978) ... .

Conservation of *Marstonia* Baker, 1926 and of *Amnicola lustrica* Pilsbry, 1890 (Mollusca: Gastropoda). OPINION 1108, October, 1978: (1) Under the plenary powers, the specific name *lustrica* Say, 1821, as published in the binomen *Paludina lustrica*, is hereby suppressed for the purposes of both the Law of Priority and the Law of Homonymy. (2) The following names are hereby placed on the Official List of Generic Names in Zoology with the name numbers specified: (a) *Amnicola* Gould & Haldeman, 1840 (gender: feminine), type-species, by subsequent designation by Herrmannsen, 1846, *Paludina porata* Say, 1821 (Name Number 2061); (b) *Marstonia* Baker, 1926 (gender: feminine), type-species, by original designation, *Amnicola lustrica* Pilsbry, 1890 (Name Number 2062). (3) The following names are hereby placed on the Official List of Specific Names in Zoology with the Name Numbers specified: (a) *limosa* Say, 1817, as published in the binomen *Paludina limosa* (Name Number 2640); (b) *lustrica* Pilsbry, 1890, as published in the binomen *Amnicola lustrica* (specific name of type-species of *Marstonia* Baker, 1926) (Name Number 2641). (4) The generic name *Euamnicola* Fischer & Crosse, 1891 (a junior objective synonym of *Amnicola* Gould & Haldeman, 1840) is hereby placed on the Official Index of Rejected and Invalid Specific Names in Zoology with the Name Numbers specified: (a) *lustrica* Say, 1821, as published in the binomen *Amnicola lustrica*, and as suppressed under the plenary powers in (1) above (Name Number 1037); (b) *lacustris* Pilsbry, 1891, as published in the binomen *Amnicola lacustris* (an erroneous subsequent spelling or junior objective synonym of *Amnicola lustrica* Pilsbry, 1980) (Name Number 1038). (6) The name AMNICOLIDAE Tryon, 1862 (type-genus *Amnicola* Gould & Haldeman, 1840) is hereby placed on the Official List of Family-Group Names in Zoology with the Name Number 489.

Proposed Futher Use of the Plenary Powers in the Case of the Generic Name *Pleurocera* Rafinesque, 1818 (Class Gastropoda). Z.N.(S.)83. OPINION 1195, November, 1981: (1) the authorship of the specific name *acutus*, as published in the binomen *Pleurocerus acutus*, is to be cited as "Rafinesque *in* Blainville, 1824". (2) Under the plenary powers, all designations of type species for the nominal genus *Pleurocera* are hereby set aside and *Pleurocerus acutus* Rafinesque *in* Blainville, 1824 is hereby designated as type species of that genus. (3) The following generic names are hereby placed on the *Official List of Generic Names in Zoology* with the Name Numbers specified: (a) *Pleurocera* Rafinesque, 1818 (gender, feminine), type species, by designation under the plenary powers as in (2) above, *Pleurocerus acutus* Rafinesque *in* Blainville, 1824 (Name Number 2137); (b) *Lithasia* Haldeman, 1840 (gender: feminine), type species, by monotypy, *Anculosa (Lithasia) geniculata* Haldeman, 1840 (Name Number 2138). (4) The following specific names are hereby placed on the *Official List of Specific Names in Zoology* with the Name Numbers specified: (a) *acutus* Rafinesque *in* Blainville, 1824, as published in the binomen *Pleuroceras acutus* (specific name of type species of *Pleurocera* Rafinesque, 1818) (Name Number 2768); (b) *geniculata* Haldeman, 1840, as published in the combination *Anculosa (Lithasia) geniculata* (specific name of type species of *Lithasia* Haldeman, 1840) (Name Number 2769).

IDENTIFICATION AND MORPHOLOGY

Shell Morphology

All freshwater snails possess a shell, which is a hard, calcareous structure that covers the soft parts of the animals bodies, providing protection. In most snails, the shell is twisted in a continually increasing spiral. The characteristics of this shell are different for each species. Therefore, the individual characters of the shells of freshwater snails (see Figs. 1, 2) are very important in species recognition and usually for generic and familial placement as well. Especially useful are the size (Fig. 3) and general form (Figs. 4, 5, 6) of the shell. Among the many species, the shell may take various shapes (Fig. 4), yet, for any one species, the shell shape is usually quite constant (excepting, of course, individual differences and the minor clinal, populational and ecophenotypic variations exhibited by some species). The shells among the various species may vary from very elongate (Fig. 5a,b) to nearly globose (Fig. 4c), depressed (Fig. 4d) and discoidal (Fig. 4e).

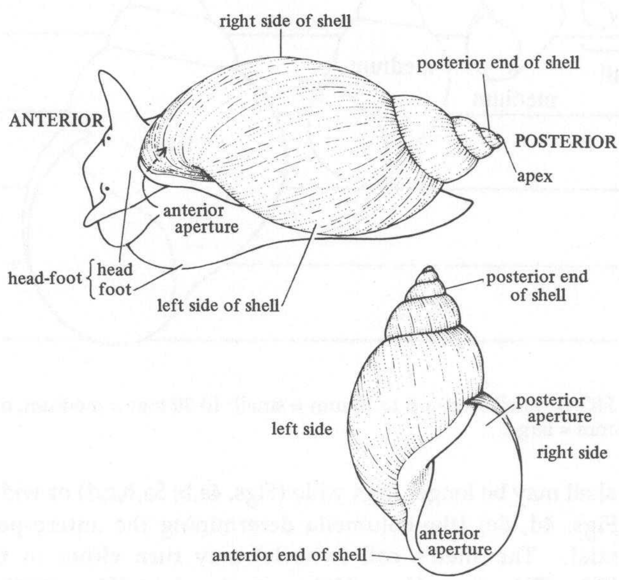


FIG. 1. Orientation of the shell in relation to the snail.

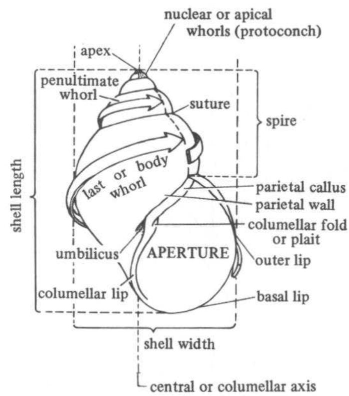


FIG. 2. Shell terminology.

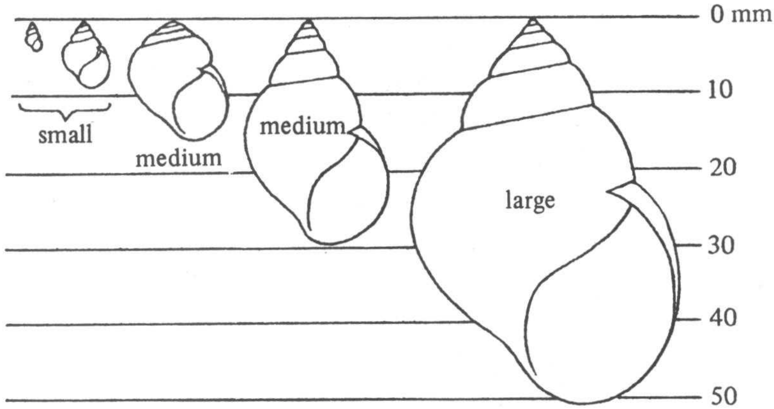


FIG. 3. Shell sizes: up to 10 mm = small; 10-30 mm = medium; over 30 mm = large.

The shell may be longer than wide (Figs. 4a,b; 5a,b,c,d) or wider than long (Figs. 4d, 5e) [the columella determining the antero-posterior shell axis]. The shell's coil (whorls) may turn either to the left (Figs. 773a, 774a, Sect. V, p. 218) or to the right (Figs. 773b, 774b),

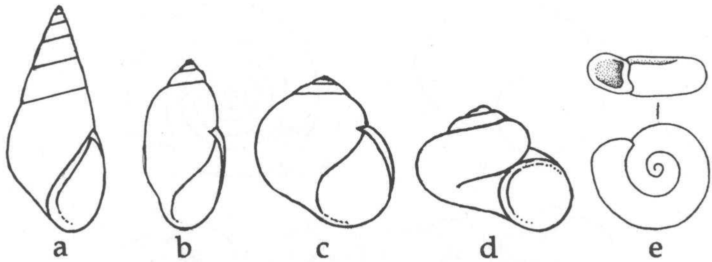


FIG. 4. Shell shapes. **a**, Elongate conic; **b**, elongate cylindrical; **c**, globose; **d**, depressed; **e**, discoidal.

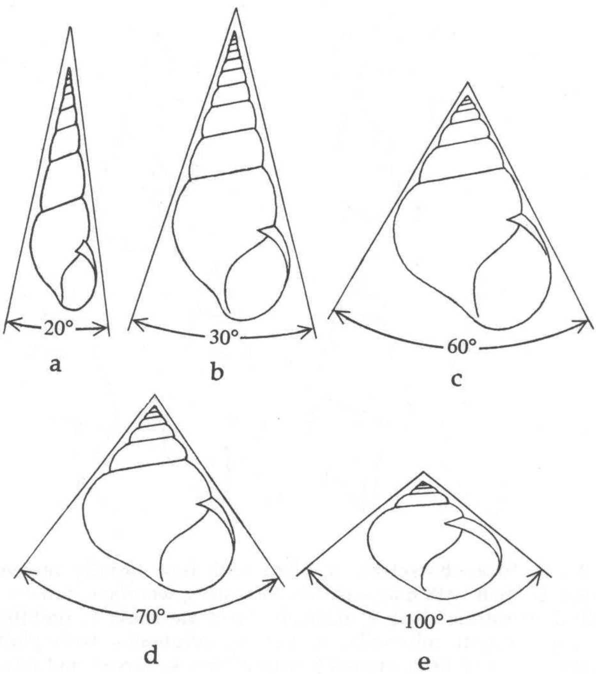


FIG. 5. Shell shapes. **a**, Narrowly conic; **b**, elongately conic; **c**, broadly (ovately) conic; **d**, globosely conic; **e**, depressed conic.

be round (Fig. 776a, Sect. V, p. 220), angular, flattened (Fig. 776b), or shouldered (Fig. 776c,) and may have impressed (Fig. 776a) or shallow sutures (Fig. 776b) The shell may have few (Fig. 6a)

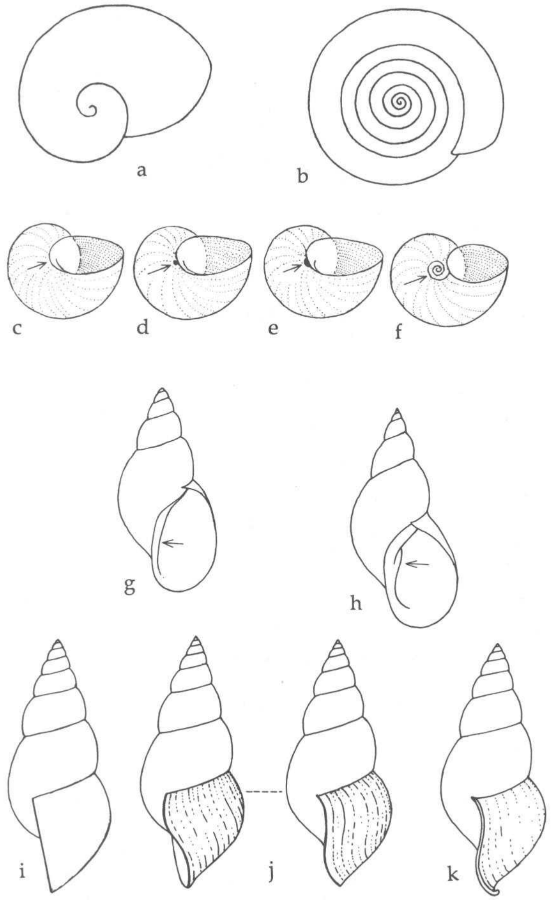


FIG. 6. Shell characters. **a**, Shell with few, rapidly increasing whorls; **b**, shell with many, slowly increasing whorls; **c**, imperforate shell; **d**, perforate shell; **e**, rimately perforate shell; **f**, umbilicate shell; **g**, straight columella; **h**, twisted columella, with plait; **i**, straight apertural lip; **j**, curved apertural lips; **k**, curved and reflected lip.

or many (Fig. 6b) whorls, may lack an opening (umbilicus) at its "base" (Fig. 6c), or may have either a narrow (Fig. 6d) or wide (Fig. 6f) opening. The columella or central axial column of the shell may be straight (Fig. 6g) or twisted (Fig. 6h) and may or may not end abruptly. The outer margin of the shell aperture may be either

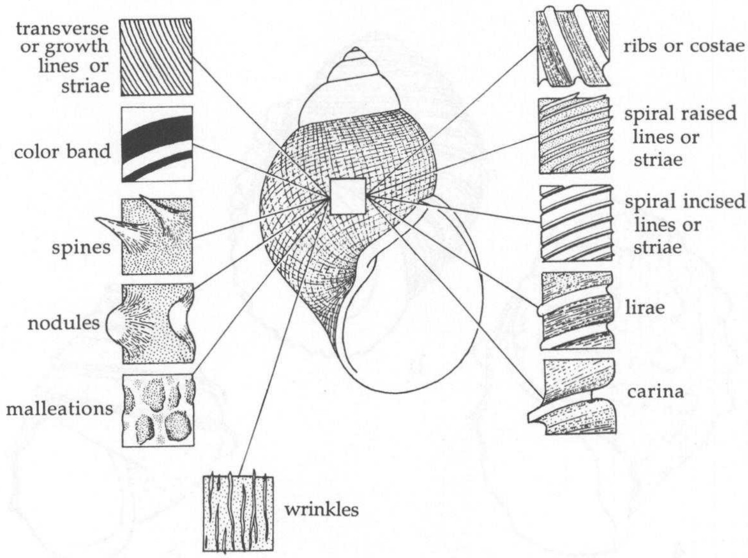


FIG. 7. Shell surface characters.

straight (Fig. 6i) or variously curved (Fig. 6j) and is sometimes turned back or reflected (Fig. 6k). The surface of the shell may be marked in various ways, i.e., it may be differentially colored (Fig. 8f) or sculptured (Figs. 7, 8), or it may be simply unicolored and smooth. The sculpturing of the shell, i.e., its surface texture, is sometimes almost perfectly smooth, but usually there is a definite three-dimensional pattern which is characteristic for the species. One pattern possessed by nearly all shells, in addition to any other pattern they may have, is a series of close-set, more or less equidistant lines paralleling the shell aperture. These are lines indicating incremental shell growth, and are most commonly referred to as "growth lines," but also as "transverse lines" or "transverse striae" (see Fig. 7). On the shells of some species, somewhat larger and more noticeable transverse elevations more distantly apart are superimposed on the growth lines. These are called "riblets." When such shell surface structures are even larger and strikingly noticeable, the are called "ribs" or "costae" (see also Fig. 8d). Similar shell surface elevations running perpendicular (i.e., in the direction of the shell's spiral) to the growth lines are called "lirae" (see also Fig. 8b). When such

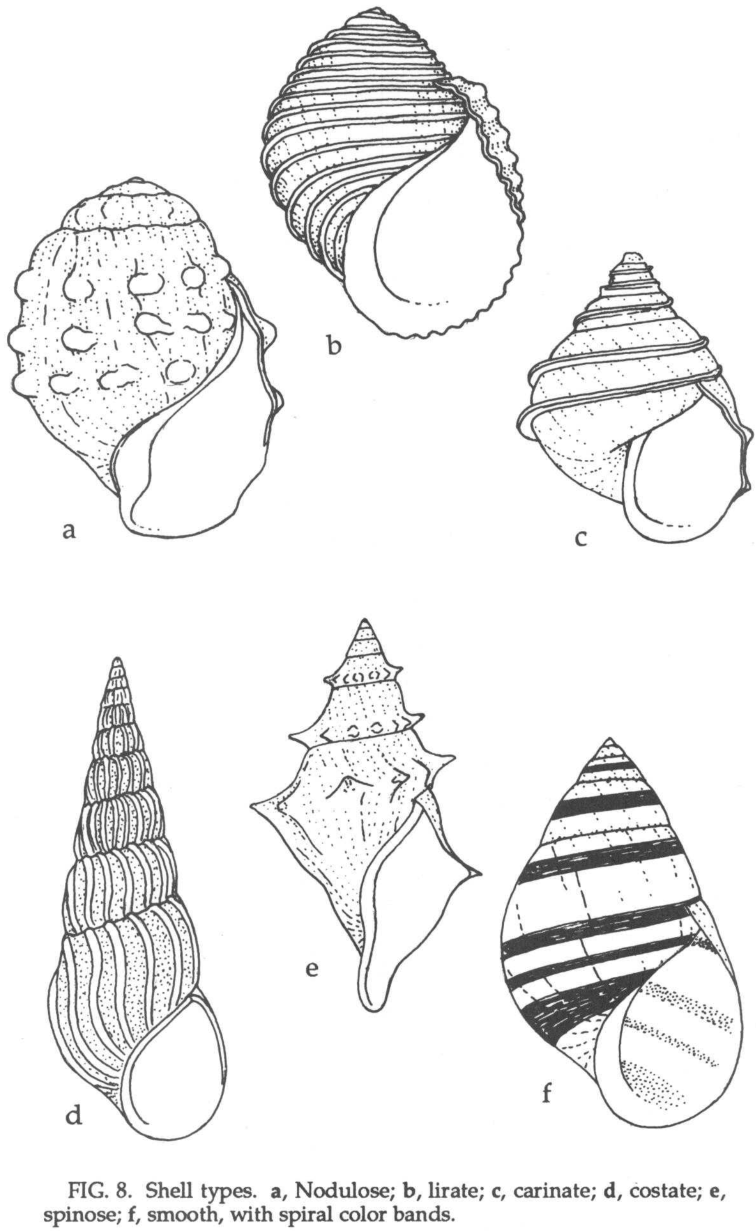


FIG. 8. Shell types. **a**, Nodulose; **b**, lirate; **c**, carinate; **d**, costate; **e**, spinose; **f**, smooth, with spiral color bands.

