Freshwater Snails of Africa and their Medical Importance

David Brown

Revised 2nd edition

Taylor&Francis
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Second Edition

TO CHRISTOPHER WRIGHT
who introduced me to Africa and its snails
TO GEORG MANDAHL-BARTH
for the pleasures of his friendship and conversation
AND TO MY WIFE JULIA
for loving encouragement

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Preface

This edition is extensively revised to take account of advances made since 1980. At first it seemed that new material could be inserted here and there in the text of the 1st Edition, but the outcome is an almost entirely rewritten book. During the last 14 years, new species have been described and changes have been made in classification; much new information has been published about the ecology and distribution of snails and their relationships with trematode parasites. The number of new references added probably exceeds the total cited in the 1st Edition. The arrangement of the book remains much the same; the major changes are the addition of a checklist of species and the replacement of the appendix about techniques by a bibliography of identification and snail distribution.

A few years after the publication of the 1st Edition, malacologists and parasitologists suffered a deep shock and loss in the early death of Christopher Wright (1928–1983). To we his remaining colleagues it is a satisfaction that the research group founded by Chris continues to flourish as his memorial; it will soon have completed 40 years of contributing to knowledge of snails and schistosomes.

Many people and institutions have contributed, directly or indirectly, to this book. Some are named, but probably not all who deserve to be, in the Acknowledgements below. Looking further back, I was attracted to the study of freshwater biology in the English midlands by the enthusiasm of H.P.Moon of Leicester University. From dissecting the heads of mayfly larvae, I moved in 1959 to unravelling the reproductive organs of planorbid snails, as a result of the Medical Research Council (MRC) seeking to strengthen expertise in the United Kingdom on the taxonomy of the snail hosts of schistosomes in Africa. The MRC sent me to join Chris Wright at the British Museum (Natural History), now named The Natural History Museum, where he was building up the research group that became the Experimental Taxonomy Unit. Here I benefited from the resources of a great museum and the stimulus of colleagues exploring new ways of characterizing species of snails and schistosomes. This laboratory has been my base ever since; its continuity has been invaluable in enabling me to make what I hope has been good use of extensive periods of fieldwork in Africa.

It was many years before I began to feel any familiarity with the extensive literature on the freshwater snails of Africa and their parasites. I hope this book

will make it easier for students to find their way. I would like to think too that specialists, whether in applied or academic fields of study, will share my enjoyment in attempting to take a broad view of the freshwater snail fauna of a large continent.

David Brown
London, January 1994

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Chapters and sections of this book have been criticized by the following: D.W.Taylor 4 (Physidae) and 12 (faunal origins), V.R.Southgate 5, D.Rollinson 7, C.C.Appleton 8, J.M.Jewsbury 8 and F.S.McCullough 8. These friends have corrected errors, pointed to things of value that might be included and suggested improvements to clarify the text. I am most grateful to them all. For omissions and mistakes that may remain I am entirely responsible.

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I am indebted to Simon Tillier for making available to me for study the large collection, mostly then unidentified, of the late G.Ranson (Muséum National d'Histoire Naturelle, Paris).

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The base maps used to show distributions (Figs 69–74, 116–128, 151) are reproduced by kind permission of Goode Base Map Series, University of Chicago.

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The manuscript benefited greatly from careful copyediting by Dr Ann Lackie.

Changes in place names and journal titles

Names of some countries, towns and lakes used in the literature have been changed in recent decades. Commonly encountered names so affected are listed here.

Official recent name	*Past name, or other name in use*
States	
Benin (Republic of)	Dahomey
Botswana	Bechuanaland
Burkino Faso	Upper Volta
Central African Republic	Oubangui Chari (part of French Equatorial Africa)
Congo (Republic)	Brazzaville Congo (part of French Equatorial Africa)
Equatorial Guinea	Spanish Guinea
Ethiopia	Abyssinia
Ghana	Gold Coast
Guinea	French Guinea
Guinea Bissau	Portuguese Guinea
Lesotho	Basutoland
Malagasy Republic	Madagascar
Malawi	Nyasaland
Mali	French Sudan
Namibia	South West Africa
Tanzania (mainland)	Tanganyika
Yemen Arab Republic	Yemen or North Yemen
Yemen, People's Democratic Republic	South Yemen or Aden Protectorate
Zaire	Belgian Congo (Leopoldville Congo)
Zambia	Northern Rhodesia
Zimbabwe	Southern Rhodesia
Towns	
Banjul	Bathurst

Official recent name	*Past name, or other name in use*
Chipata	Fort Jameson
Kabwe	Broken Hill
Kalemié	Albertville
Kinshasa	Leopoldville
Kisangani	Stanleyville
Likasi	Jadotville
Lubumbashi	Elizabethville
Maputo	Lourenço Marques
Ndjamena	Fort Lamy
Ubundi	Ponthierville
Lakes	
Abaya	Margherita
Mobuto	Albert
Turkana	Rudolf

Names of some long-established scientific journals cited in the reference lists in this book have been changed in recent years.

Bulletin of Epizootic Diseases in Africa has become *Bulletin of Animal Health and Production in Africa*.

Cahiers de l'Office de la Recherche Scientifique et Technique Outre-Mer (ORSTOM), *série Hydrobiologie* has become *Revue d'Hydrobiologie tropicale*.

Proceedings of the Malacological Society of London has become *Journal of Molluscan Studies*.

Revue de Zoologie Africaine is also known as *Journal of African Zoology*.

Zeitschrift für Parasitenkunde has become *Parasitology Research*.

Chapter 1.
Introduction

There are about 400 species of freshwater snail (including the limpets) in Africa. Most are known only to specialists, but some are all too familiar to residents and visitors alike, as the source of the 'peril in the water'—the microscopic cercariae that produce the parasitic infection in man that causes the disease schistosomiasis (bilharzia). To find out more about the species of snail which are the intermediate hosts for schistosomes became a priority about 40 years ago, when the World Health Organisation and some national health authorities began to give serious consideration to the possibility of controlling schistosomiasis. The resulting financial support for malacological studies has advanced knowledge of many species besides those of medical or veterinary importance. Collectors have searched areas where the aquatic molluscan fauna was unknown. Whole animals have been obtained for the study of many species described by earlier taxonomists from only empty shells. Comparative morphology, and the use of biochemical and cytological characters in taxonomy, as well as growing knowledge of distribution and ecology, are all contributing to a better understanding of the species as biological units, and of their histories. Studies focused on the remarkable radiation of prosobranch snails in Lake Tanganyika are providing new insights into the processes of speciation within ancient lakes.