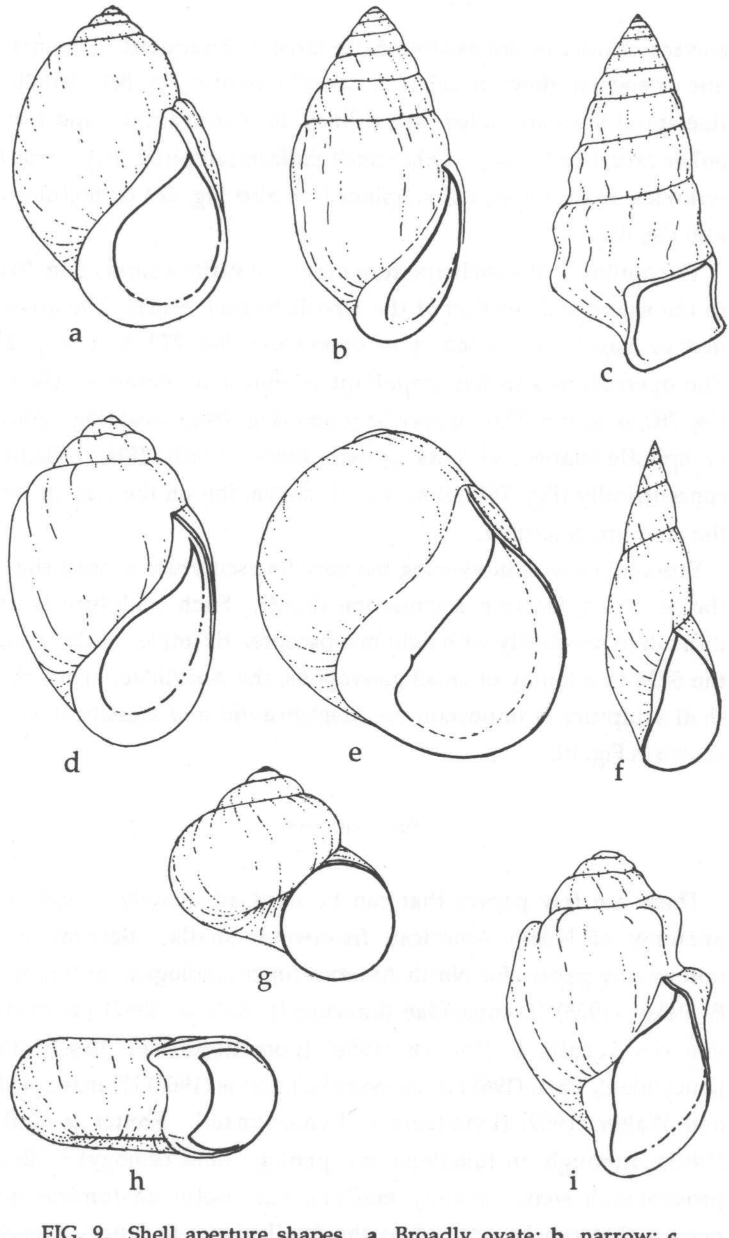


FIG. 9. Shell aperture shapes. **a**, Broadly ovate; **b**, narrow; **c**, rectangular; **d**, elongately ovate; **e**, semicircular; **f**, D-shaped; **g**, round; **h**, lunate; **i**, fusiform or spindle-shaped.

surface structures are exceptionally large and reduced in number to one or several, they are called "carinae" (see also Fig. 8c). Small and fine spiral lines are called "spiral lines" or "spiral striae," and may be either raised or incised. Other shell surface sculpture may consist of wrinkles, malleations, hairs, spines (see also Fig. 8e) or nodules (see also Fig. 8a).

The outline of the shell aperture may take various forms (Fig. 9) due to the shape and relation of the whorls to each other. The aperture may or may not be closed by an operculum (Fig. 772, Sect. V, p. 218). The operculum also has important recognition characters (Sect. V, Fig. 780, p. 220; p. 223). It may be round (Fig. 780a), oval (Fig. 780b,c,d) or spindle-shaped, and its growth lines spirally (Fig. 780a,b) or concentrically (Fig. 780c,d) arranged, depending on the way in which the aperture is formed.

Especially useful in viewing the very fine sculpture of snail shells is the Scanning Electron Microscope (SEM). Such sculpture is often difficult to see clearly with light microscopes. Examples of the value of the SEM in a family of small gastropods, the Ancylidae, in which the shell sculpture is important for identification and classification, are shown in Fig. 10.

Soft Anatomy

There are few papers that can be used adequately as guides to anatomy of North American freshwater snails. Several of the noteworthy papers for North America (in chronological order) are H. B. Baker (1925) [Lymnaeidae (Lancinae)], Abbott (1952) [Thiaridae], van der Schalie & Dundee (1956) [Pomatiopsidae], Basch (1959) [Ancylidae], Dazo (1965) [Pleuroceridae], Davis (1967) [Pomatiopsidae] and Walter (1969) [Lymnaeidae (Lymnaeinae)]. Fretter & Graham (1962), although on functional morphology (and ecology) of British prosobranch snails (mainly marine), has useful anatomical information that can be applied at the family level to North American freshwater snails (Neritidae, Valvatidae, Viviparidae, Ampullariidae, Bithyniidae and Hydrobiidae).

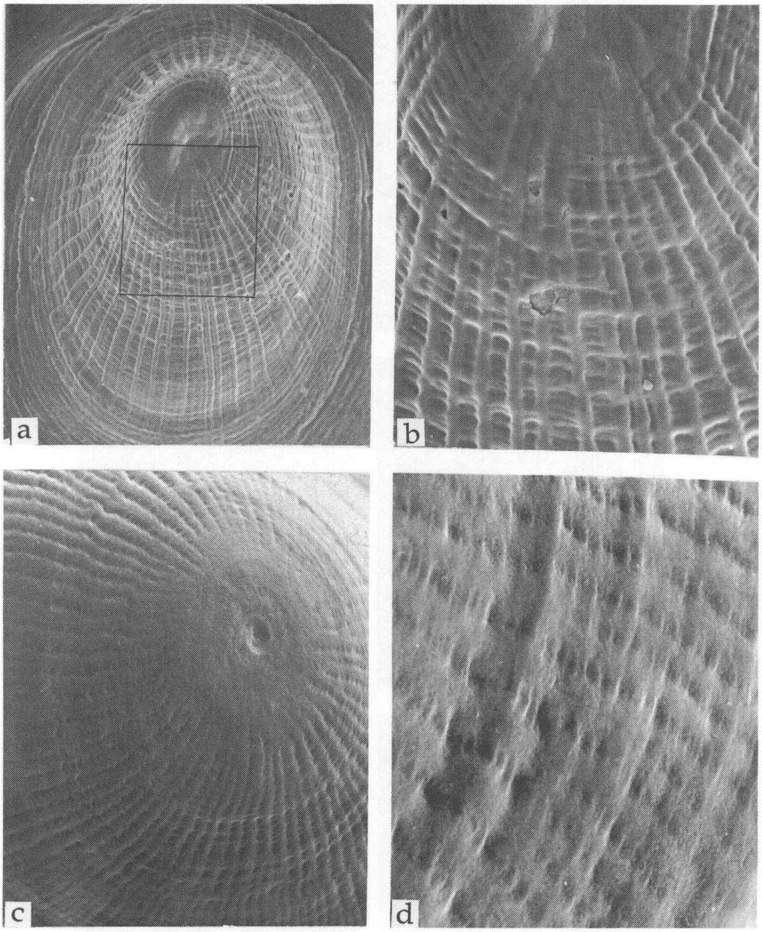


FIG. 10. Apical shell surface sculpture of some North American freshwater limpets (Ancylidae). **a, b**, *Rhodacmea filosa,* apical sculpture of strong radiating and weaker cords (b is an enlargement of the area marked in a); **c**, *Ferrissia walkeri;* apical sculpture of prominent radiating, regularly spaced, narrow grooves; **d**, *F. shimeki,* apical sculpture similar to *F. walkeri.* SEM photographs; a, ca. x52; b,c, ca. x190; d, ca. x625.

External Anatomy

Shelled snails have a peculiarly coiled body with asymmetrically arranged visceral organs. Because of the coiled body, most snails

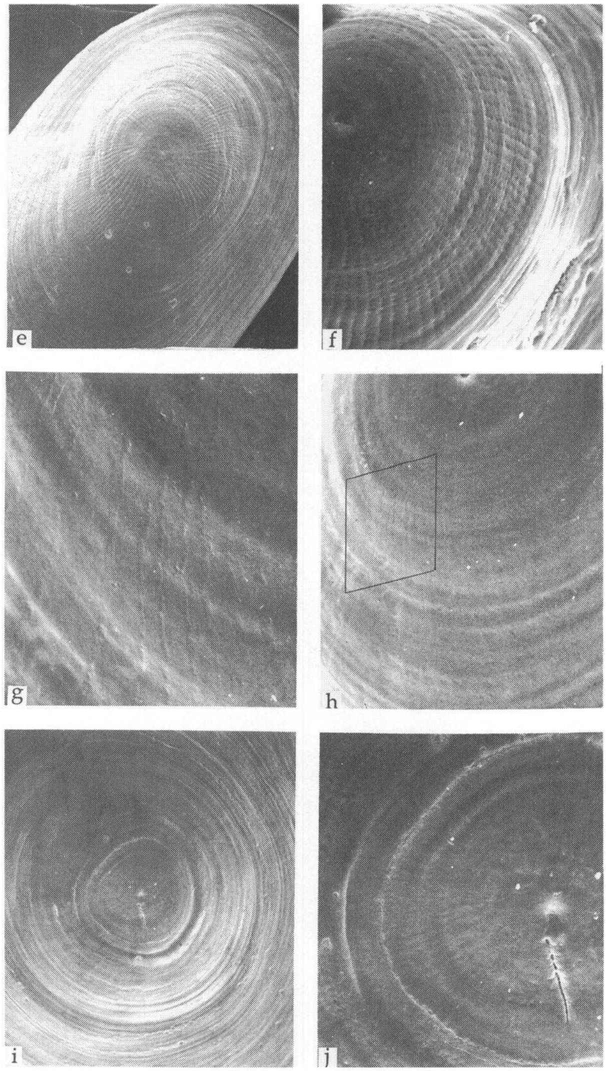


FIG. 10 (cont.). SEM photographs of ancylid apical shell sculpture (cont.). **e**, *Ferrissia "californica" [fragilis]*, with apical sculpture similar to *F. shimeki* and *F. walkeri*; **f**, *F. shimeki*; **g**, **h**, *Hebetancylus excentricus*, in which the apical sculpture is very weak and shallow, with a radiating pattern (under the light microscope, the apex looks smooth, or nearly so); **i**, **j**, *Laevapex diaphanus*, with apical sculpture of very faint, irregularly spaced, very shallow, radiating grooves (like *H. excentricus* and *L. fuscus*, the apex looks more or less smooth under the light microscope). e, i, ca. x44; f, h, j, ca. x134; g, ca. x440.

have a coiled shell, which exhibits spiral symmetry. However, in the limpet-shaped aquatic gastropods, the shell has lost its spiral form and may be more of less bilaterally symmetrical. External aspects of the head and foot may appear to be bilaterally symmetrical as well, but the internal organs nevertheless display the typical asymmetry of gastropods. This asymmetry of the gastropods makes dissection difficult for beginning students of molluscan anatomy and taxonomy.

When a shelled snail is active, the head and foot protrude from the shell aperture, while the visceral mass remains within the shell. Nearly all snails can withdraw their head-foot into the shell when disturbed or during unfavorable climatic periods. This withdrawal is accomplished by the contraction of the columellar muscle, which is formed by a coalescence of muscle fibers from the foot which attach to the shell's columella. In a coiled shell, the columellar muscle insertion is the only attachment of the snail's body to the shell. In operculated snails (i.e., mostly the prosobranchs), the operculum, which is attached to the posterior dorsal surface of the foot, reaches the peristome last when the snail withdraws and thus effectively seals the shell aperture.

In gastropods, the foot is a wide, dorsally convex and ventrally flat, muscular organ, covered with a tough skin containing numerous mucous glands. The integument is generally pigmented by melanin granules, especially on the dorsum and sides.

The head is rather well separated from the foot in prosobranch snails, but in pulmonate snails it is not externally delimited from the foot (hence the term "head-foot" is often applied to these two combined structures in pulmonates). The head bears two tentacles in freshwater snails; at the base of each of the tentacles is an eye. The tentacles are tactile sensory structures, and may vary from one taxon to another in degree, color and arrangement of pigment, in shape, in bluntness of the tip, in length, and in possession and arrangement of surface ciliation.

Externally, gastropods have a number of orifices for various of the organ systems. These openings are the mouth, anus, mantle cavity or pulmonary cavity, the nephridiopore and the male and female reproductive openings. The mouth may be little more than an opening in the head, but in many snails it is placed at the end of a rather long anterio-ventrally directed proboscis. This is especially noticeable in the prosobranchs. In the pulmonates, the proboscis is much shorter, and is often referred to as a "snout." The mouth is at the anterior end, medianly placed on the ventral side, as would be expected. However, the other end of the digestive tract, the anus, is not located posteriorly, but, because of torsion, is placed anteriorly. Near it are the nephridiopore and, on the side of the foot, the female gonopore. The male opening in pulmonate snails is on the head-foot, near one of the tentacles. Torsion also brings the mantle cavity and its external opening forward. Except for the medianly placed mouth, the side of the body on which these various openings are located depends on the direction of coiling of the snail. The openings are on the right side in dextral snails and on the left side in sinistral snails (see Fig. 773, Sect. V, p. 218).

The external characteristics of the snails' bodies are useful in identification and are often especially pertinent in classification. For example, among the prosobranchs, the Valvatidae have two structures lacking in other North American freshwater operculates (Fig. 781, Sect. V, p. 220): an externally protruding bipectinate gill and a mantle tentacular appendage. In Valvatidae and male Neritidae, an external penis is located on the head under the right tentacle. In other North American freshwater prosobranch snails, the penis, when present, is located elsewhere. In the Viviparidae, each male has a noticeable thickened right tentacle, which functions as a modified penis. In the Bithyniidae, Hydrobiidae (Figs. 83, 85-92, Sect. IV, pp. 94, 95) and Pomatiopsidae (Fig. 18, p. 51 (B)), the males have a large external male organ located dorsally behind the head. Males in the Pleuroceridae (Fig. 18, p. 61 (A)) lack male intromittent organs. [Males are absent in *Melanoides tuberculata* and *Thiara granifera* (Thiaridae).]

The Thiaridae have very noticeable papillae projecting from the mantle collar (Fig. 18A,B, p. 54). The closely related pleurocerid snails lack such mantle papillae, as do the other North American freshwater prosobranchs. The Ampullariidae have a long siphon, used to take air into the lung portion of the mantle cavity. Such a structure is lacking in other freshwater prosobranchs. The Bithyniidae have a peculiar lobe or siphon (external accessory excretory organ?) on the right side of the body near the mantle cavity opening.

The pigmentation patterns of the mantle in the Hydrobiidae often have distinctive specific patterns (e.g., see Figs. 83-94, Sect. IV, pp. 94, 95). But especially useful for taxonomic recognition in the Hydrobiidae are the external male copulatory organs, the verge and penis, which are distinctive for many of the genera, and can be used also to recognize subfamilies (Fig. 82, Sect. IV, p. 94). In some hydrobiid groups, such aspects of the external soft anatomy are *essential* for identification, because the various taxa in these groups have shells which are relatively uniform or have few distinctive characteristics. In such groups as these, identification is very difficult for samples in which only empty shells are available. In these cases, identification can be aided by taking into account the known distributions of the various species, and by making especially careful observations of shell characters.

Among the pulmonates, the Acroloxidae, Planorbidae (see Fig. 773a, Sect. V, p. 218) and Ancylidae have pseudobranchs (false gills), but the Lymnaeidae and Physidae do not; the lymnaeids have broad, flat, triangular tentacles (see Fig. 1, p. 25; 773b, Sect. V, p. 218), while the tentacles of members of the other freshwater pulmonate families are filiform; the Physidae have digitate mantle lobes, while the mantle border is smooth in the other pulmonate families. Within the Physidae, the number and arrangement of the digitate mantle lobes have some taxonomic significance. In the Ancylidae, the arrangement of the dorsal shell adductor muscles are useful for generic recognition (Fig. 11, pp. 38, 39), as are mantle pigmentation patterns.

Internal Anatomy

In some families, characters of the internal soft anatomy are important in classification, and often identification as well, because the shells of various of the lower taxa do not exhibit clearly any distinguishing features. For this reason, it is of some practical value to be familiar with the organ systems of freshwater snails.

The two most conspicuous organ systems in a snail are the digestive system (Fig. 12, p. 41; Fig. 18, pp. 50, 56, 59, 63, 70) and the reproductive system (Fig. 18, pp. 49, 51, 52, 58, 61, 62, 65, 68, 73). Together, the two systems make up the greater portion of a snail's body mass. In the digestive system, the mouth opening leads into a short buccal atrium, the pharynx or oral cavity (Fig. 12b, p. 41; Fig. 18, p. 55). The alimentary tract then expands into a relatively large, highly muscular buccal mass, which contains the radula, radular sac, jaw and odontophoral cartilage. Salivary ducts open into the oral cavity near the radular sac. Leading posteriorly from the buccal mass is the esophagus, a long,

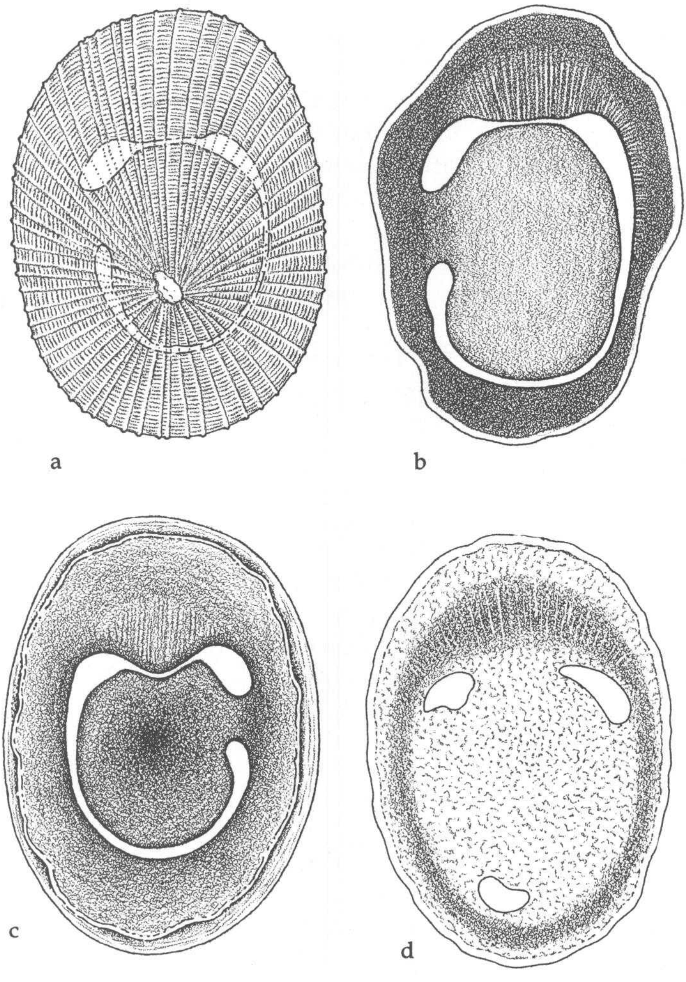


FIG. 11. Shell adductor muscles in freshwater limpets (Ancylidae). **a**, *Rhodacmea filosa*, shell adductor muscles showing through the translucent shell; **b**, *R.* *"cahawbensis"* [*elatior*], dorsal mantle; **c**, *R. elatior*, underside of mantle with rest of animal removed; **d**, *Ferrissia rivularis*, dorsal mantle.

narrow tube which leads to the stomach. Running along side the esophagus are the salivary glands.

In freshwater pulmonate snails, the stomach consists of an anterior expanded crop, a large bulbous gizzard, and a posterior pylorus. The crop is a vestibule for food accumulation before it passes into the

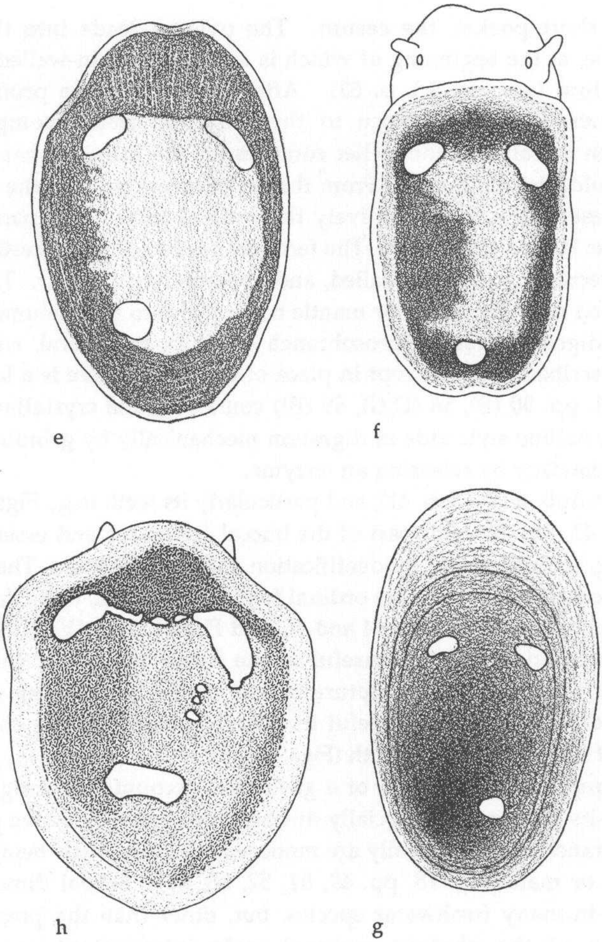


FIG. 11 (cont.). Shell adductor muscles in freshwater limpets (Ancylidae) (cont.). e, *Ferrissia "tarda"* [*rivularis*], dorsal mantle; f, *F. parallela*, dorsal mantle (with snail's head protruding from anterior part); g, *F. parallela*, underside of shell showing adductor muscle attachment scars; h, *Laevapex* sp., dorsal mantle.

gizzard. The gizzard is a highly muscular organ for grinding food. The pylorus is a short expansion of the alimentary tube between the gizzard and the intestine. Into the posterior pylorus empty the ducts from the digestive glands. Leading from the posterior pylorus is a small, short pocket, the cecum. The pylorus leads into the prointestine, at the beginning of which is a relatively thin-walled cavity, the atrium (see Fig. 18, p. 63). After the atrium, the prointestine continues a short distance to the muscular pellet compressor. Between the atrium and pellet compressor, the intestine has a large inner fold, the typhlosole. From the pellet compressor to the rectum, the intestine is a long, relatively thin-walled tube. This part of the intestine lacks a typhlosole. The terminal section of the digestive tract is the rectum. It is thick-walled, and apparently glandular. The anus is located near the posterior mantle collar, close to the pneumostome.

The digestive tract of prosobranch snails is, in general, similar to that described above, except in place of the cecum there is a large sac (Fig. 18, pp. 50 (B), 56 (D,G), 59 (B)) containing the crystalline style. The crystalline style aids in digestion mechanically by grinding food, and chemically by releasing an enzyme.

The radula (Fig. 13, p. 41), and particularly its teeth (e.g., Figs. 14, 15, 16, pp. 43, 44, 45), both part of the buccal apparatus and essential for feeding, are also useful in identification and classification. The radula is especially valuable at the ordinal (e.g., see Fig. 782, Sect. V, p. 222) and familial (e.g., see Figs. 14 and 16, and Fig. 81, Sect. IV, p. 94) levels of identification, but it is useful in the lower systematic categories as well. As with fine sculpture of the shell, the scanning electron microscope is especially useful for clearly distinguishing characteristics of the small radular teeth (Figs. 15, 16).

The reproductive system of a gastropod accounts for a significant part of its body mass, especially during reproductively active periods. Prosobranch snails generally are monosexual, individuals being either female or male (Fig. 18, pp. 49, 51, 52, 58, 61). Sexual dimorphism occurs in many freshwater species, but, other than the presence or absence of the obvious external male intromittent organ, the dimorphism is confined mainly to size, females in some species being somewhat larger than males.

The snail's primary sex gland, the gonad, is located posteriorly or apically in the visceral mass, and generally is covered by or embedded in the digestive gland. The male gonad, the testis, produces great numbers of male sex cells, spermatozoa (sperm), which are stored until copulation in one or more seminal vesicles in the proximal part of the male tract (e.g., see Fig. 18, p. 51). During mating, the sperm pass from the seminal vesicle(s) through the sperm duct, past or through the prostate gland and continue on through the narrow

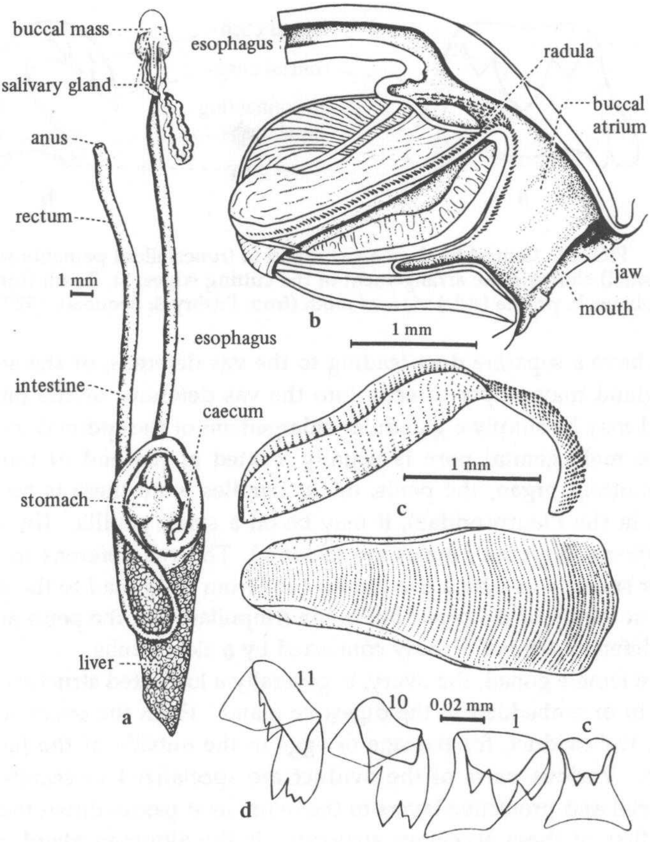


FIG. 12 The radula of a freshwater pulmonate snail (*Biomphalaria*) and its relation to the alimentary system. **a**, The alimentary system, mainly dorsal view; **b**, longitudinal section through the buccal mass, showing the orientation of the radula as viewed from the right side; **c**, right side and dorsal views of the radula; **d**, four teeth from one transverse row of the radular ribbon; c= central tooth, 1 = 1st tooth (a lateral tooth) to the right of the central tooth; 10,11 = 10th and 11th teeth (marginal teeth) to the right of the central tooth. From Barbosa et al. (1968), after Demian.

ciliated vas deferens to the genital pore for transfer to the female for fertilization. Among the various taxa, there are many variations in the parts of this basic system. For example, the seminal vesicle may be a single sac-like structure, or it may consist of many acini along the sperm duct, or it may be simply an enlargement of the sperm duct (vas deferens). The prostate gland also may take many forms, and

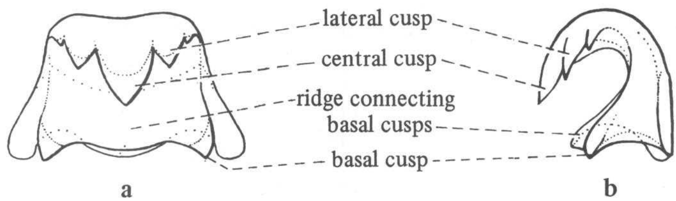


FIG. 13. Central tooth of a gastropod (a truncatelloid pomatiopsid snail) showing the arrangement of the cutting edges. **a**, Tooth from above; **b**, profile (side) view of tooth (from Pilsbry & Bequaert, 1927).

may have a separate duct leading to the vas deferens, or the acini of the gland may empty directly into the vas deferens, or the prostate gland may be simply a glandular enlargement of the sperm duct.

The male genital pore is usually located at the end of the male intromittent organ, the penis, or, in families were there is no penis (e.g., in the Pleuroceridae), it may be on a small papilla. [In *Thiara granifera* (Thiaridae), males are lacking.] The vas deferens in freshwater snails is usually a continuous tube from the gonad to the genital pore at the tip of the penis, but in the Ampullariidae, the penis and the vas deferens are not directly connected by a closed tube.

The female gonad, the ovary, is generally a lobulated structure lying next to or embedded in the digestive gland. From the ovary leads a duct, the oviduct, for passage of eggs to the outside of the female's body. Various parts of the oviduct are specialized to secrete food material and protective layers to the ovum as it passes down the tract. The first of these accessory structures is the albumen gland, which coats the egg with albumen to nourish the developing embryo. Next distally is either a jelly gland or a capsule gland, which secretes a protective layer. Other specializations of the tract include a bursa copulatrix, which receives the male intromittent organ during copulation, and a seminal receptacle, which is a pouch for storing male sex cells from the mating partner until they are needed for fertilization. The nature of the various parts of the female tract may vary considerably among the various gastropod families.

The Valvatidae differ from the other freshwater prosobranch families in being hermaphroditic. Here the gonad produces both male and female sex cells, and the duct leading from the gonad is a hermaphrodite duct, which allows passage of both types of sex cells.

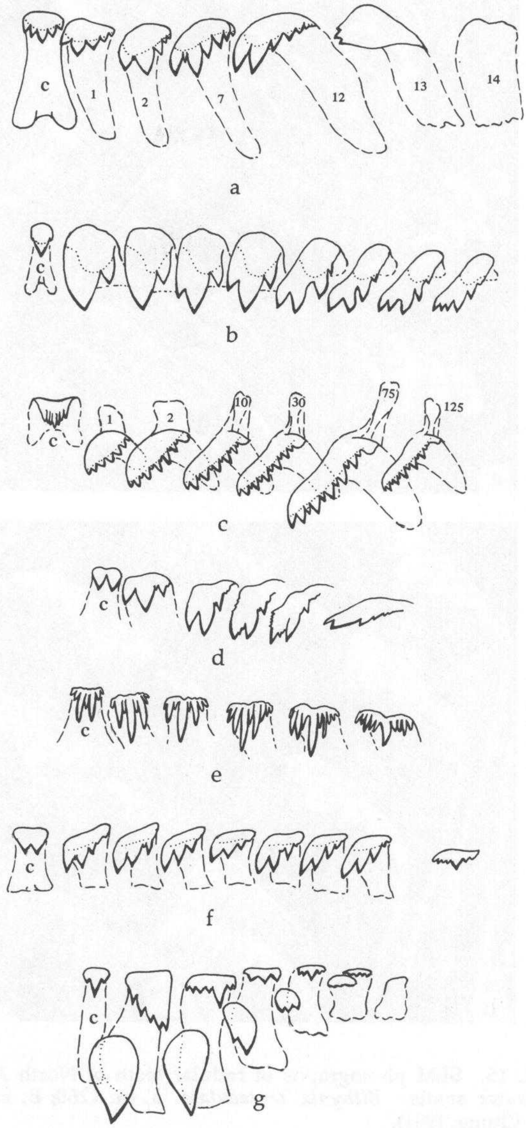


FIG. 14. Radulae of North American Pulmonata. **a**, Acroloxidae; **b**, Lymnaeidae; **c**, Physidae; **d**, **e**, Planorbidae; **f**,**g**, Ancylidae. **c** = Central tooth; numbers refer to vertical rows of radular teeth counted distally from the median row of central teeth. Fig. 14a adapted from H.B. Baker (in Walker, 1925); b,c from F.C. Baker (1928); f,g from Basch (1963).

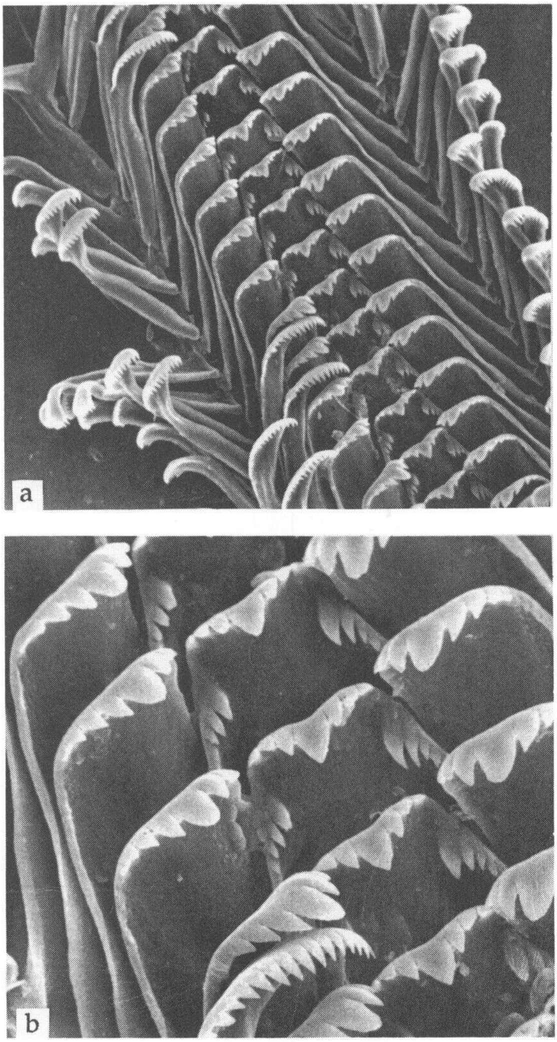


FIG. 15. SEM photographs of radular teeth of North American freshwater snails. *Bithynia tentaculata*. **a**, ca. x260; **b**, ca. x735. (From Chung, 1984).

In *Valvata*, each animal has two genital openings, the male opening at the tip of the penis on the head or neck, and the female opening near the entrance into the mantle cavity.

Pulmonate snails are *all* hermaphroditic, and like *Valvata*, each

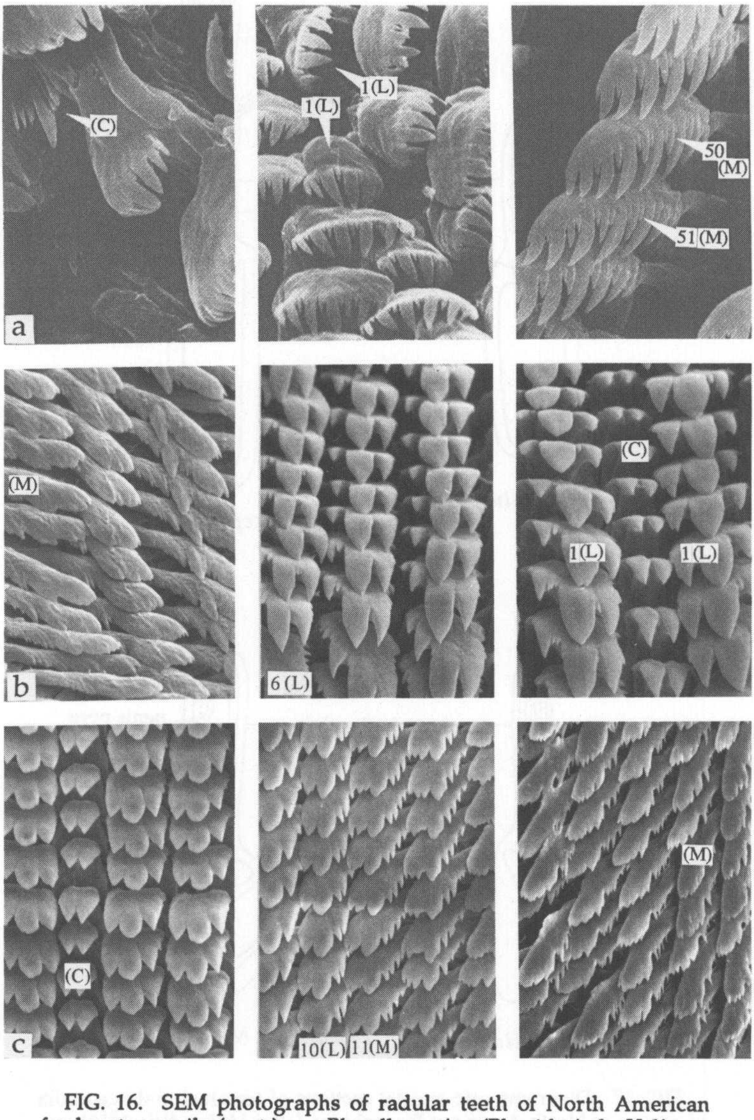


FIG. 16. SEM photographs of radular teeth of North American freshwater snails (cont.). **a**, *Physella gyrina* (Physidae); **b**, *Helisoma anceps* (Planorbidae); **c**, *Planorbella trivolvis* (Planorbidae). (c) = central tooth; L = lateral tooth; M = marginal tooth; 1 = a tooth of the 1st vertical row [counted distally from the central tooth]; 2 = tooth of the 2nd vertical row; 6 = a tooth of the 6th vertical row, etc. Fig. a is from Te & Mardinly (1974). Fig. a, ca. x1660; Figs. b, c, ca. x595.