The first edition of this book provided the first comprehensive review of freshwater snails for the whole of Africa. During the 14 years since its publication considerable advances have been made in all the main fields of study: taxonomy, ecology, distribution and snail-borne parasitic infections. The catalogue of species is incomplete, but the actual number may be less than 400 and thus is not large compared with some other kinds of invertebrate in Africa, e.g. landsnails and some insect groups. Because the number of species is moderate, it is possible in a volume of reasonable size to review them systematically, and also summarise their ecology, distribution and relationships with parasites. I hope therefore that this book will be useful to a variety of readers: taxonomists, medical malacologists, parasitologists, freshwater biologists in general and biogeographers—indeed all who are interested in the life of the great continent of Africa.

Besides the African mainland including the Mediterranean region, this account covers islands in the Atlantic and Indian Oceans, among them the Cape

Verde Islands, Madagascar and the Mascarene group. Many endemic species and genera live in the tropical area: the fauna of northern Africa is very different, having species that occur also in parts of Europe, the Near East and South West Asia. A few species have been introduced, apparently by man in recent historical time. Africa south of the Sahara, together with Madagascar, was known to early biogeographers as the 'Ethiopian Region', but since the name Ethiopia was adopted by the territory formerly called Abyssinia, the replacement term 'Afrotropical Region' has come into use (Crosskey & White, 1977). Considerable areas of this region, however, do not experience a tropical climate, notably the highlands of eastern Africa and the temperate zone of South Africa. The Palaearctic Region includes North West Africa: it is not fully understood what factors, past or present, determine the southern limits of palaearctic species, and the northern limits of the afrotropical ones. There appears to be a formidable barrier in the Sahara Desert, but freshwater habitats were widespread in this region less than 10 000 years ago. Yet aquatic molluscs have made remarkably few movements through this apparently broad highway that was available between north and south. The slender thread of the Nile has been the main route taken by snails from tropical Africa to the Mediterranean coast.

Since it is difficult to define ecological limits for the freshwater fauna, I include species of brackish/marine affinity which might be encountered in coastal streams, estuaries and lagoons, including the mangrove habitat. Africa has many saline inland waters, but these do not have a specialised snail fauna, except perhaps in North West Africa.

Scientific study of African freshwater snails began nearly 250 years ago, in association with the penetration of the continent by European traders and explorers. Full justice cannot be done here to a story that needs a book to itself; our present knowledge owes much to men who suffered great hardships, ill health and risked their lives. Collectors in East Africa are the subjects of a continuing series of most interesting accounts published in *The Conchologists' Newsletter* (Verdcourt, 1979–1993). Notable pioneers in this area and elsewhere include M.Adanson (1757; Senegal, 1749–53), F.Krauss (1848; South Africa, 1838–40), G.Tams (Angola, 1841–42; molluscs reported by Dunker, 1853), W.Peters (Mozambique and Zambezi valley, 1843–47; molluscs reported by Martens, 1860, 1879), F.Welwitsch (Angola, 1853–60; molluscs reported by Morelet, 1868), J.Speke (Lake Tanganyika and Lake Victoria, 1858 and 1859; molluscs reported by Woodward, 1859, and Dohrn, 1864), J.Kirk (Lake Nyasa, 1859; molluscs reported by Dohrn, 1865), C.F.Jickeli (1874; north east Africa, 1870–71). In these days of the package tour to game-parks it is startling to read Adanson's account of his thoughts when setting sail from France in 1749: he would be, he reflected with pleasure, the first naturalist to visit tropical Africa.

Then in his early twenties, Adanson spent four years moving from one trading post to another in Senegal, collecting all kinds of biological specimens and especially molluscs. In 1757 was published his *Histoire naturelle du Sénégal,* a volume devoted entirely to molluscs and now held to be the beginning of their

scientific study (Fischer-Piette, 1942). Adanson described shells, anatomy and habitats; he used a binomial system of nomenclature, one year before Linnaeus introduced his own system. From fresh water he described *'Le Coret'* (now *Afrogyrus coretus*) and *'Le Bulin'* (now *Bulinus senegalensis*), which was to become the type of the genus *Bulinus*. Nearly 160 years later the discovery in Egypt of the life cycle of *Schistosoma haematobium* would make *Bulinus* one of the most intensively studied snails in the world.

Unfortunately, some later authors did not share Adanson's interest in anatomy as well as conchology. During the 19th century numerous species were hastily named according to trivial differences between shells, while important anatomical characteristics went unnoticed, partly because of a want of materials to dissect. Something of the political scramble for Africa can be seen in the promptness with which authors published names for 'new shells'. A modern student bewildered by long lists of synonyms due to conchologists such as J.R. Bourguignat will be tempted to dismiss this activity as hopelessly unscientific. But some early writers were well aware of the limitations of their materials, often a few shells picked up hurriedly by travellers who were concerned above all with surviving their hazardous daily lives. Shells are still important in molluscan taxonomy, and a knowledge of conchology is usually necessary in order to identify a species, even though its systematic place may depend on the anatomy and bio-chemical properties of the animal within.

The first scientific expeditions to study freshwater organisms in tropical Africa were sent by The Royal Society in 1895 and 1899 to Lake Tanganyika, partly to investigate the remarkable prosobranch snails brought to notice by shells that John Speke collected in 1858. But it was the discovery that *Bulinus truncatus (=contortus)* and *Biomphalaria alexandrina (=Planorbis boissyi)* are the intermediate hosts for the parasites causing human schistosomiasis in Egypt (Leiper, 1915, 1918), that led to the modern phase in the study of African freshwater snails. For some time though, authorities responsible for health in Africa were preoccupied with other diseases, especially malaria, and there was little progress in knowledge of the intermediate hosts of schistosomes. Nonetheless, professional and amateur malacologists were busy and two outstanding monographs appeared, both still indispensable today, describing the snails of the former Belgian Congo (Pilsbry & Bequaert, 1927) and South Africa (Connolly, 1939). After the 1939– 45 World War interest in African schistosomiasis increased through the influence of the World Health Organisation (Farooq, 1973); growing awareness of an urgent need for improved snail taxonomy led to the meeting in Paris in 1954 of the 'Study Group on the Identification and Classification of the Bilharzia Snail Vectors (Equatorial and South Africa)'. There was growing interest too in the common parasites of livestock with snail intermediate hosts (schistosomes, amphistomes and liver flukes). Funds were made available by the WHO and national governments for malacological research, and substantial support continues to be given to investigations in the laboratory and the field. Increasing prevalence of

schistosomiasis continues to be a problem in human populations living nearby man-made lakes, dams and irrigation schemes (Hunter *et al.,* 1993). Studies on snail taxonomy and distribution are major activities of the Experimental Taxonomy Division of The Natural History Museum, London (formerly the British Museum (Natural History)) and the Danish Bilharziasis Laboratory, Copenhagen. An outstanding national survey of snail distribution was carried out in the Republic of South Africa in the Institute for Zoological Research, Potchefstroom University. Today there are staff trained in malacological work in the universities and public health laboratories of many African countries.