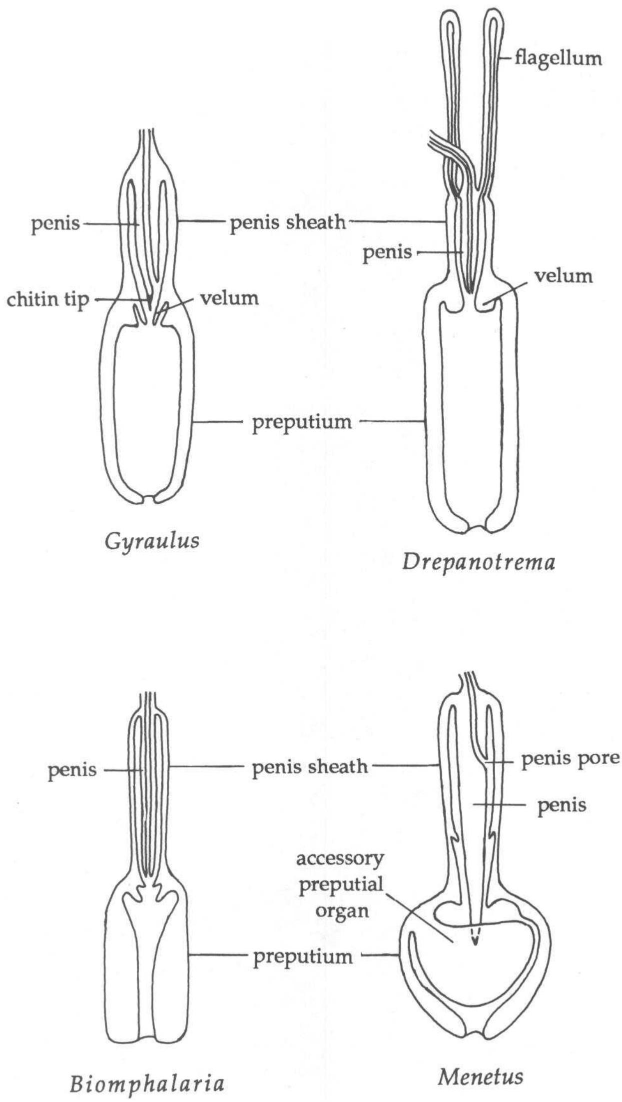


FIG. 17. Diagrammatic sagittal sections of terminal male genitalia of genera of North American Planorbidae (after Hubendick, 1955).

individual has a complete male and female system (Fig. 18, pp. 62 (A), 65; Fig. 19, pp. 68, 73). The gonad, an ovotestis, is embedded in the digestive gland, or as in the Planorbidae, precedes the digestive gland

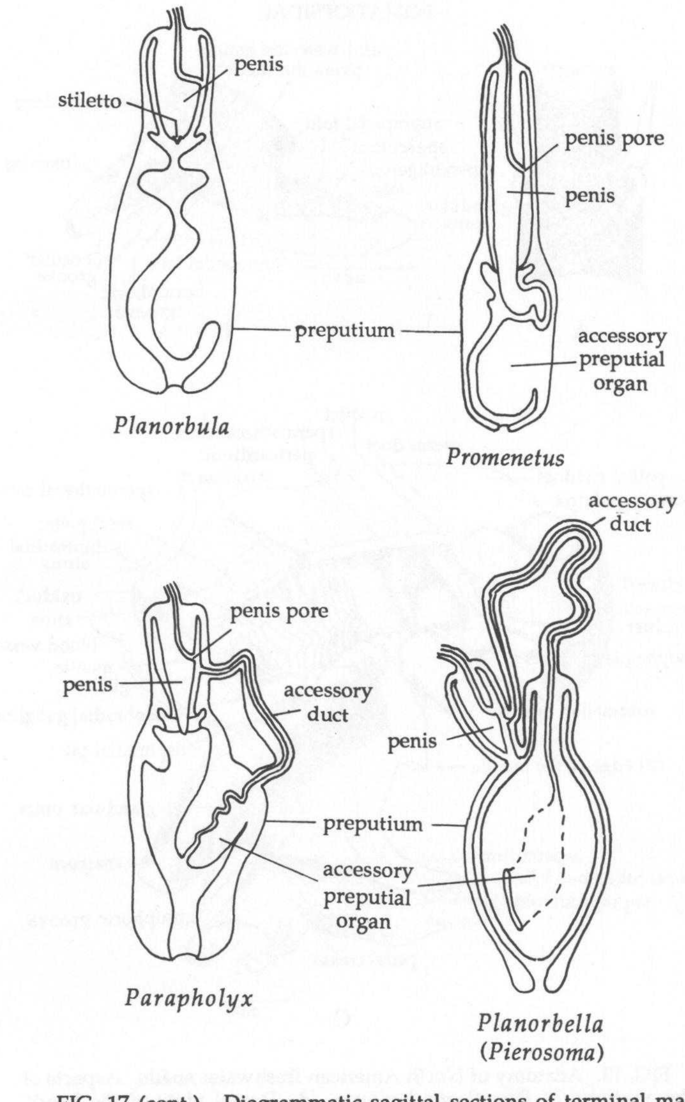


FIG. 17 (cont.). Diagrammatic sagittal sections of terminal male genitalia of genera of North American Planorbidae (cont.). (After Hubendick, 1955).

apically. The hermaphrodite duct also serves as a seminal vesicle, being either enlarged and convoluted, or having outpocketings along its course. Where the genital duct bifurcates into separate male and

POMATIOPSIDAE

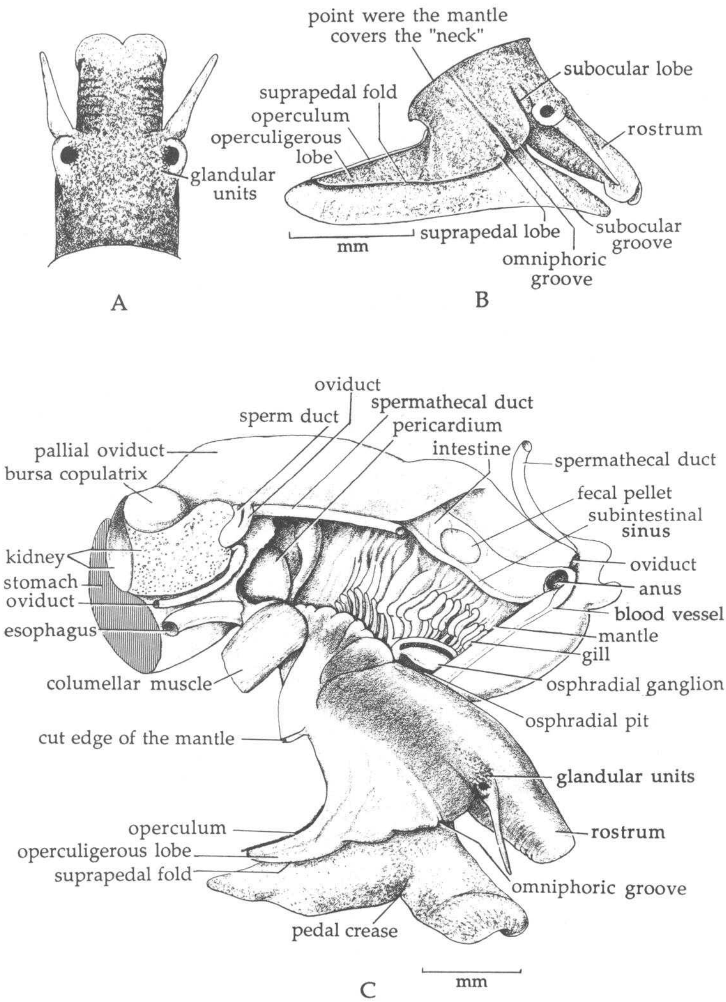


FIG. 18. Anatomy of North American freshwater snails. Aspects of the anatomy of *Pomatiopsis lapidaria*. **A**, Dorsal view of the head; **B**, head-foot, right side; **C**, head, foot and mantle region. (From Davis, 1967).

female tracts, there is a small insemination pocket where fertilization takes place (Fig. 18, p. 65 (B)). Here the sperm from the male-functioning mating partner, which have travelled up the female tract,

POMATIOPSIDAE

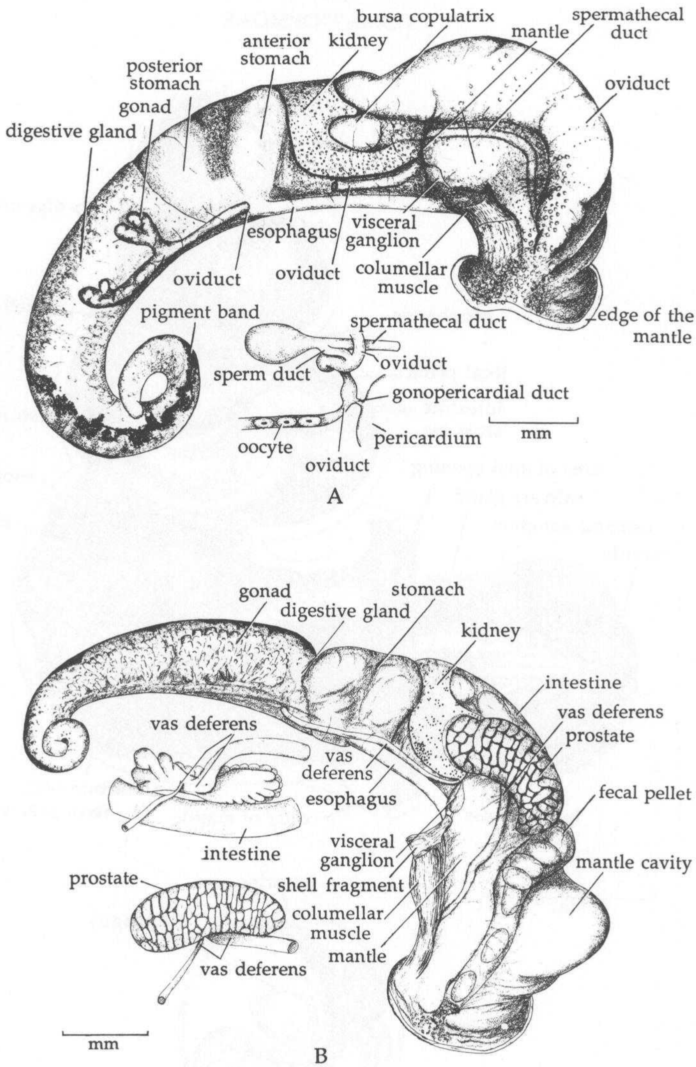


FIG. 18 (cont.). *Pomatiopsis lapidaria* (cont.). Uncoiled viscera. **A**, Female; **B**, male. (From Davis, 1967).

meet the ovum, which has just arrived from the ovotestis.

The male system in pulmonate snails consists of a prostate gland (Fig. 18, p. 65; Fig. 19, pp. 68, 73), of differing shapes and construction in

POMATIOPSIDAE

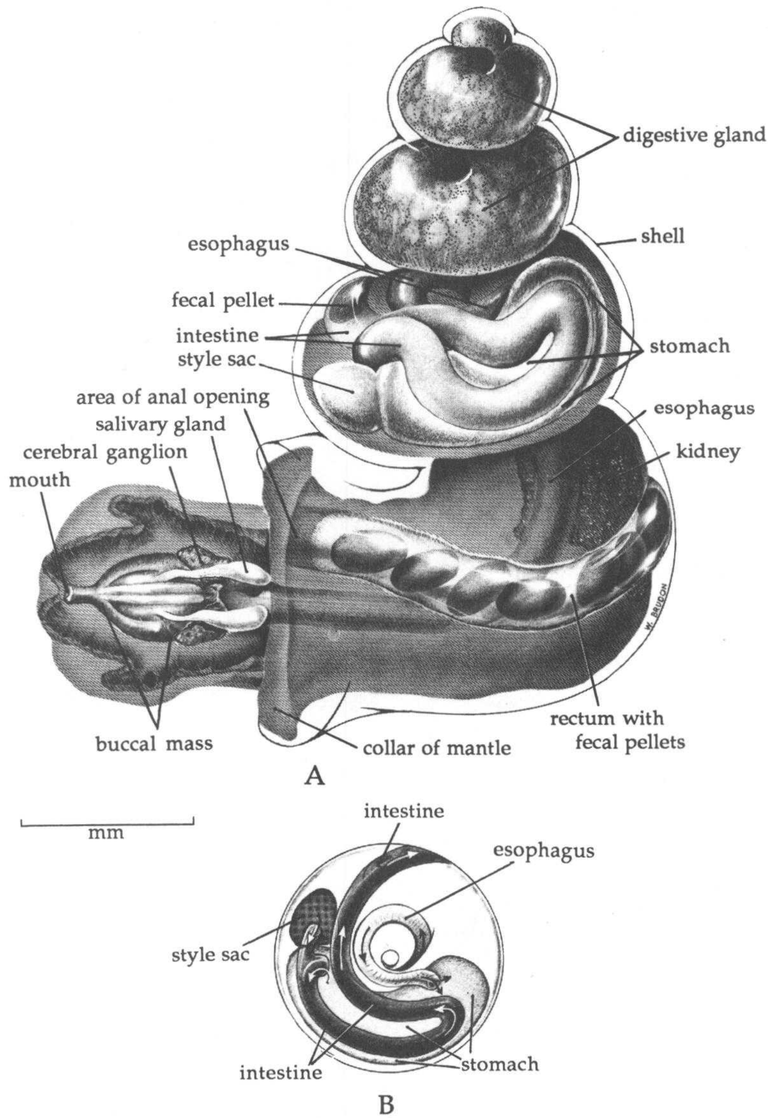


FIG. 18 (cont.). *Pomatiopsis cincinnatiensis*. **A**, Digestive system; **B**, spatial relationship of the esophagus, stomach, crystalline style and intestine. (From van der Schalie & Dundee, 1956).

POMATIOPSIDAE

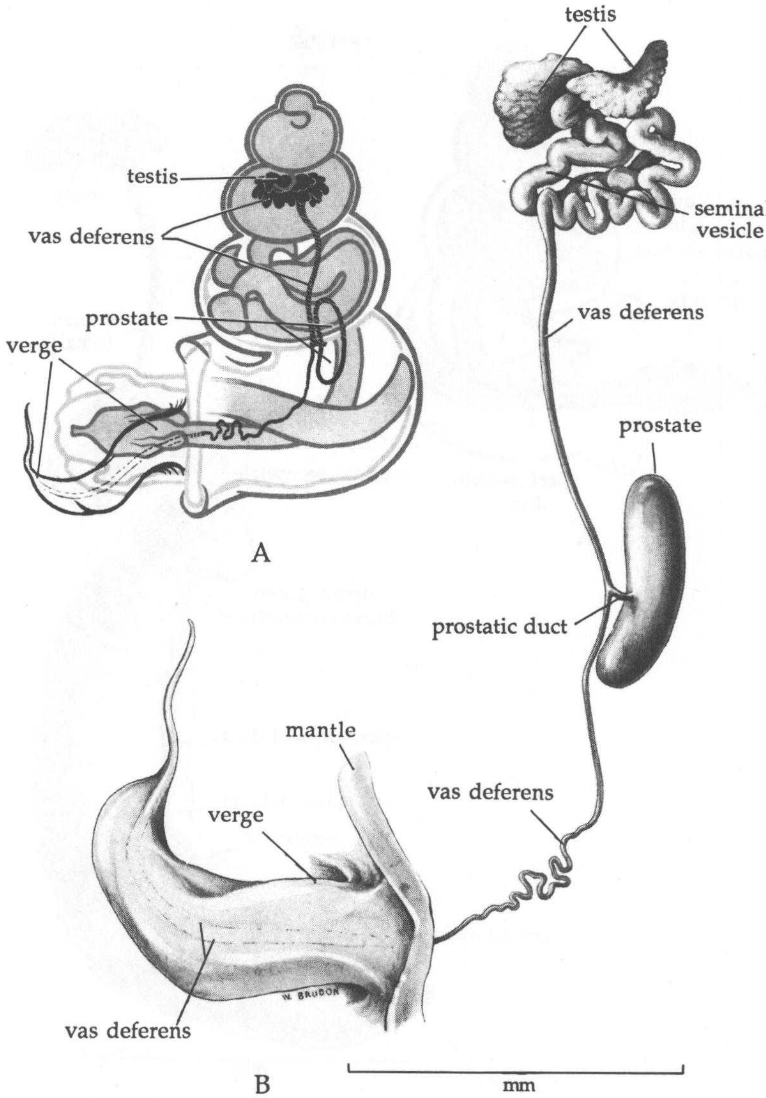


FIG. 18 (cont.). *Pomatiopsis cincinnatiensis* (cont.). Male reproductive system. **A**, position of the male organs in the snail; **B**, male organs. (From van der Schalie & Dundee, 1956).

POMATIOPSIDAE

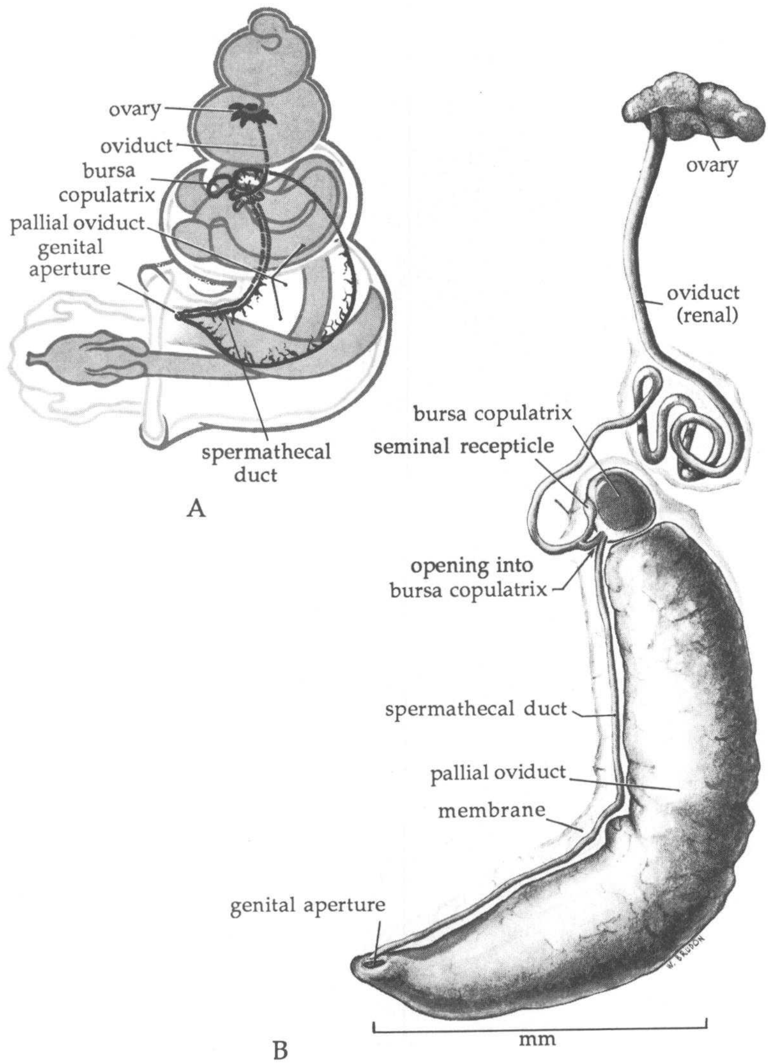


FIG. 18 (cont.). *Pomatiopsis cincinnatiensis* (cont.). Female reproductive system. **A**, Position of the female organs in the snail; **B**, female organs. (From van der Schalie & Dundee, 1956).

different taxa, from which leads a long, narrow, muscular vas deferens. The vas deferens courses through the body wall along the side of the foot (Fig. 18, p. 65 (A)) before entering the head-foot hemocoel near the male genital opening. The vas deferens joins the penis, which is also in the hemocoel (Fig. 18, p. 62 (A)). The penis in freshwater pulmonates is contained in a penis sheath, which connects distally to the tubular preputium (Fig. 18, p. 65 (A)). The preputium is attached to the body wall at the male gonopore.

Pulmonate snails differ from prosobranchs in carrying the penis internally when not sexually active. The preputium and penis sheath are everted by turgor pressure during copulation, and withdrawn by penial retractor muscles after completion of mating. In some families, the penis and preputium vary considerably between various taxa, in which case these structures are given considerable taxonomic attention (e.g., see Fig. 17, pp. 46, 47).

The female system in pulmonate snails (see Fig. 18, p. 65 (A); Fig. 19, p. 73 (B)) consists of the albumen gland, nidamental gland, uterus, seminal receptacle (spermatheca) and vagina (that part of the female duct between the opening of the seminal receptacle and the female genital pore).

Freshwater gastropods obtain oxygen by gills (in the Prosobranchia) or by a lung (in the Pulmonata). The gill is usually well hidden within the protective enclosure of the mantle cavity (Fig. 18, pp. 48, 54, 59, 60). In most of the freshwater prosobranchs, the unipectinate gill is attached to the wall of the mantle cavity and consists of a long series of parallel, often triangularly-shaped, leaflets. In the Valvatidae, the gill is bipectinate, and, when the snail is active, it protrudes to the exterior from the mantle cavity (Fig. 781, sect. V, p. 220).

The lung in freshwater pulmonate snails is located in the same general area as the mantle cavity in prosobranchs (Fig. 18, p. 62 (A)). The surface of the lung is highly vascularized (Fig. 18, p. 64 (B)) to facilitate O_2/CO_2 exchange. The lung is generally reduced in freshwater limpets, where oxygen uptake is mainly through other body surfaces. While freshwater pulmonates do not have true gills, three families, the Acroloxidae, Planorbidae and Ancylidae (Fig. 19, p. 69) have secondarily derived gills, called "pseudobranchs."

The respiratory pigment in nearly all gastropods is hemocyanin, but in the Planorbidae it is hemoglobin, which gives the planorbid body a red appearance (unless the color of the blood is masked by body melanin pigment).

THIARIDAE

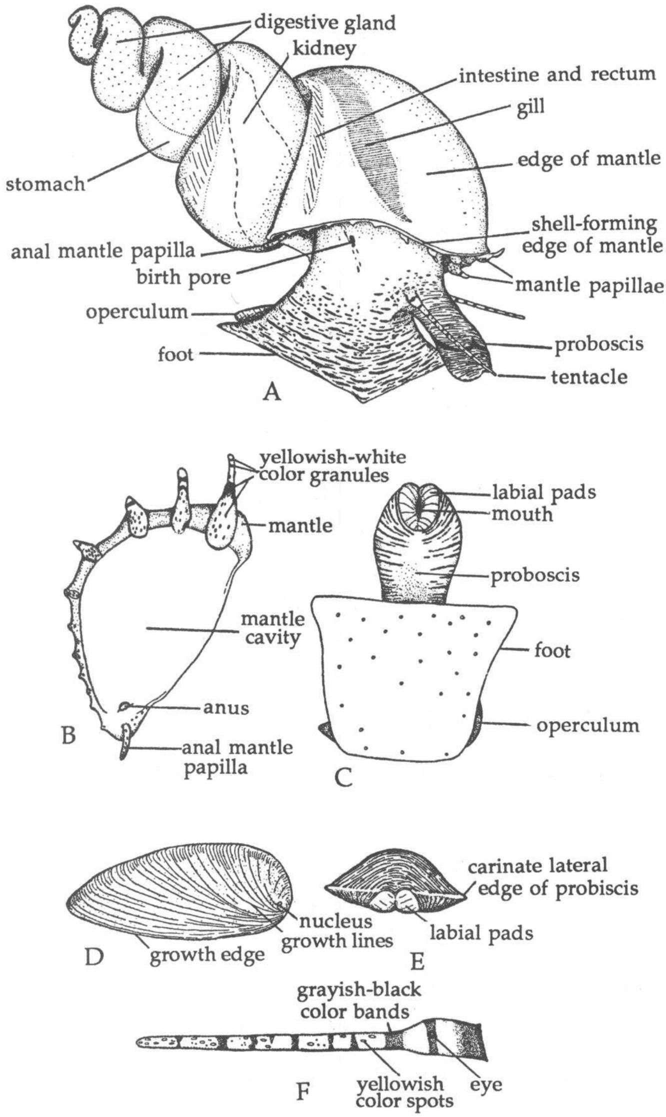


FIG. 18 (cont.). *Thiara granifera.* **A**, Right side of the animal; **B**, mantle edge, frontal aspect. **C**, underside of crawling animal; **D**, operculum; **E**, proboscis, anterior view; **F**, right tentacle, dorsal view. (From Abbott, 1952).

THIARIDAE

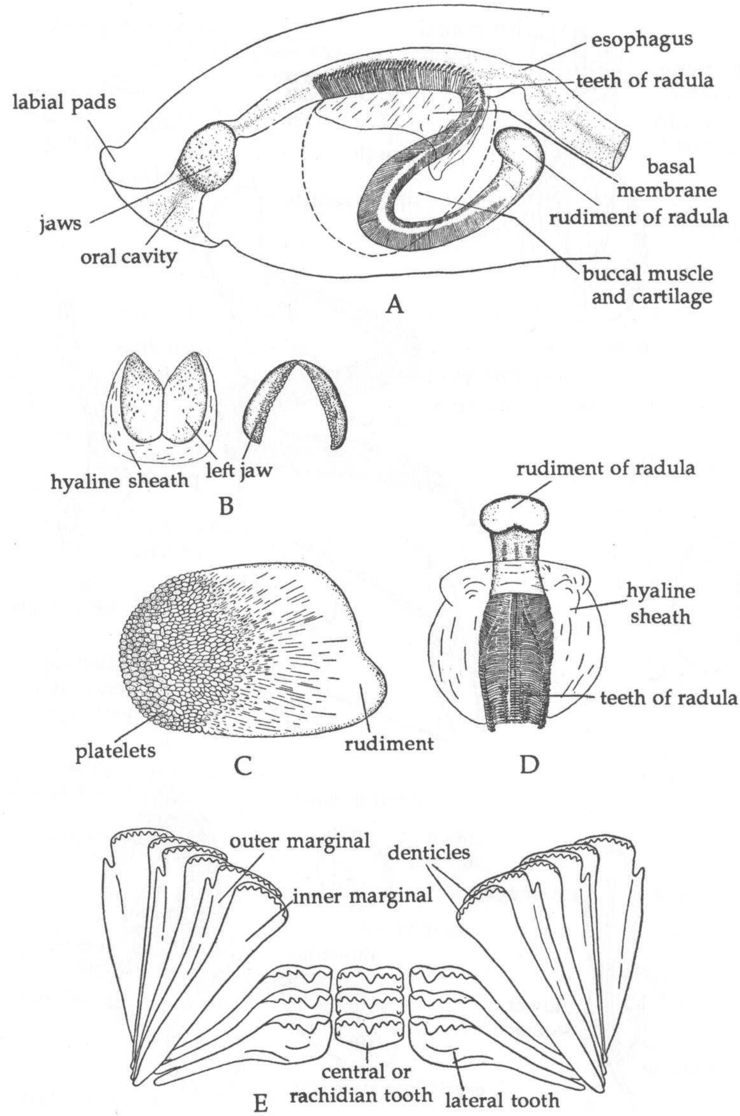


FIG. 18 (cont.). *Thiara granifera* (cont.). **A**, Proboscis, sagittal section; dotted lines indicate limits of buccal muscle and cartilage; **B**, jaws; dorsal (on left) and anterior (on right) views; **C**, outer view of right jaw; **D**, radula, dorsal view; **E**, three rows of radular teeth. (From Abbott, 1952).

THIARIDAE

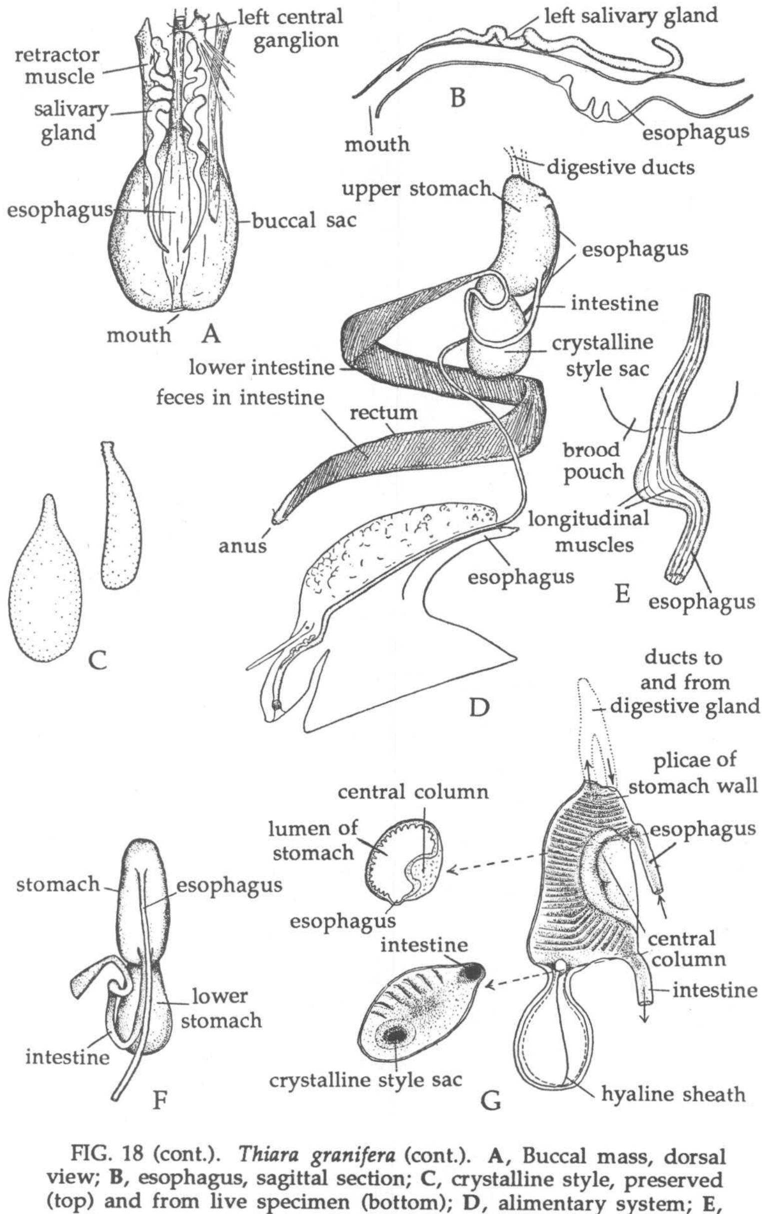


FIG. 18 (cont.). *Thiara granifera* (cont.). **A**, Buccal mass, dorsal view; **B**, esophagus, sagittal section; **C**, crystalline style, preserved (top) and from live specimen (bottom); **D**, alimentary system; **E**, esophagus beneath the brood pouch, dorsal view; **F**, stomach; **G**, interior of stomach. (From Abbott, 1952).

THIARIDAE

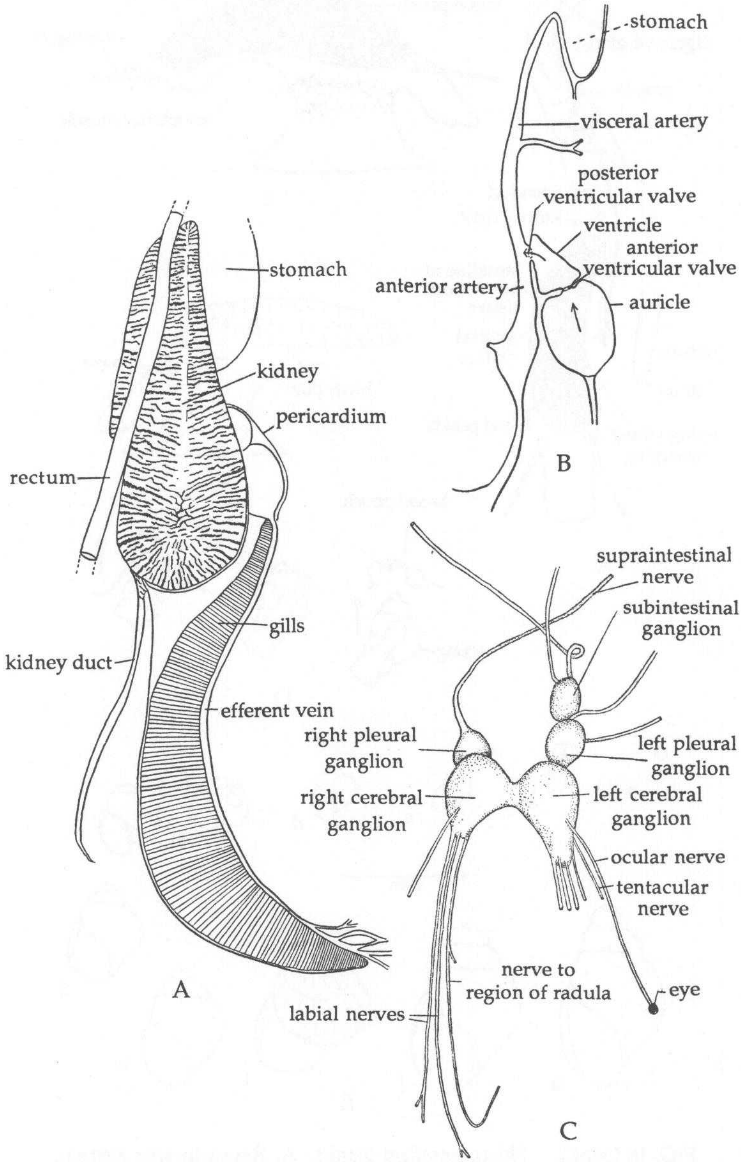


FIG. 18 (cont.). *Thiara granifera* (cont.). **A**, Kidney and gill; **B**, heart and adjacent arteries; **C**, central ganglia and their nerves, dorsal view. (From Abbott, 1952).