The first half of this book is mostly a systematic survey of the snails (Chapters 2–4), beginning with glossaries, keys for identification to genera and a checklist of species: there follows a synopsis of species, with brief notes on ecology, distribution and parasites. Relationships are then described between snails and schistosomes (Chapter 5) and with other parasites (Chapter 6). Because the degree of susceptibility to infection with schistosomes varies so greatly among species of *Bulinus,* from complete resistance to full compatibility, this genus has been much studied in order to improve the definitions of species, and to reach an understanding of variation within them. An account of the still developing species-concepts in *Bulinus* and a consideration of reasons for the success of this genus occupies Chapter 7. The objective of reducing transmission of schistosomiasis through reducing the numbers of snails has been the motive for many studies of snail ecology and distribution. Whether to rely on molluscicides for controlling snails, or to place more emphasis on non-chemical means (biological control and environmental modifications), has been thoroughly debated; measures that can be sustained by the local community seem to offer the best prospect for successful snail control in Africa (Chapter 8). Local surveys are the essential basis for understanding the ecology and distribution of snails on a larger scale: Chapter 9 describes selected snail faunas in areas of not more than a few hundred square kilometres, and consideration is given to some of the biotic factors that influence occurrence locally (aquatic vegetation, food supply and dispersal). Abiotic factors (physical and chemical) are reviewed in Chapter 10, with particular reference to distribution in the field and experiments in the laboratory. Physicochemical factors are discussed further in relation to growth, life cycles and population dynamics (Chapter 11). My attempt to present the African freshwater snail fauna in a continental perspective (Chapter 12) owes much in its arrangement to the late R.E.Moreau's *The Bird Faunas of Africa and its Islands* (1966). By concentrating first on Mediterranean Africa and then southern Africa, we can look at the transition between the snail faunas of the Palaearctic and the Afrotropical regions, and then view the progressive subtraction of tropical species as they reach their various southern limits of penetration into the cooler southern tip of the continent. For other areas it seemed the most effective treatment was to analyse the snail assemblages found in the major lakes and river systems. The Appendix provides a selected bibliography of guides to the identification of freshwater snails and studies of distribution,

arranged according to geographical region. In this edition I have not attempted to review methods of study, because of the wide variety of techniques in use, and the difficulty of giving an account of practical value in a limited number of pages. Technical information will be found in many of the references listed, especially in Chapters 5–11.

There are good reasons for studying the freshwater snails of Africa, besides the objective of controlling snail-transmitted diseases. Snails are an important part of the freshwater ecosystems on which depend the inland fisheries that are a valuable source of human food. From the purely scientific point of view there is much of interest in the uniquely African events that have occurred in the evolution of many snail lineages. The strange and beautiful snails of Lake Tanganyika are one of the wonders of the living world: may enlightened governments in eastern Africa cooperate to preserve them for the interest and enjoyment of future generations of their people. The well-being of human societies in Africa depends much on conserving water and supplying uncontaminated water to people. Wherever living standards rise and the threat of schistosomiasis recedes, it may be that a rich snail fauna will come to be appreciated as a sign of healthy and sustainable aquatic ecosystems, on which the water supply depends.

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Chapter 2.
Systematic Synopsis: Introduction, Glossary, Identification Keys, Checklist

The synopsis of species to be presented in Chapters 3 and 4 covers Africa, Madagascar and the Mascarene Islands, and includes snails likely to be found in moderately saline coastal habitats such as mangrove swamp. Two families are dominant (Table 2.1), the Thiaridae and the Planorbidae, which together contribute about half of the totals for both genera and species. Few species found in tropical Africa occur also north of the Sahara Desert, and likewise few species of the Mediterranean region extend southwards into the tropics. Faunal composition and biogeography are discussed in Chapter 12; here the contributions of the different families are briefly summarised.

Prosobranchs are most varied in the larger lakes and rivers. Neritidae scarcely penetrate the inland waters of Africa apart from the lower Nile and streams in North West Africa. Viviparidae live usually in lakes and rivers; African species belong to either *Bellamya* or *Neothauma,* which is confined to Lake Tanganyika. Ampullariids are successful in seasonally flooded habitats, being able to breathe air, while *Lanistes* also has species adapted to fast-flowing streams and benthic life in Lake Malawi. Many species classified in the Hydrobiidae occur in northern Africa, particularly in the Maghreb area, but the hydrobiid fauna known from the tropical region is comparatively poor. The Pomatiopsidae is represented by a small group of species concentrated in the coastal regions of southern Africa. There is one widespread genus of the Bithyniidae, *Gabbiella,* which in habitats ranges from rainpools to large lakes; some specialised bithyniids are restricted to rapidly flowing rivers in western Africa. Assimineids are scarce in African inland waters; the few strictly freshwater species are associated with springs in eastern Africa and with rapids of the lower Zaire River. The Thiaridae is well represented in fresh and brackish waters; *Melanoides* and *Cleopatra* occur almost throughout tropical Africa. Many thiarids are restricted to the Zaire Basin or to a particular lake, especially Tanganyika (Chapter 12), while *Potadoma* is characteristic of streams in western forests (*Melanatria* occupies this niche in Madagascar). Although the Melanopsidae is widespread in the Mediterranean area it is absent from the Nile and further south. The Potamididae is confined to brackish water.