THIARIDAE

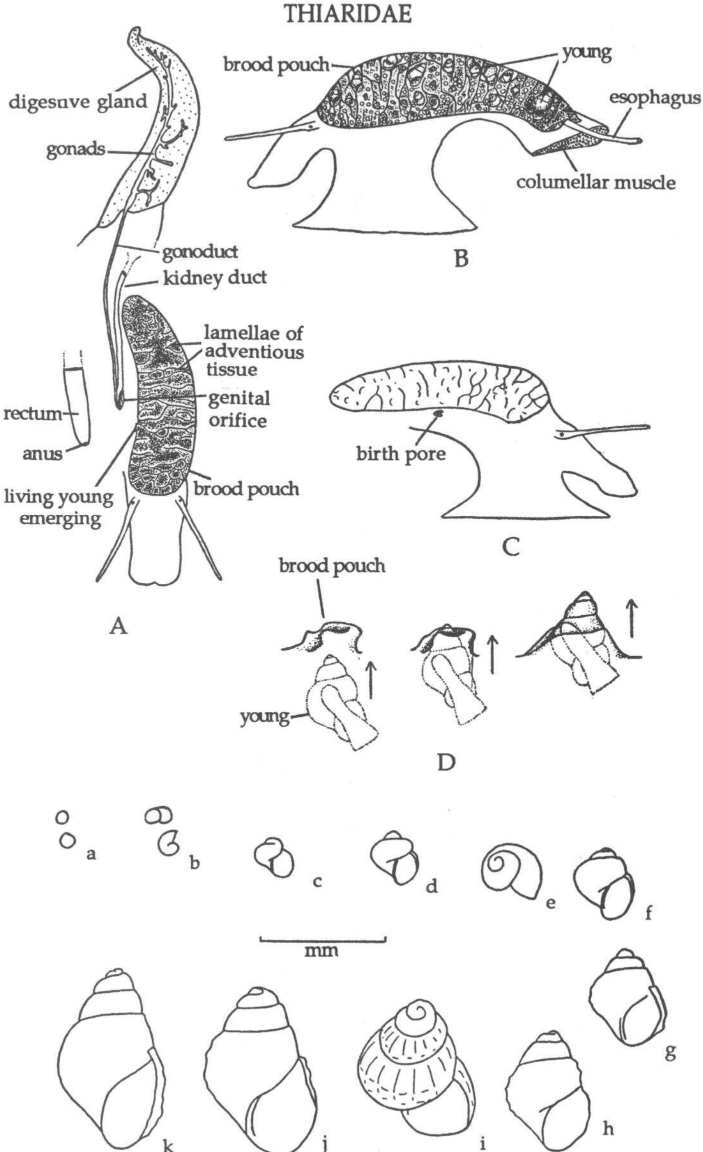


FIG. 18 (cont.). *Thiara granifera* (cont.). **A**, Reproductive system, dorsal view. **B, C**, left and right sides of animal, showing young in the brood pouch; **D**, young snails emerging from birth pore; **E**, eggs and young from brood pouch, showing development from fertilized egg (a) to a shell of four whorls (k). (From Abbott, 1952).

PLEUROCERIDAE

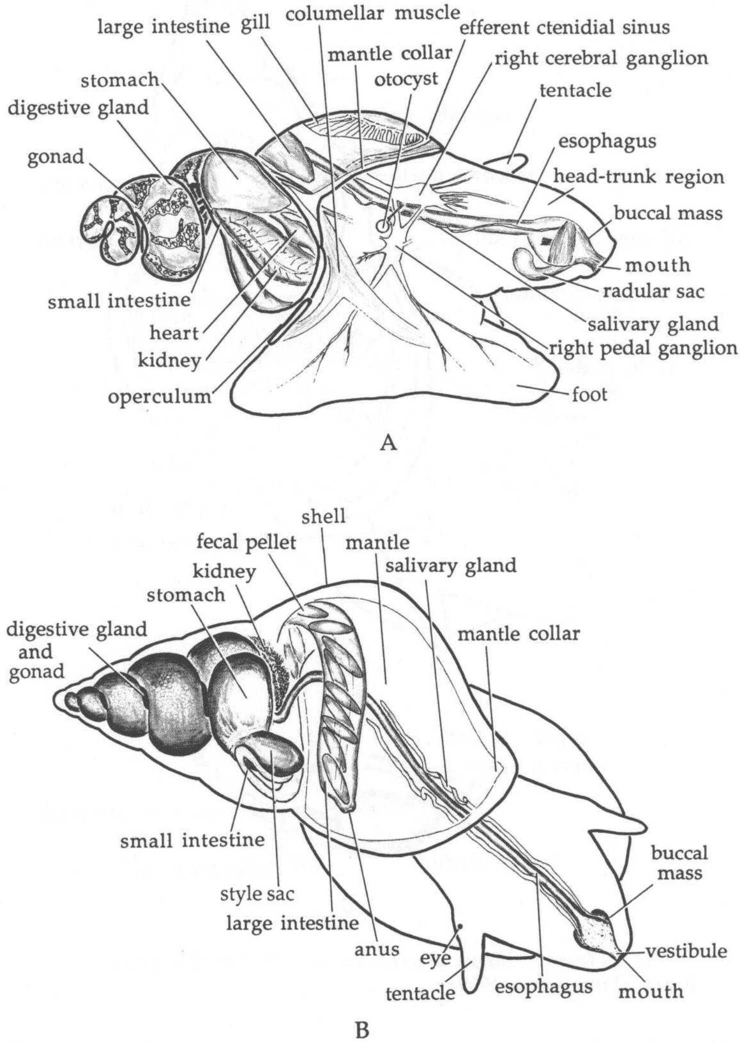
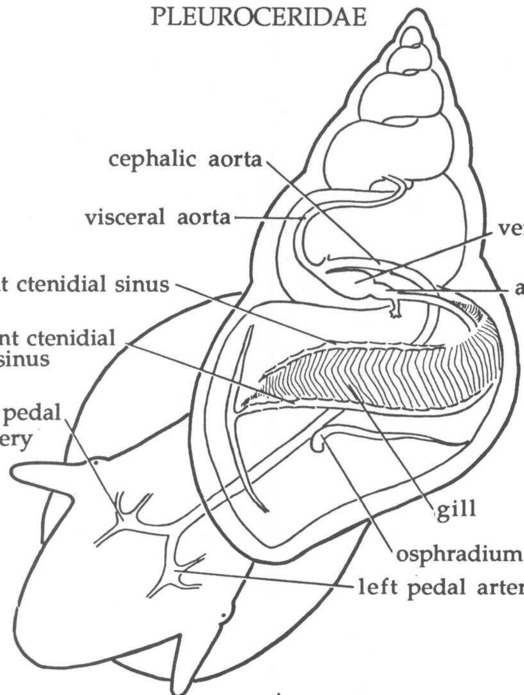


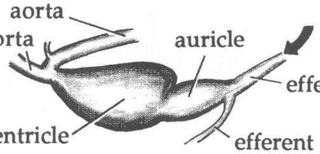
FIG. 18 (cont.). *Elimia livescens*. **A**, Lateral view, right side; **B**, digestive system, dorsal view. (From Dazo, 1965).

The excretory system of mollusks consists of a metanephridium (kidney) and its duct(s). The kidney is closely associated with both the reproductive and circulatory systems. In freshwater gastropods, the

PLEURORCERIDAE



A



B

FIG. 18 (cont.). *Elimia livescens* (cont.). **A**, Circulatory system; **B**, heart. (From Dazo, 1965).

kidney lies along side the pericardium, with its contained heart (Fig. 18, pp. 57, 64; Fig. 19, pp. 67, 72). The kidney in the Acroloxidae and Ancylidae differ from the other freshwater pulmonate snails in being serpentine in shape (Fig. 19, pp. 72 (A), 73 (A)).

The nervous system in freshwater gastropods (Fig. 18, p. 57 (C); Fig. 19, pp. 71, 72) has a concentration of paired nerve centers (ganglia) in the anterior hemocoel. The cerebral ganglia receive nerves from the

PLEUROCERIDAE

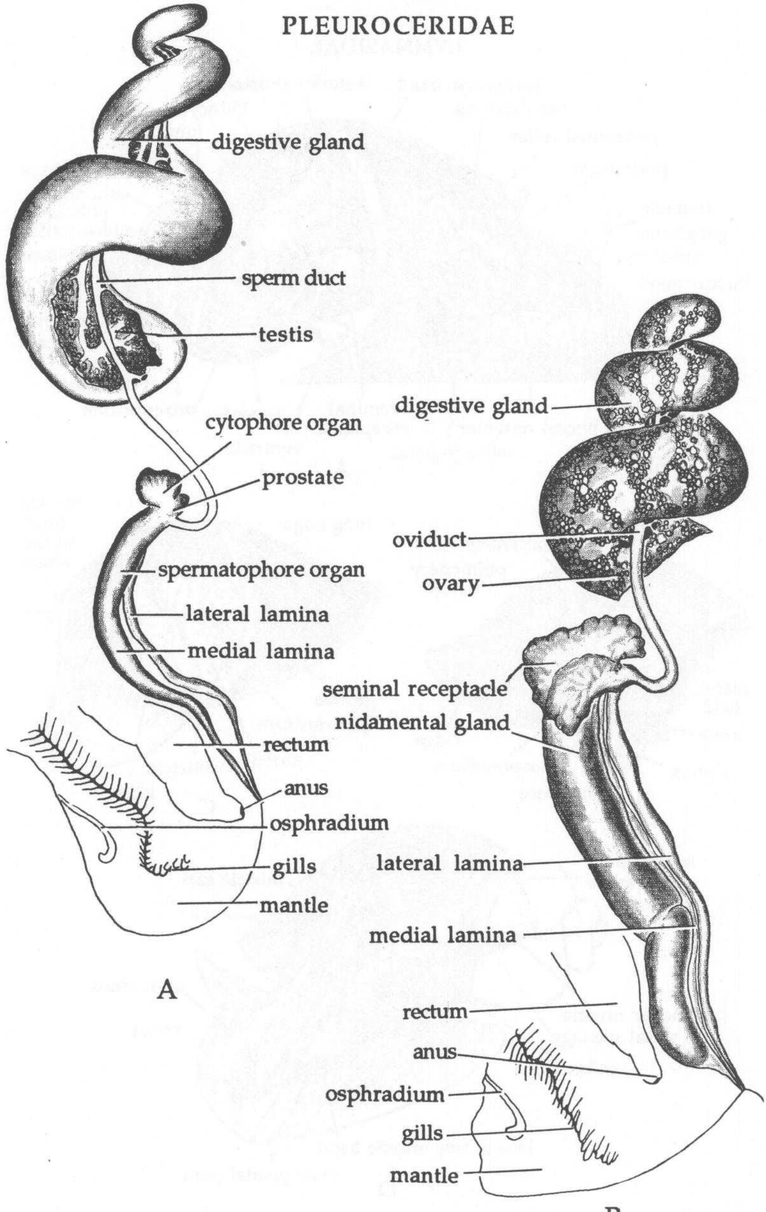


FIG. 18 (cont.). *Elimia livescens* (cont.). Reproductive system. **A**, Male; **B**, female. (From Dazo, 1965).

LYMNAEIDAE

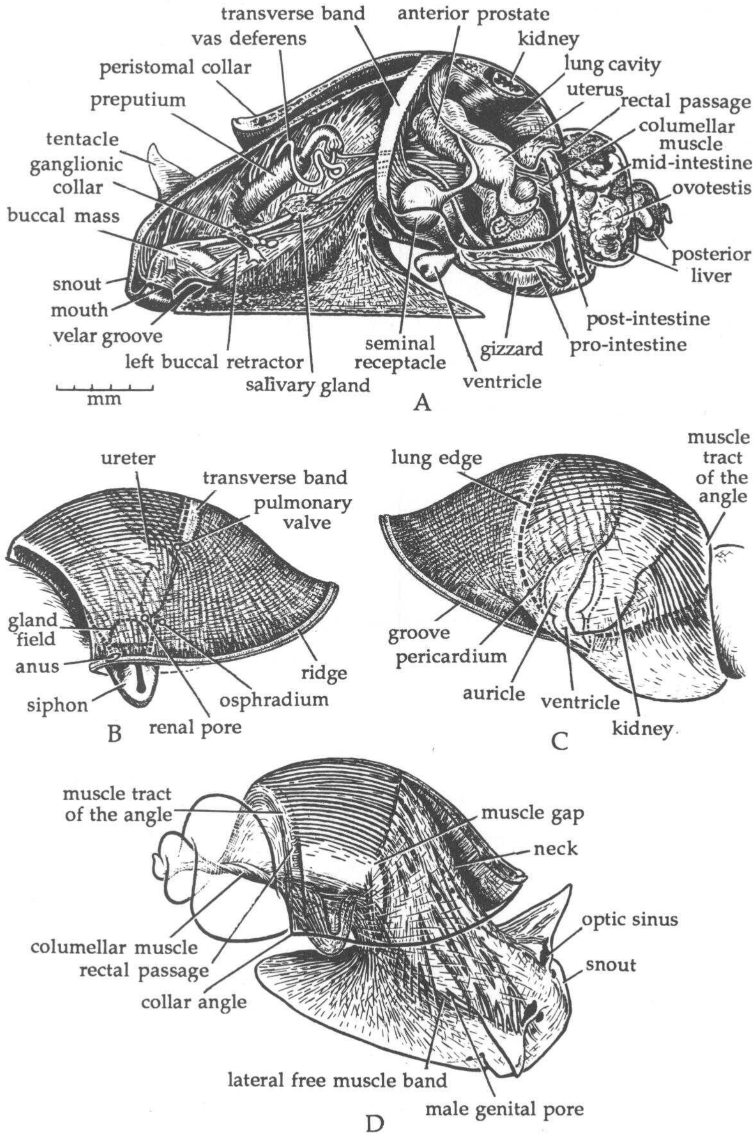


FIG. 18 (cont.). *Stagnicola emarginata*. **A,** Section through left side, showing organs; **B,C,** right and left sides of lower mantle and underlying structures; **D,** musculature. (From Walter, 1969).

LYMNAEIDAE

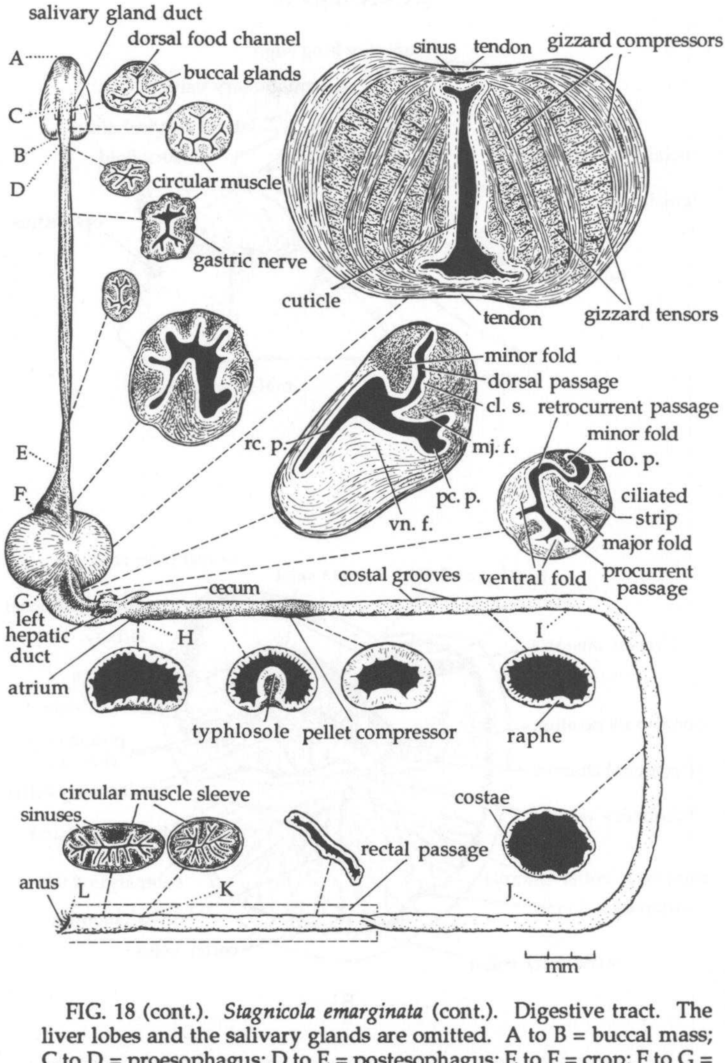
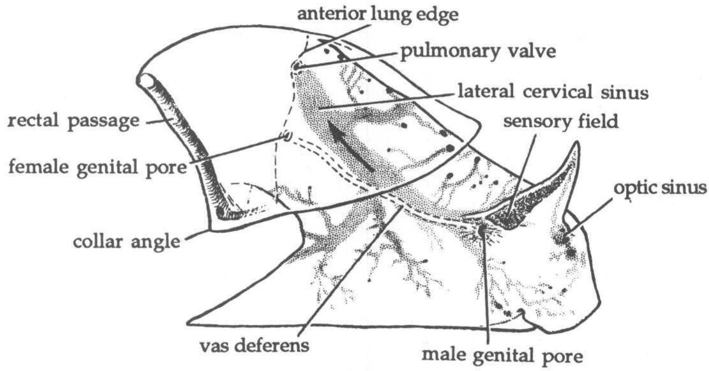


FIG. 18 (cont.). *Stagnicola emarginata* (cont.). Digestive tract. The liver lobes and the salivary glands are omitted. A to B = buccal mass; C to D = proesophagus; D to E = postesophagus; E to F = crop; F to G = gizzard; G to H = pylorus; H to I = prointestine; I to J = midintestine; J to K = postintestine; K to L = rectum. cl.s. = ciliated strip; do.p. = dorsal passage; mj.f. = major fold; pc.p. = procurrent passage; rc.p. = retrocurrent passage; vn.f. = ventral fold. (From Walter, 1969).

eyes and tentacles, the pleural ganglia receive nerves from the body walls, and the pedal ganglia receive nerves from the foot. The cerebral and pleural ganglia are arranged around the anterior

LYMNAEIDAE



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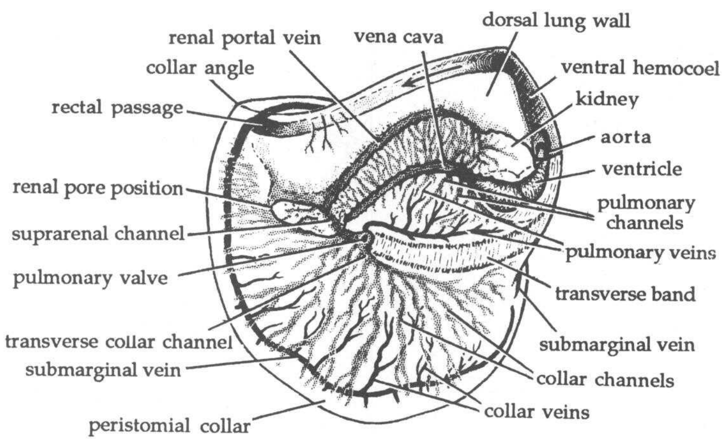

B

FIG. 18 (cont.). *Stagnicola emarginata* (cont.). **A**, Venous pathways in the wall of the anterior part of the animal; **B**, venous sinuses in the peristomial collar, roof of the lung and kidney. (From Walter, 1969).

esophagus, and the pedal ganglia are beneath the esophagus. The nervous systems of North American freshwater prosobranchs and pulmonates are basically similar.