Of the pulmonates, ellobiids are confined to brackish coastal waters, while the strictly freshwater groups are most abundant in the smaller waterbodies,

including seasonal rainpools. Although *Lymnaea natalensis* is the most widely distributed freshwater snail in Africa, the number of lymnaeid species in the Afrotropical region is surprisingly few. Ancylids occur in most kinds of habitat; clean well-oxygenated waters are suitable for *Ancylus* (in N Africa) and *Burnupia* (E and S Africa), while *Ferrissia* thrives in stagnant conditions. The Planorbidae is well represented in temporary waters, where *Bulinus* survives in dry mud for

Table 2.1. Composition of the gastropod fauna of the fresh and brackish waters of the African continent (according to the checklist at the end of this chapter, and likewise excluding the Hydrobiidae of northern Africa). For each family the number of genera is followed in brackets by the number of species, which is approximate for some genera. Introduced species are included.

Prosobranchs		
Neritidae	4	(17)
Viviparidae	2	(19)
Ampullariidae	5	(28)
Valvatidae	1	(1)
Littorinidae	1	(2 plus)
Hydrobiidae (tropical region only)	3	(13)
Pomatiopsidae	1	(10)
Bithyniidae	9	(35)
Assimineidae	5	(11)
Thiaridae:		
non-thalassoid	6	(78)
thalassoid (of Lake Tanganyika)	17	(31 plus)
Melanopsidae	1	(1)
Potamididae	4	(4)
Total prosobranchs	59	(250 approximately)
Pulmonates		
Ellobiidae	5	(7 plus)
Lymnaeidae	1	(6)
Ancylidae	3	(5 plus)
Planorbidae:		
Planorbinae	11	(40)
Bulininae	2	(31)
Physidae	2	(2)
Total pulmonates	24	(91 approximately)
Overall totals	83	(341 approximately)

many months (Chapters 7, 10). *Biomphalaria* is rather less successful in seasonal pools and perhaps for this reason is not so well established in the drier parts of

northern Africa. Few species of Physidae occur in Africa and perhaps all were introduced following European settlement.

The introduction by man of exotic freshwater snails into Africa (see Chapter 12) seems to have begun with physids in the nineteenth century and has resulted in the appearance of *Lymnaea columella, Helisoma, Amerianna* and *Indoplanorbis*. Deliberate introductions have been made of *Helisoma* and *Marisa* for the attempted biological control of snail hosts for schistosomes (Chapter 8).

Organisation of systematic synopsis

Information is given under species-headings about taxonomy, habitat and ecology, distribution and parasites. Ecology and distribution are considered more fully in Chapters 9–12, and parasites in Chapters 5 and 6. The species are mostly recognisable from the shell; for a few their identification may depend on examination of the radula and soft organs. Cytological and molecular data are available for only a few genera. As knowledge of genetic relationships increases and morphological comparisons are made in more detail, taxonomic changes will be likely. At present evolutionary relationships within the larger families are not clear enough for genera and species to be arranged in a phylogenetic manner with any confidence; use will be made here of geographical distribution and sometimes simply alphabetical order.

Taxonomy

A type locality given by the original author of a species may be supplemented here by information in brackets. The terms holotype, paratype and syntype are used as defined in the Glossary: General. Commonly used synonyms are mentioned and references are given to publications useful for exploring the taxonomic history of a species; the single most valuable compilation of names is that of Pilsbry & Bequaert (1927), which covers an area far larger than the Congo Basin.

Characterisation of species

The size given is of a fully grown shell (see Glossary: Shell), but not necessarily the largest known; populations may be found where the maximum is unusually large or small. Attention should be given to scales of magnification in the figures as they may vary within a group. Outstanding characteristics are described as briefly as practicable, with emphasis on the shell and gross anatomical parts wherever possible. References are given also to biochemical and cytological data of current or potential taxonomic application. The institution where particular material is stored may be indicated by an abbreviation listed below.

Habitat and ecology

Reference is made to observations in the field and also to studies of ecological factors in the laboratory.

Distribution

Geographical ranges when extensive are summarised and details may be found in the legends to the distribution maps grouped at the ends of Chapters 3 and 4.

Parasites

Summaries are given of the medical and veterinary importance of a snail as known from the natural transmission of parasites and of responses to experimental infection in the laboratory.

Abbreviations and symbols

BMNH	The Natural History Museum, London: Mollusca Collection. Formerly the British Museum (Natural History).
BME	Experimental Taxonomy Division of the Department of Zoology, The Natural History Museum.
DBL	Danish Bilharziasis Laboratory.
MNHN	Muséum National d'Histoire Naturelle, Paris.
E	East, eastern.
N	North, northern.
NW	North-West, north-western.
S	South, southern.
SE	South-East, south-eastern.
SW	South-West, south-western.
‰	Total concentration of dissolved salts (salinity) as parts per thousand.
<	Smaller than.
>	Larger than.
●	A locality for a living population or one believed to have been alive when found.
○	A locality for 'sub-fossil' shells, usually of Late Pleistocene-Holocene age.

Glossary (General, Shell, Operculum, Radula)

Extensive glossaries of malacological terms are given by Malek (1985) and Burch (1985) and include anatomical terms for which there is not space here. Lincoln *et al.* (1982) provide a comprehensive dictionary of systematic, ecological and biogeographical terms.

General terms

allopatric Used of species occupying different geographical areas.

Arabia Used here of the Arabian Peninsula southwards from the northern border of Saudi Arabia.

Basommatophora A group of pulmonates, possessing one pair of tentacles with eyes at their bases.

East Africa Kenya, Uganda and Tanzania.

form A minor variant or subset of a species; a morph.

holotype The single specimen indicated as the type of a named species by the original author or the single specimen when no type was specified but only one was available.

Mascarene islands Mauritius, Réunion and Rodrigues.

morph See form.

Near East Used here for the area comprising Iraq, Israel, Jordan, Lebanon, Palestine and Syria.

North West Africa Morocco, Algeria and Tunisia.

paratype Any type specimen there may be additional to the holotype.

Prosobranchia, prosobranch A major group of streptoneuran Gastropoda, with gills (branchia or ctenidia) situated in the mantle cavity and anterior to the heart; usually with an operculum.

pseudobranch A gill-like respiratory organ developed in some aquatic pulmonates.

Pulmonata, pulmonate A major group of euthyneuran Gastropoda, with the mantle cavity serving as a lung; usually lacking an operculum.

sympatric Used of species occurring together in the same geographical area.

syntype Any of two or more type specimens when a holotype is not established.

taxon A taxonomic group of any rank, considered to be sufficiently distinct to be treated as a separate unit.

type(s), type specimen(s) Used as neutral terms for specimens without asserting their precise status in taxonomy.

type locality The locality of origin for the type(s) of a species.

type species The species designated as the type of a genus or subgenus.