LYMNAEIDAE

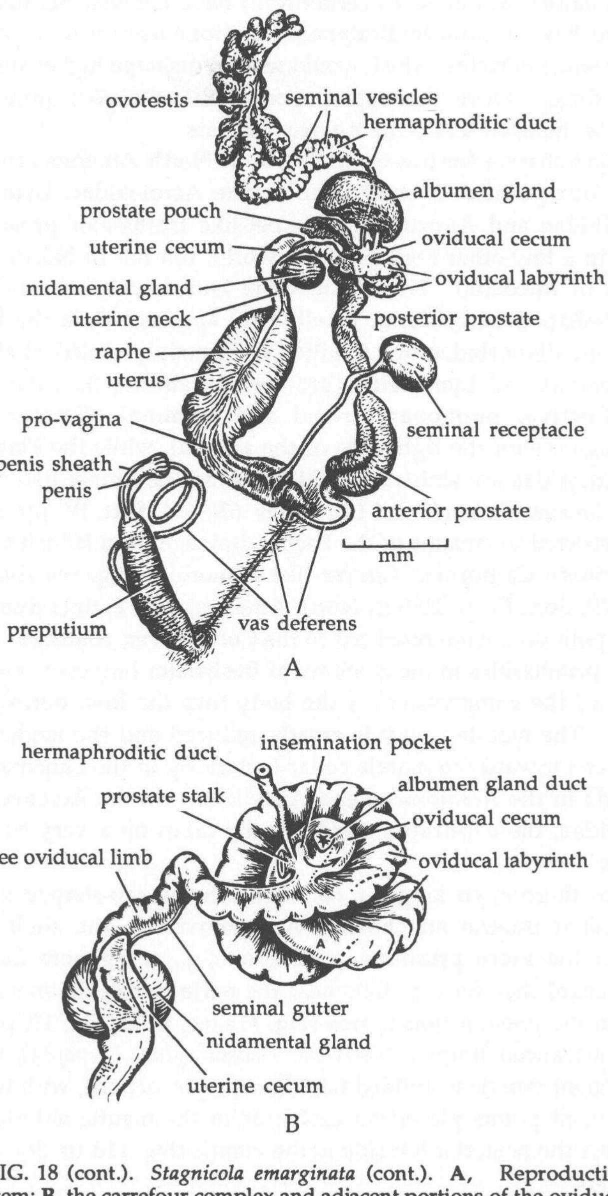

FIG. 18 (cont.). *Stagnicola emarginata* (cont.). **A**, Reproductive system; **B**, the carrefour complex and adjacent portions of the oviducal and uterine divisions of the female tract. (From Walter, 1969).

Freshwater gastropods with cap-shaped shells that have lost their coiled nature would seem certainly to have evolved because of the need to have a more hydrodynamic contour necessary to withstand strong water currents, which would tend to dislodge higher shells with more drag. Once the cap-shaped shells evolved, some of the "limpets" invaded lentic, quiet-water habitats.

Limpet-shaped freshwater mollusks in North America are restricted to four pulmonate snail families, the Acroloxidae, Lymnaeidae, Planorbidae and Ancylidae. [Limpet-like freshwater prosobranchs occur in a few other regions of the world, but not in North America (north of Mexico).] The Acroloxidae and Ancylidae contain *only* limpet-shaped (ancyliform, patelliform) species, while the Lymnaeidae and Planorbidae are families with mainly coiled shells. The Acroloxidae and Lymnaeidae are dextral families (i.e., the external reproductive, pulmonary, renal and terminal alimentary tract openings are on the right side of the animal), while the Planorbidae and Ancylidae are sinistral. In North America, limpet-like lymnaeid snails (genera *Fisherola* and *Lanx*; Figs. 632-634, Sect. IV, pp. 179, 181) are restricted to streams of the Pacific drainage from British Columbia to northern California. Limpet-like Planorbidae (genus *Amphigyra*; Fig. 749, Sect. IV, p. 209) in North America, now extinct due to man-made pollution, were restricted to the Coosa River, Alabama.

The peculiarities in the anatomy of freshwater limpets is mainly the result of the compression of the body into the low, obtuse-conical shape. The mantle cavity is greatly reduced and the nephridium is displaced toward the mantle collar (anteriorly in the Lancinae and to the side in the Acroloxidae and Ancylidae). In the Acroloxidae and Ancylidae, the nephridium additionally takes on a very convoluted shape.

Since there is no longer a columella in the cap-shaped shell, the columellar muscle attachments have moved to the shell surface, and in the more primitive condition (e.g., see genera *Lanx* and *Rhodacmea*) they form a circle near the perimeter of the mantle, open only in the pneumostomal area (Fig. 11a,b,c, p. 38; Fig. 19, p. 67). In more advanced limpets (*Ferrissia, Hebetancylus, Laevapex*), the shell attachment muscle is divided into three major sections, with two main attachment points placed on each side of the mantle anteriorly and one near the posterior left side of the mantle (Fig. 11d (p. 38), Fig. 11e-h (p. 39)).

LYMNAEIDAE (LANCINAE)

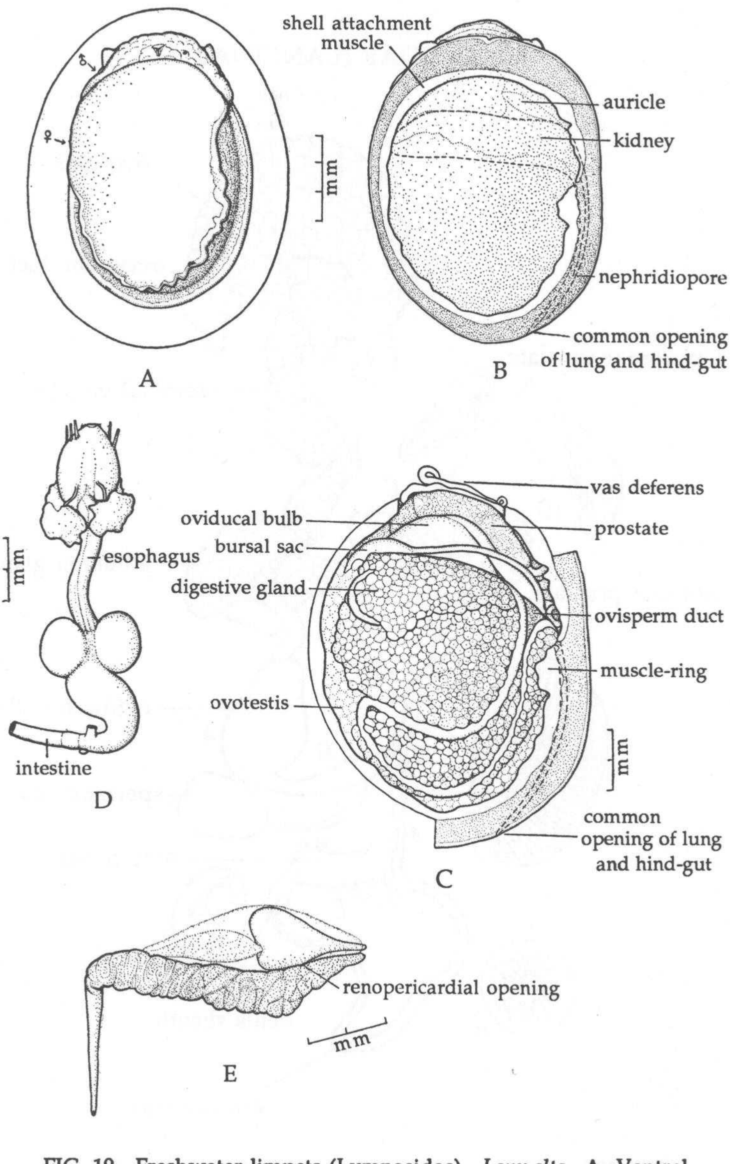

FIG. 19. Freshwater limpets (Lymnaeidae). *Lanx alta*. **A**, Ventral view; **B**, dorsal view; **C**, dorsal view of visceral mass, with most of the mantle cut away; **D**, anterior portion of the digestive tract; **E**, kidney, pericardium and heart. (From H.B. Baker, 1925).

LYMNAEIDAE (LANCINAE)

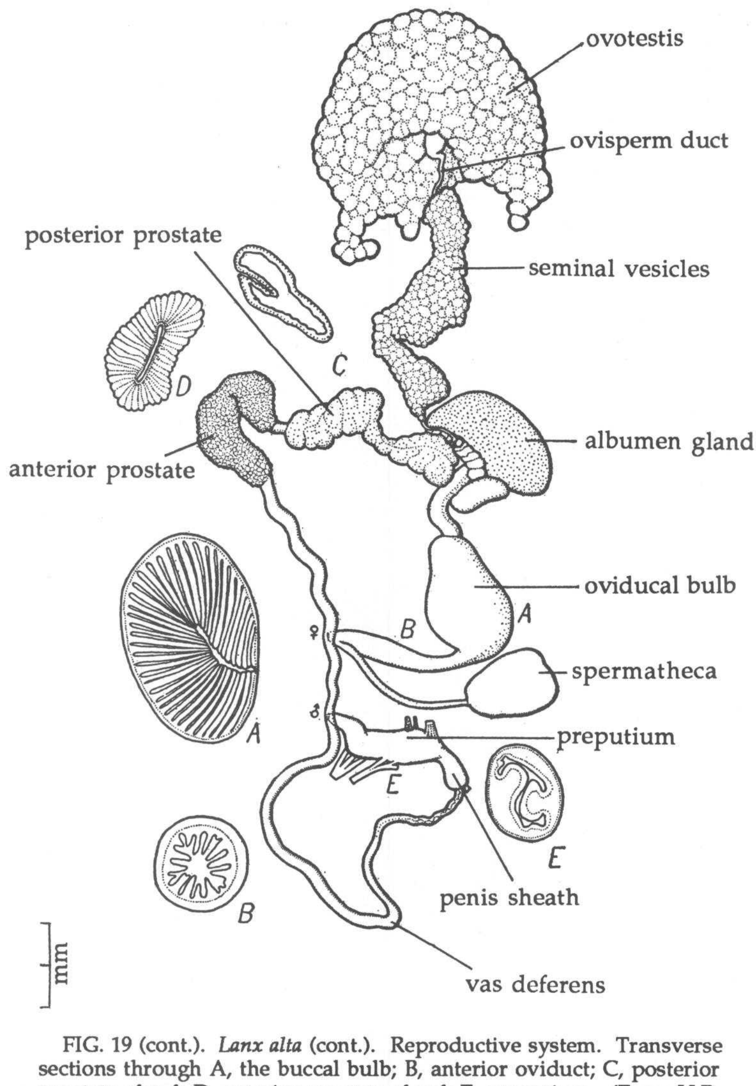

FIG. 19 (cont.). *Lanx alta* (cont.). Reproductive system. Transverse sections through A, the buccal bulb; B, anterior oviduct; C, posterior prostate gland; D, anterior prostate gland; E, preputium. (From H.B. Baker, 1925).

ANCYLIDAE

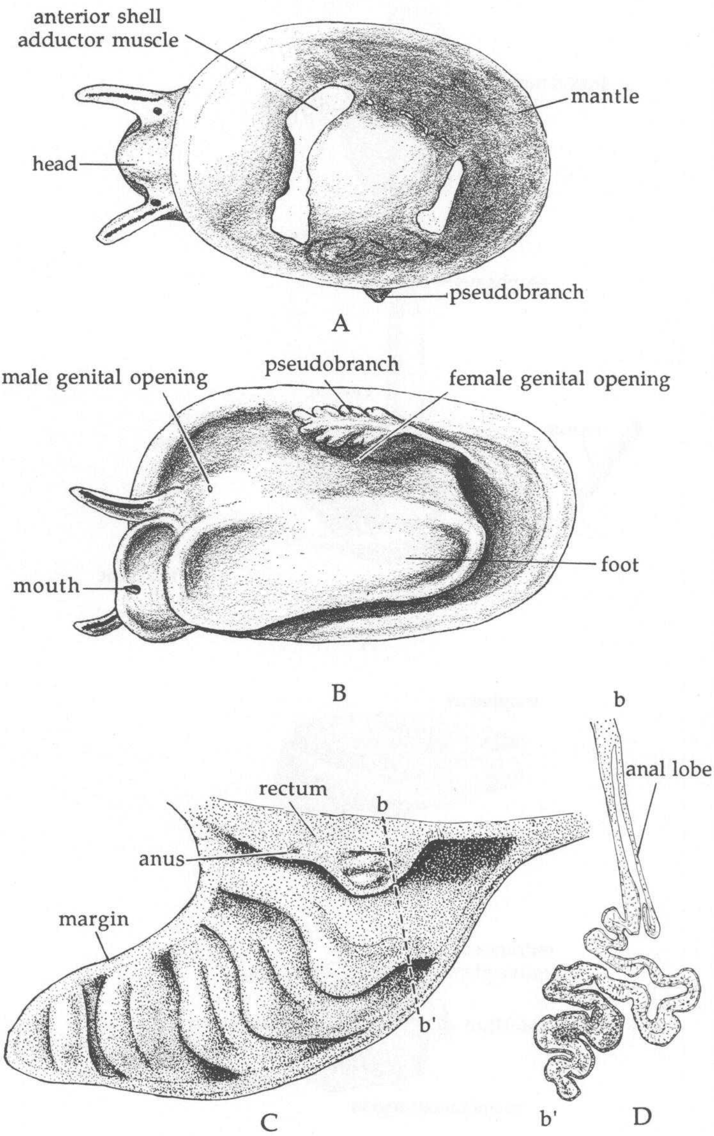

FIG. 19 (cont.). Freshwater limpets (cont.) (Ancylidae). *Laevapex fuscus*. **A**, Dorsal view; **B**, right oblique ventral view; **C**, pseudobranch; **D**, cross section of pseudobranch at dotted line (b—b') on Fig. C. (From Basch, 1959).

ANCYLIDAE

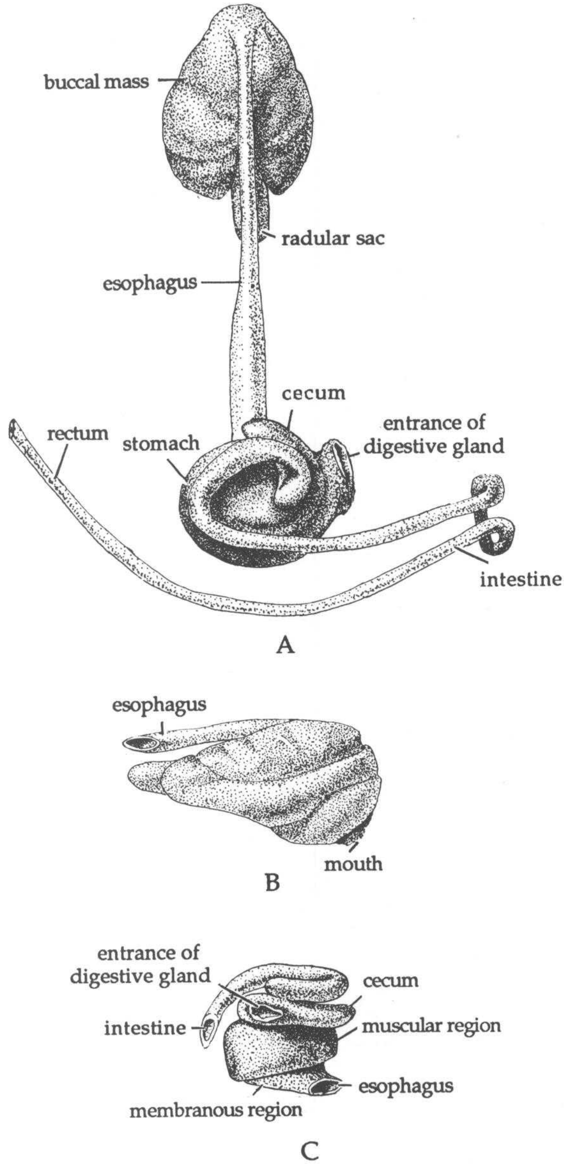

FIG. 19 (cont.). *Laevapex fuscus* (cont.). Digestive system. **A**, Entire system (dorsal view), except for the digestive gland; **B**, buccal mass, right side; **C**, stomach, right side. (From Basch, 1959).