West Africa The area south of the Sahara and extending westwards from the Cameroon/Nigeria border.

Shell

angular Used of the shell surface when it forms an angle rather than an evenly curved contour.

aperture The opening or 'mouth' of the shell (surrounded by the lip or peristome).

apex The tip of the spire. base The part of the shell furthest from the apex.

body whorl The last complete whorl of a spired shell.

calcareous, calcified Composed of calcium carbonate; of white or chalky appearance.

callus A layer of calcareous material; often deposited on the columella and nearby surface (Figs 1a,d).

cap-like The limpet form; a shell with little or no coiling, e.g. Ancylidae.

carina (plural: carinae) A conspicuous spiral ridge running along an angular contour, like the keel of a boat (Fig. 2b).

columella The internal column around which the whorls turn; the axis of a spiral shell, solid or with a cavity that may be open below forming the 'umbilicus'.

columellar Used of those parts of the lip and inner margin of the aperture that lie near the columella; a columellar plate is a well-defined layer of callus (Figs 1a–d, 4b,e).

conic, conical Shaped like a cone, tapering from a wide circular base to a point.

decollate Used of a shell when the upper whorls are normally detached (Figs 3c, 6f).

depressed Used of shells broader than high; spire short (Fig. 3d).

dextral Used of a spired shell having its aperture on the observer's right side when the spire points upwards (Fig. 2a).

diameter Maximum distance across a discoid shell. **discoid** Coiled horizontally, round and flat (Fig. 11b).

embryonic whorl See **protoconch**.

fusiform Used of a shell with its sides slightly curved, tapered at both ends (Figs 10a, 49a).

globose Used of a shell when its height and width are about equal (Fig. 27c).

globosely conic Used of a shell when the height is about 1.20 times the width (Fig. 3e).

growth lines or ridges Fine lines on the surface, parallel to the lip, indicating brief phases of growth.

height For spired shells the greatest distance between the apex and the base (also termed the length). For discoid shells the height may be measured of the last whorl at the lip. For a cap-like (ancylid) shell the vertical distance between the summit and the base.

imperforate Lacking an umbilical opening.

inner lip That part of the apertural lip in the columellar-parietal region.

lamella (plural: lamellae) See **septum**.

length See **height**.

limpet See **cap-like**.

lip The outermost edge of the last whorl surrounding the aperture.

malleated Used of a surface when small areas are flattened.

microsculpture Fine surface structure seen under magnification.

narrowly conic Used of slender spired shells; height about 3 times width (Fig. 6d).

neritoid, neritiform Used of shells with a greatly expanded last whorl and of the shape common in the Neritidae (Figs 1a,d).

nodule A small rounded projection from the shell surface; described as nodular if many are present.

nuclear whorl See **protoconch**.

outer lip That part of the lip opposite to the columellar-parietal region.

ovate Egg-shaped in outline; one end narrower than the other.

ovately conic Used of spiral shells when the height is about 1.5 times the width (Fig. 5a).

parietal Used of the area between the upper attachment of the outer lip and the columella.

perforate Used of a spired shell with a narrow umbilical opening.

periostracum Thin outer layer of proteinaceous material covering the shell.

periphery The outermost edge of a whorl seen in outline.

peristome The entire apertural lip.

plate see **columellar**.

protoconch The shell formed by a young snail within the egg capsule.

punctae Small pits; punctate microsculpture.

radial Used of sculptural elements diverging from the apex of a cap-like shell.

reflected Used of the apertural lip when it is turned outwards, e.g. the columellar lip reflected over the umbilical area.

ribs Conspicuous regularly-spaced transverse ridges.

rimate Used of a shell with a narrow, slit-like umbilical opening.

sculpture Surface structures; raised (e.g. ribs, nodules) or sunken (e.g. punctae).

septum (plural: septa) Elongate projection from the internal shell wall.

shoulder A blunt angle in a whorl near the suture.

sinistral Used of a spired shell with its aperture on the observer's left side when the spire points upwards (Fig. 3b).

sinuous Used of the outer lip when its margin is wavy (Figs 4a,c).

size Measurements given in the text for coiled shells are height followed by width (diameter). For cap-like shells, the dimensions are length and width of the base, followed by height.

small: greatest dimension less than 10 mm.

medium: greatest dimension 10–30 mm.

large: greatest dimension more than 30 mm.

spiral Running along the whorl in the direction of growth.

spire That part of a spired shell rising above the upper attachment of the lip.

stepped Used of a spired shell with a succession of shouldered whorls.

striae, striation Fine lines on the surface, raised or incised.

subfossil Used of shells which are not old enough to be fossilised but come from extinct populations of Late Pleistocene-Holocene age; e.g. in the Saharan area.

suture The line of attachment between two whorls.

transverse At a right angle to the direction of growth, i.e. parallel to the lip.

tubercle A conspicuous blunt projection from the surface.

turreted Used of a slender high-spired shell.

umbilicate Used of coiled shells with an opening, the 'umbilicus', at the base, formed when the inner sides of the coiled whorls do not join (see also **perforate)**. In a discoid shell the umbilicus and underside are taken here to be beneath when the aperture is facing the observer on their righthand side (Figs 11b–d; see also the account of Planorbidae).

whorl One complete turn or coil of a spiral shell.

width The maximum distance across the shell at a right angle to its height.

Operculum

apophysis (plural: apophyses) A projection from the internal surface (Figs 8a–d, 15).

calcareous, calcified Made partly of calcium carbonate; hard, inflexible, opaque.

concentric Growing in a series of zones with the same centre (Fig. 8e).

corneous Made partly or entirely of 'horn-like' proteinaceous material; flexible and translucent.

multispiral Growing spirally with many whorls (more than 3) (Fig. 8g).

nucleus The earliest formed part of the operculum.

paucispiral Growing spirally with few whorls (up to about 3) (Fig. 9c).

subspiral Growing in increments which follow the beginning of a spiral path but turn through less than 180 degrees.

Radula

basal lobe A projection from the posterior margin on the basal plate of the central tooth (Figs 36c–g).

cusps Small pointed cutting blades situated either on the crown of a tooth or below on the basal plate (basal cusps or denticles).

central tooth The middle (median or rachidian) tooth in a transverse row.

denticles One or more pairs of cusps on the basal plate of the central tooth (Figs 36c–g).

ectocone The cusp on the outer (lateral) side of the mesocone.

endocone The cusp on the inner (median) side of the mesocone.

lateral teeth Teeth lying between the central and marginal teeth; there is only a single lateral tooth on each side in the prosobranch taenioglossate radula (Figs 44, 52e), but many in the pulmonate radula.

marginal teeth Teeth at the lateral margins of the radula, differing in shape from the central and lateral teeth; there are only two marginal teeth on each side in the taenioglossate radula (Figs 44, 52e), but many in the pulmonate radula.

mesocone The middle of the 3 major cusps on the inner lateral teeth of the pulmonate radula (Fig. 105).

rhipidoglossate The type of prosobranch radula with many teeth in each transverse row, though only few are conspicuous.

taenioglossate The type of prosobranch radula with only 7 teeth in each transverse row: central, one pair lateral and 2 pairs marginals (Figs 44, 52e).

Identification keys

Keys are given here for identification to family and genus; a series of regional keys for identification to species is published by the Danish Bilharziasis Laboratory (e.g. Brown & Kristensen, 1989).

Freshwater snails from our geographical area found with an operculum attached can be identified immediately as members of the subclass Streptoneura (commonly known as prosobranchs); only a single African prosobranch is reported to lack an operculum (*Septariellina* of the Assimineidae, restricted to the lower Zaire River). All other species lacking an operculum belong to the Pulmonata within the subclass Euthyneura. But the operculum though normally present may be small and inconspicuous (e.g. *Septaria* of the Neritidae and *Soapitia* of the Bithyniidae) or deeply withdrawn into the aperture, or it may have been lost from a preserved specimen. Yet whether or not the true condition regarding the operculum is known, the student will soon learn to recognise the limited number of aquatic pulmonate families.

An occasional problem may be a landsnail fallen into the water; some are discoid (Fig. 97a) and misleadingly like the Planorbidae (Verdcourt, 1958). The mainly terrestrial family Succineidae includes some species that live on emergent aquatic plants and may turn up in the collecting net; their shells resemble certain lymnaeids, but the tentacles are very different (Figs 12a,b; Key to pulmonate families). Marine shells have sometimes been mistaken for a freshwater species (*Brondelia* Bourguignat, 1862 and *Ancylus turtoni* Connolly, 1939), while *Afrocanidea* of Connolly (1929) was thought to be estuarine but has not been re-discovered in brackish or fresh water.

The first key is designed to identify shells as prosobranch or pulmonate using only characters of the empty shell. In later keys to families and genera, use becomes necessary of the operculum, radula and soft organs. Unfortunately there is not space in this book to describe anatomy sufficiently; sources of information include Mandahl-Barth (1958), Brown (1965), Starmühlner, (1969), Meier-Brook (1983) and Malek (1985). These simple rules are helpful:

the only sinistral prosobranch is *Lanistes*,
all strongly sculptured shells are prosobranch,
all large shells over 30 mm in height or width are prosobranch,
discoid shells are pulmonate except for *Marisa* (Ampullariidae) and *Hadziella* (Hydrobiidae).

Key to the main gastropod groups: prosobranchs and pulmonates

1 A With operculum .....prosobranch
B Lacking operculum or condition not known 2
2 A Shell cap-like 3
B Shell discoid 4
C Shell with pointed spire 5
3 A Large (reaching over 20 mm); Indo-Pacific coasts ....***Septaria*** (prosobranch)

B Small (<10 mm long), apex coiled; rapids of lower Zaire River ....***Septariellina*** (prosobranch)
C Small (<10 mm long), apex may be hooked but not coiled; widespread in fresh waters .....**ANCYLIDAE** (pulmonate)
4 A Large (reaching 50 mm diameter), with light and dark spiral bands; introduced into Sudan .....***Marisa*** (prosobranch)
B Smaller (rarely 25 mm, usually <10mm) ....**PLANORBINAE** and ***Indoplanorbis*** (pulmonate)
5 A Sinistral 6
B Dextral 7
6 A Shell larger (commonly >25 mm high or wide), strongly built, may have spiral bands .....***Lanistes*** (prosobranch)
B Smaller (rarely reaching 25 mm high), fragile, without spiral bands. ....***Amerianna, Bulinus,*** **PHYSIDAE** (pulmonate)
7 A Shell with lamellae projecting from the inner wall of the aperture; in coastal brackish water. .....**ELLOBIIDAE** (pulmonate)
B Shell with sharply pointed spire, thin-walled, smooth, pale-coloured and lacking bands or other pigmented marks ....**LYMNAEIDAE** (pulmonate)
C Shell of varied shape from depressed to narrowly conic; often thick-walled, smooth or strongly sculptured; may have pigmented patterns. ....Prosobranch (many genera)

Prosobranch families
(excluding Thiaridae endemic to Lake Tanganyika and the discoid *Marisa*)

1 A Shell cap-like 2
B Shell not cap-like 3
2 A Large (reaching over 20 mm long); Indo-Pacific coasts ....**NERITIDAE** part ***(Septaria)***
B Small (<10 mm long), apex coiled; in rapids of the lower Zaire River. ....**ASSIMINEIDAE** part ***(Septariellina)***
3 A Whorls few and rapidly increasing, spire low, aperture 'D-shaped' (Figs 1a–d,f); operculum strongly calcified, with one or two internal apophyses (Figs 8a–d). In tropical Africa restricted to coastal areas .. ..**NERITIDAE**
B Whorls generally more numerous, spire higher and more conical; operculum calcareous or entirely corneous, without apophyses 4
4 A Shell globose, up to about 10 mm high; with pigmented markings, bands or entirely dark. Neritoid snails found only in rapidly flowing rivers in Sierra Leone .....**BITHYNIIDAE** part ***(Sierraia)***
B Shell variously shaped, small to large 5
5 A Shell ovately conic, smooth reaching about 15 mm high; operculum calcified. In NW Africa only .....**BITHYNIIDAE** part ***(Bithynia)***
B Shell variously shaped, small to large 6
6 A Shell more than 10 mm high (Figs 2,3,6,7). Central radular tooth without basal denticles (Figs 36a,b; 52) 7
B Shell <10mm high (Figs 4,5). Central tooth with or without basal denticles (Figs 36c–g; 44) 12