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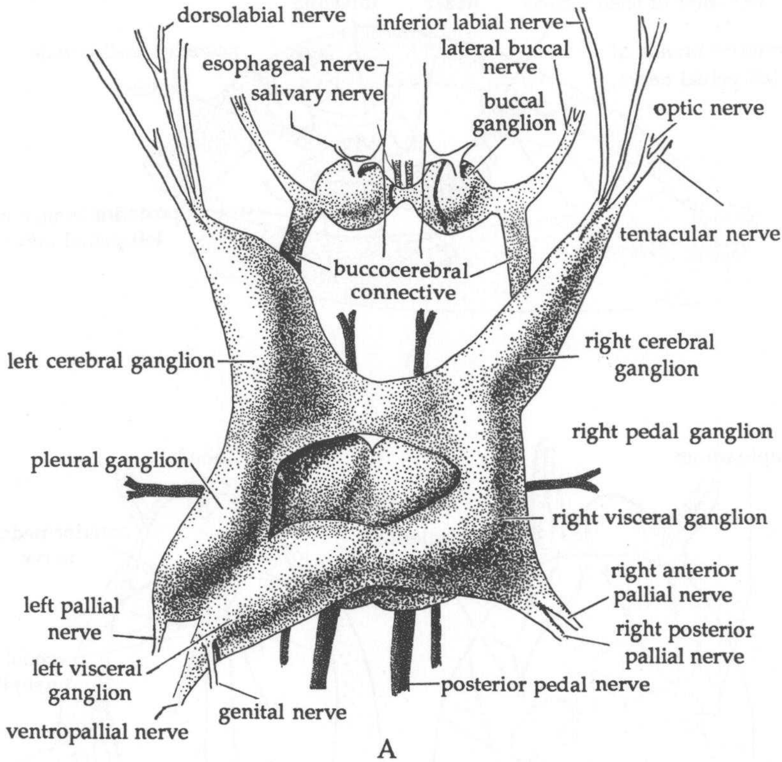

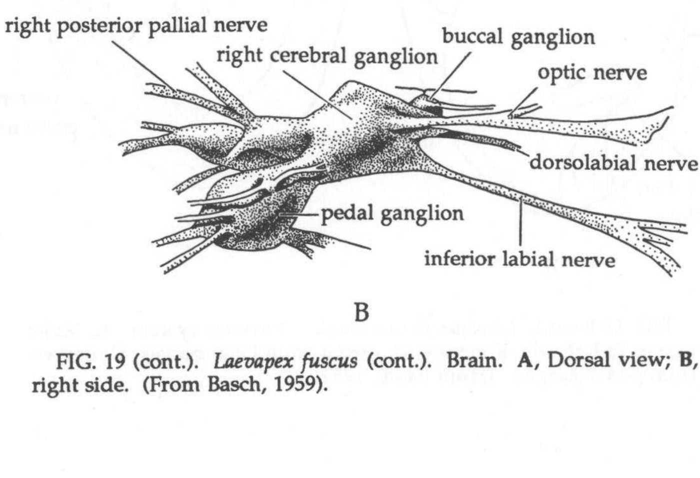

FIG. 19 (cont.). *Laevapex fuscus* (cont.). Brain. **A**, Dorsal view; **B**, right side. (From Basch, 1959).

ANCYLIDAE

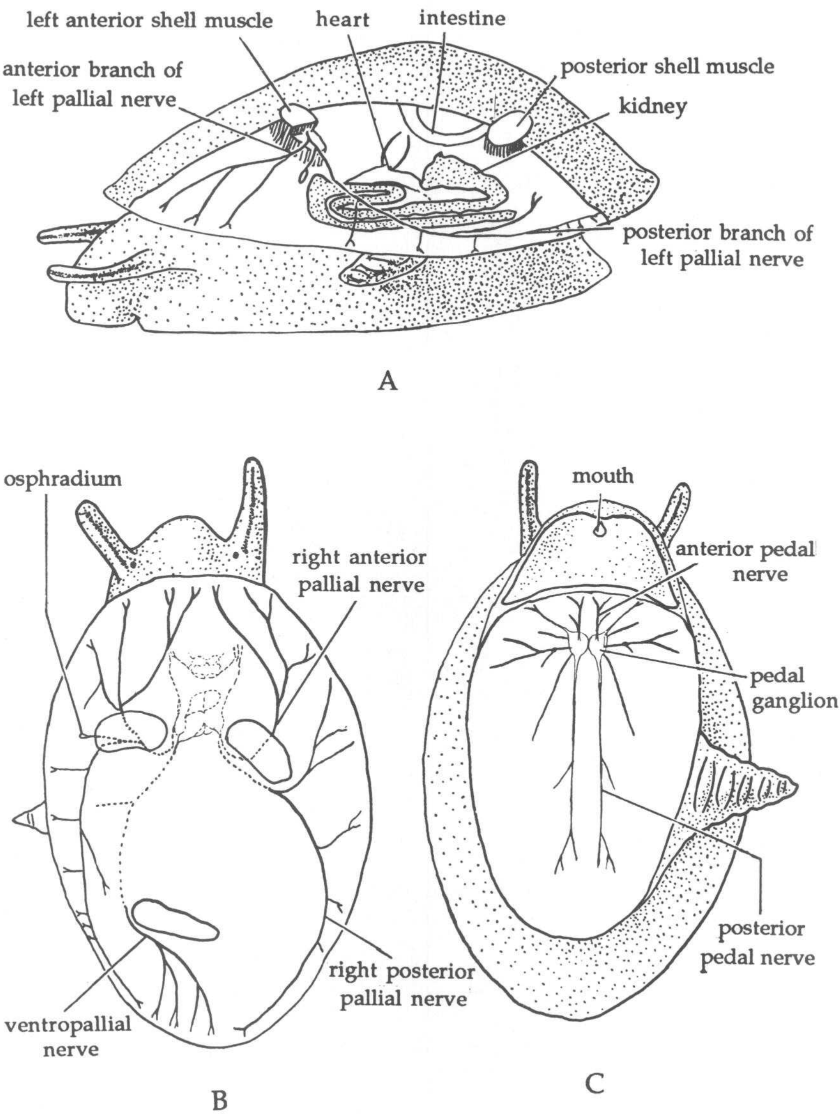

FIG. 19 (cont.). *Laevapex fuscus* (cont.). Nervous system. **A**, Major nerves to left side of mantle; **B**, dorsal superficial nerves; **C**, nerves from pedal ganglia. (From Basch, 1959).

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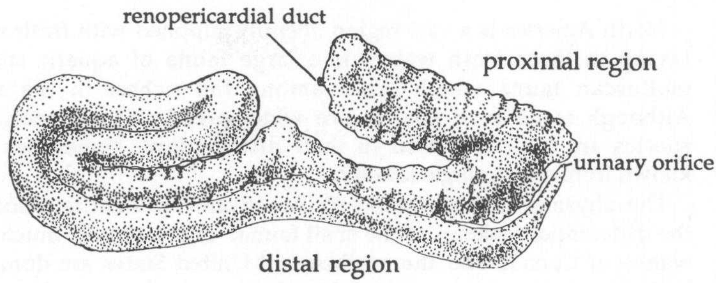

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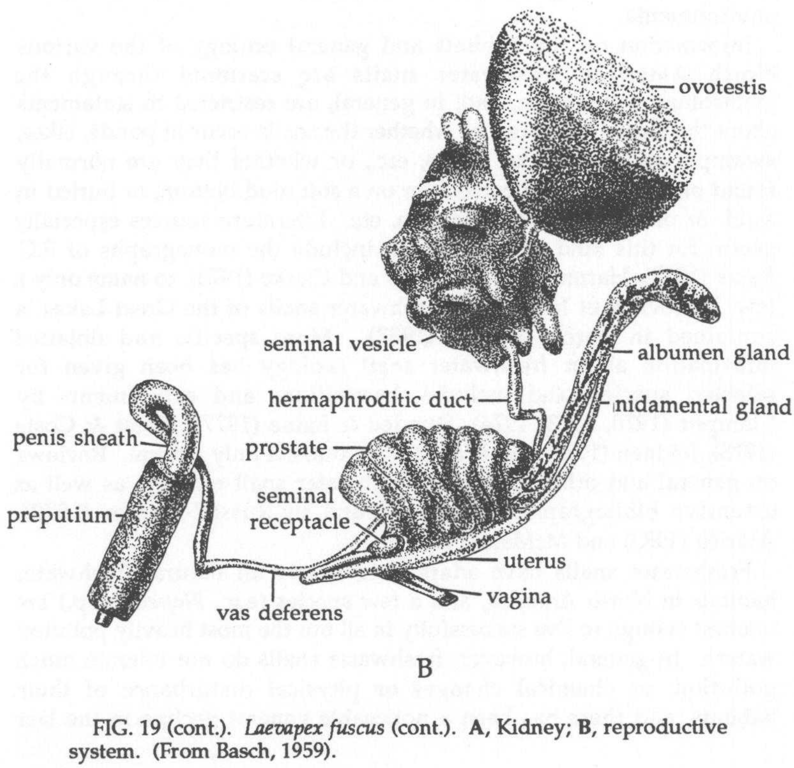

B

FIG. 19 (cont.). *Laevapex fuscus* (cont.). A, Kidney; B, reproductive system. (From Basch, 1959).

III. HABITATS AND DISTRIBUTION

HABITATS

North America is a vast region liberally supplied with fresh waters. Living in these fresh waters is a large fauna of aquatic snails, a molluscan fauna which ranks among the richest in the world. Although some snail species are wide-spread and common, other species are very restricted in their distributions, sometimes being known from only a single locality.

The physiography of the North American continent is reflected in the differential makeup of the snail fauna. For example, much of the waters of Canada and the northcentral United States are dominated by lentic environments, and so there is a preponderance of pond and lake species. In the southeastern United States, lakes were very rare before the advent of man-made impoundments, most of the fresh waters in this region being lotic in nature. Similarly, the aquatic habitats of this region are dominated by snails adapted to lotic environments.

Information on the habitats and general ecology of the various North American freshwater snails are scattered through the malacological literature, and, in general, are restricted to statements about the snails' habitats, i.e., whether the snails occur in ponds, lakes, swamps, ditches, creeks, rivers, etc., or whether they are normally found on rocks in swift current, or on a soft mud bottom, or buried in sand, or on submerged vegetation, etc. Literature sources especially useful for this kind of information include the monographs of F.C. Baker (1928), Harmon & Berg (1971) and Clarke (1973), to name only a few. A review of habitats of freshwater snails of the Great Lakes is contained in Burch & Jung (1987). More specific and detailed information about freshwater snail ecology has been given for selected species, and include observations and experiments by Clampitt (1970, 1973, 1974), Dundee & Paine (1977), Horst & Costa (1975), Jokinen (1978) and Wall (1977), to name only several. Reviews on general and other aspects of freshwater snail ecology, as well as extensive bibliographies, can be found in Russell-Hunter (1978), Aldrich (1983) and McMahon (1983).

Freshwater snails have adapted to nearly all natural freshwater habitats in North America, and a few species (e.g., *Physella* spp.) are tolerant enough to live successfully in all but the most heavily polluted waters. In general, however, freshwater snails do not tolerate much pollution, or chemical changes or physical disturbance of their habitats, and there has been a noticeable general decline in the last several decades in the local distribution and abundance of many species of freshwater snails.

North American aquatic snails have radiated into various kinds of freshwater habitats, with most species being restricted more or less to one or only several types of habitats. There are a few ubiquitous species, of course, but the restriction of species to specific types of habitats is the general rule. Examples of habitat restrictions for freshwater snails in the Great Lakes region are given below.

Deep water lake species: *Birgella subglobosa, Hoyia sheldoni, Valvata sincera sincera, Stagnicola contracta.*

Open shore lake species: *Valvata winnebagoensis, Lymnaea stagnalis sanctaemariae, Stagnicola catascopium, S. emarginata, S. nasoni, S. walkeriana, S. woodruffi, Physella gyrina sayi, P. magnalacustris, P. parkeri, P. vinosa, Planorbella (Pirosoma) corpulenta whiteavesi, P. (Pirosoma) truncata.*

Quiet bay or pond species: *Valvata piscinalis, V. sincera nylanderi, V. winnebagoensis, Viviparus georgianus, Cipangopaludina chinensis malleata, C. japonica, Bythinia tentaculata, Amnicola (Lyogyrus) pilsbryi, Elimia livescens haldemani, Acella haldemani, Bulimnea megasoma, Fossaria cyclostoma, F. galbana, Pseudosuccinea columella, Radix auricularia, Stagnicola elodes, Gyraulus (Torquis) parvus parvus, Helisoma anceps royalense, Menetus (Micromenetus) dilatatus, Planorbella campanulata campanulata, P. campanulata collinsi, P. multivolvis, P. (Pirosoma) corpulenta corpulenta, P. (Pirosoma) pilsbryi, Planorbula armigera, Ferrissia fragilis, F. parallela, F. walkeri, Laevapex fuscus.*

Marsh species: *Stagnicola elodes, Promenetus exacuous.*

Mud-flat species: *Fossaria obrussa, F. exigua.*

Species burrowing in sand or mud in rivers or lakes: *Campeloma crassula, C. decisum, Pleurocera acuta.*

Amphibious species: *Pomatiopsis cincinnatiensis, P. lapidaria, Fossaria parva, Fossaria (Bakerilymnaea) dalli.*

Intermittant pool or stream species: *Stagnicola exilis, S. elodes* (form *reflexa*), *S. (Hinkleyia) caperata, Physella gyrina gyrina, Aplexa elongata, Gyraulus (Armiger) crista, G. (Torquis) circumstriatus.*

Riverine species: *Valvata bicarinata, V. piscinalis, Bythinia tentaculata, Somatogyrus tryoni, Pyrgulopsis letsoni, Fossaria peninsulae, Stagnicola catascopium, S. petoskeyensis, Helisoma anceps royalense, Ferrissia rivularis.*

Species with a general aquatic distribution in both perennial and intermittant waters: *Physa skinneri, P. gyrina gyrina, Gyraulus deflectus.*

Species with a general aquatic distribution, but restricted to perennial waters: *Valvata lewisi, V. tricarinata, Lioplax sulculosa, Amnicola limosa, A. (Lyogyrus) walkeri, Probythinella lacustris, Cincinnatia cincinnatiensis, Marstonia lustrica, Elimia livescens livescens, Fossaria obrussa, Lymnaea stagnalis appressa, Helisoma anceps anceps, Planorbella (Pirosoma) trivolvis.*

Shallow springs species: *Fontigens nickliniana.*

DISTRIBUTION

North America has been divided into various zoogeographical regions in regard to its non-marine molluscan fauna (Binney, 1878, 1885; Henderson, 1931; Pilsbry, 1948). The three primary regions are the Eastern American, Western American and Middle American divisions. On the Continental North American mainland north of Mexico, the Middle American Division includes only the southern tip of Florida and a small portion of southcentral Texas. The largest region, the Eastern American Division, extends westward from the Atlantic coast to the eastern limit of the Rocky mountains - an area encompassing 5/6 of the total North American land mass, and it includes the drainages flowing into the Arctic and Bering seas, the Hudson Bay, the Gulf of Mexico and Atlantic Ocean, the Great Lakes, and the St. Lawrence and Mississippi rivers (Fig. 20). The Eastern Division is characterized by such endemic freshwater snail genera as *Campeloma, Lioplax* and *Tulotoma* (Viviparidae), *Antroselates* (? Micromelanidae), *Antrobia, Aphaostracon, Birgella, Cincinnatia, Clappia, Fontigens, Gillia, Hoyia, Lepyrium, Marstonia, Notogillia, Probythinella, Rhapinema, Somatogyrus, Spilochlamys* and *Stiobia* (Hydrobiidae), *Elimia, Gyrotoma, Io, Leptoxis, Lithasia* and *Pleurocera* (Pleuroceridae), *Acella* and *Bulimnea* (Lymnaeidae), *Amphigyra, Neoplanorbis* and *Planorbula* (Planorbidae) and *Rhodacmea* (Ancylidae). The Western American Division includes about 1/8 of the total North American land mass, and contains the Interior Basin, Colorado River, Columbia River and Pacific Slope drainages. Western freshwater snail genera not found in the Eastern American Division are *Fluminicola, Fontelicella* and *Tryonia* (Hydrobiidae), *Juga* (Pleuroceridae), *Fisherola* and *Lanx* (Lymnaeidae) and *Vorticifex* (Planorbidae). Some genera, of course, occur in both Eastern and Western divisions, e.g., *Valvata* (Valvatidae), *Cipangopaludina* [introduced] (Viviparidae), *Pyrgulopsis, Amnicola* and *Horatia* (Hydrobiidae), *Pomatiopsis* (Pomatiopsidae), *Melanoides* [introduced] (Thiaridae), *Acroloxus* (Acroloxidae), *Fossaria, Stagnicola* and *Radix* [introduced] (Lymnaeidae), *Aplexa* and *Physella* (Physidae), *Gyraulus, Helisoma, Menetus, Planorbella* and *Promenetus* (Planorbidae) and *Ferrissia* (Ancylidae). Genera that occur in either the Eastern or Western divisions, but have species also in the Middle American Division, are *Neritina* (Neritinidae, = Neritidae), *Viviparus* (Viviparidae), *Marisa* [introduced] and *Pomacea* (Ampullariidae), *Pyrgophorus* and *Cochliopina* (Hydrobiidae), *Pseudosuccinea* (Lymnaeidae), *Stenophysa* (Physidae), *Drepanotrema* and *Biomphalaria* (Planorbidae) and *Laevapex* (Ancylidae).

FIG. 20. Major drainages of North America (north of Mexico).

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Corrigenda

p. 90, line 23 - *Lioplax subcarinata* Say dates from 1817 rather than 1816.

p. 144, line 40 - The author of *Elimia virginica* is Gmelin (1791) rather than Say (1817). Say's (1817) *"Lymnaea" virginica* is *Elimia livescens* (Menke 1830).

pp. 156, 158, 245 - The subspecific name in the trinominal *Leptoxis* (*Mudalia*) *carinata nickliniata* should be *nickliniana*. The spelling *nickliniata* dates from Goodrich (1942b; see References, p. 310) [*Nitocris carinatus nickliniatus*] and is an error for [*Melania*] *nickliniana Lea* 1841.

p. 176, line 21 - F.C. Baker (1928) restricted the distribution of *Stagnicola apicina* (Lea 1838) "to the region west of the Rocky Mountains, the Pacific drainage." Specimens from Michigan that he previously referred to *S. apicina*, he later (1926) named *S. walkeriana* (type locality: Madeline Island, near Bayfield, Wisconsin).

p. 247, line 11 - Under Lymnaeidae, for "three latter" read "last two."

p. 251, couplet 23 - For "with above five whorls" read "with about five whorls."

p. 288, last line - For "part of beginning" read "part or beginning."