7 A Operculum entirely concentric (Figs 8e,f) 8
B Operculum partly concentric with spiral nucleus (e.g. Figs 9a,b) or wholly spiral (Figs 8g; 9c,d,f) 9
8 A Shell dextral with conical spire (Fig. 2); Operculum entirely corneous; viviparous .....**VIVIPARIDAE**
B Dextral or sinistral, depressed to ovate, may be very large (Fig. 3); operculum corneous or calcified; oviparous ....**AMPULLARIIDAE (PILIDAE)**
9 A Basal margin of aperture with a notch (Figs 6a; 7a–c) 10
B Basal lip without notch 11
10 A Operculum multispiral. Restricted to brackish water, usually at the coast .....**POTAMIDIDAE**
B Operculum paucispiral. Found only in the NW part of Africa ....**MELANOPSIDAE**
11 A Spire conical, sharply pointed; rather smooth apart from spiral grooves; pigmented markings may form transverse bands (Fig. 7d). Operculum multispiral. Restricted to coasts, found in mangrove

swamp ....**LITTORINIDAE**

B Shell variously shaped, smooth or with strong sculpture (Fig. 6); any dark pattern is spiral rather than transverse. Operculum paucispiral (Figs 9d,f) or concentric with spiral nucleus (Figs 9g,h). In fresh and brackish water .....**THIARIDAE**

12 A Shell depressed, smooth, aperture circular, umbilicus large. Operculum multispiral (Fig. 8g). Found living only in Egypt and Ethiopia ....**VALVATIDAE**

B Commonly ovately conic (Figs 4a,c,f; 5a); if depressed then with notch in lip (Fig. 4d) or spiral ridges (Fig. 5d) 13

13 A Operculum calcareous, concentric around a spiral nucleus ....**BITHYNIIDAE** part (e.g. ***Gabbiella*)**

B Operculum entirely corneous 14

14 A Operculum small, lacking spiral structure. Found only in river in Guinea .....**BITHYNIIDAE** part ***(Soapitia)***

B Operculum paucispiral (Fig. 9c) 15

15 A Radula with accessory plate between the lateral tooth and first marginal tooth (Fig. 44) .....**ASSIMINEIDAE**

B Radula without accessory plate ....**HYDROBIIDAE** and **POMATIOPSIDAE**

Prosobranch genera of Africa within families

(excluding Thiaridae endemic to Lake Tanganyika)

Family **NERITIDAE**

1 A Shell cap-like (Fig. 1e). Operculum rectangular (Fig. 8a). SE Africa and Indo-Pacific islands .....***Septaria*** (p. 43)

B Shell hemispherical. Operculum approximately oval (Fig. 8c) 2

2 A Fully grown shell less than 4 mm high (Fig. 1f). Operculum with a single apophysis (Fig. 8b). West Africa and Indo-Pacific islands ....***Neritilia*** (p. 45)

B Fully grown shell exceeding 6 mm high. Operculum may have rib and peg (Figs 8c,d) 3

3 A Fully grown shell less than 10mm high. NW Africa and Egypt ....***Theodoxus*** (p. 36)

B Fully grown shell commonly more than 10 mm high. Tropical Africa 4

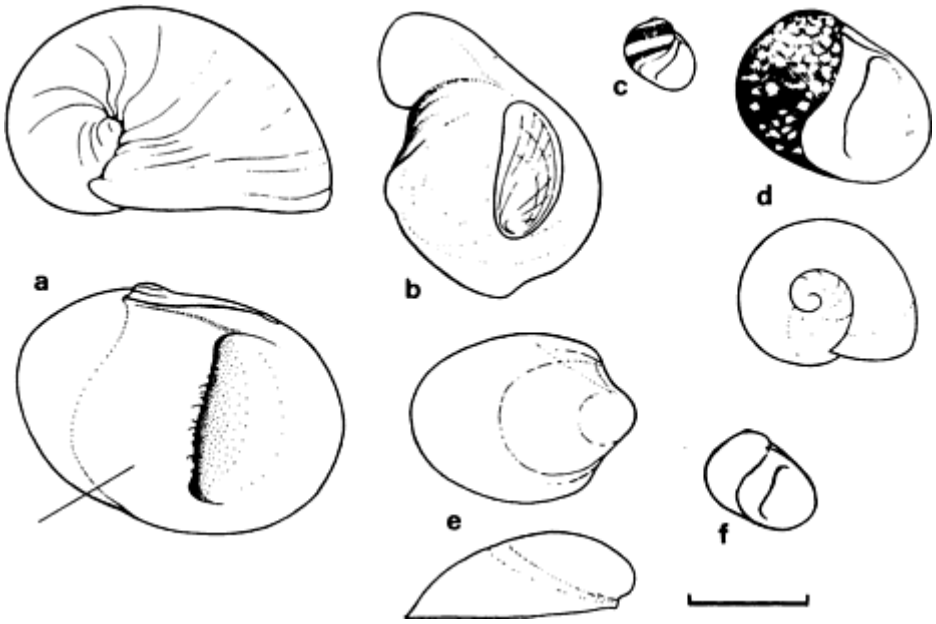


Fig. 1. Neritidae. (a) *Neritina pulligera* (two views), (b) N. *oweniana.* (c) N. *glabrata.* (d) N. *natalensis.* (e) *Septaria borbonica* (two views), (f) *Neritilia manoeli.* Scale line: 5 mm (f) or 10 mm (a–e). A guide line indicates the layer of callus on the columellar plate.

4 A Operculum with a low ridge connecting the rib and peg (Fig. 8c). No spines on the shell, which may have wing-like expansions of its aperture (Fig. 1b). Tropical coasts .....***Neritina*** (p. 39)

B Operculum with a comparatively high ridge between rib and peg (Fig. 8d). Some species have spines on the shell. Indo-Pacific islands, but not known to occur in Africa .....***Clithon*** (p. 43)

Family **VIVIPARIDAE**

A Apex sharply pointed and embryonic whorl with spiral ridges (Figs 2a– c). Fully grown shell reaching 50 mm in only one species. Widely distributed, but not known to occur in Lake Tanganyika ....***Bellamya*** (p. 46)

B Apex obtuse with smooth embryonic whorl (Fig. 2d). Fully grown shell about 60 mm high. Lives only in Lake Tanganyika ....***Neothauma*** (p. 53)

Family **AMPULLARIIDAE (PILIDAE)** (see also the discoid *Marisa*)

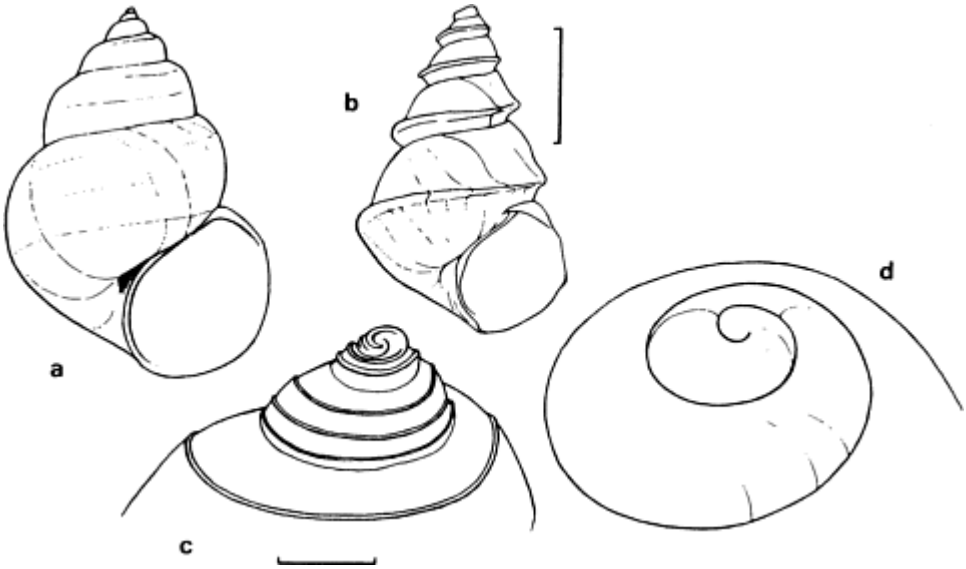


Fig. 2. Viviparidae. (a) *Bellamya unicolor*. (b) *B. trochlearis*. (c) *B. unicolor*, apex of juvenile, (d) *Neothauma tanganyicense*, apex of juvenile. Scale line: 1 mm (c,d) or 10 mm (a,b).

1 A Shell sinistral (Fig. 3b). Operculum entirely corneous ***Lanistes*** (p. 57)
B Shell dextral. Operculum either corneous or calcareous 2
2 A Shell with transverse brown bands (Fig. 3a). Sierra Leone ....***Saulea*** (p. 66)
B Any coloured bands present are spiral 3
3 A Fully grown shell exceeding 40 mm high (Fig. 3e). Operculum calcareous. Rare individuals are sinistral .....***Pila*** (p. 54)
B Fully grown shell less than 30 mm high (Fig. 3c). Operculum wholly corneous. Sierra Leone and Ivory Coast .....***Afropomus*** (p. 66)

Family **HYDROBIIDAE** (excluding North Africa) and **POMATIOPSIDAE**

1 A Outer lip of aperture strongly sinuous, columellar margin heavily thickened (Fig. 4a). SE Zaire and Zambia .....***Lobogenes*** (p. 74)
B Outer lip of aperture nearly straight. Mostly living near coasts 2
2 A Shell with stout spines. West coast, in brackish water ....***Potamopyrgus*** (p. 74)
B Shell without spines 3

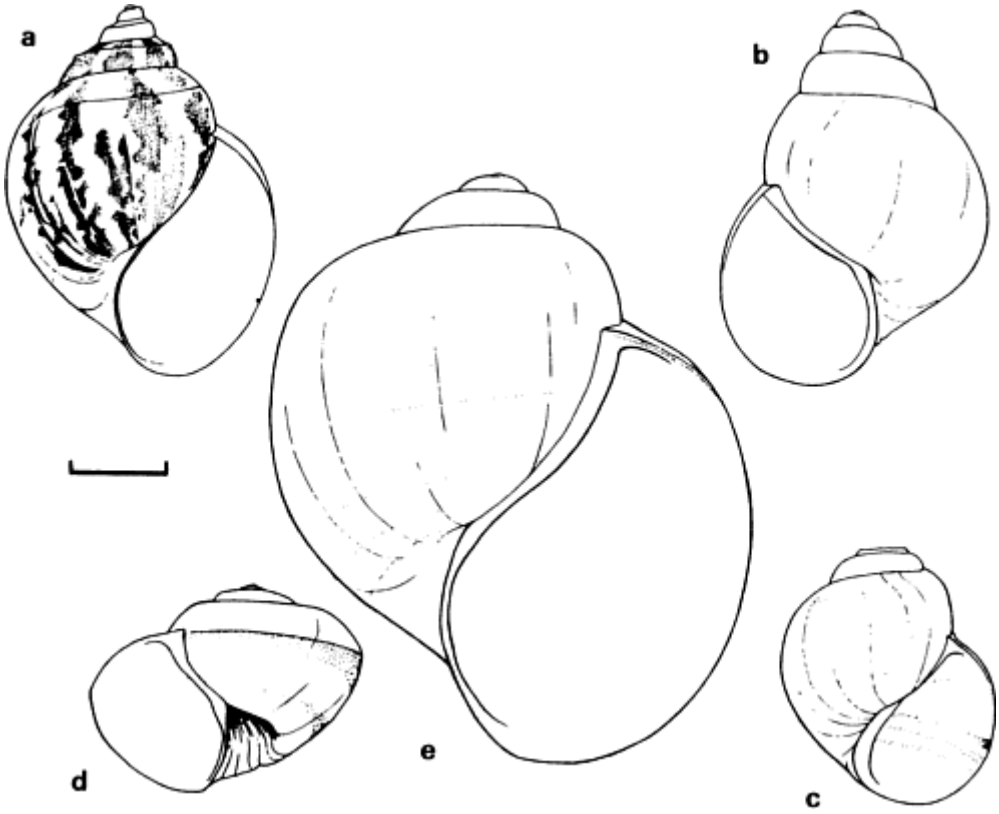


Fig. 3. Pilidae. (a) *Saulea vitrea.* (b) *Lanistes purpureus.* (c) *Afropomus balanoidea.* (d) *Lanistes carinatus.* (e) *Pila ovata.* Scale line: 10 mm.

3 A Shell varies from depressed to narrowly conical (Figs 32, 33). Central tooth with one basal denticle on each side. West coast, in brackish or fresh waters .....***Hydrobia*** (p. 70)

B Spire ovately to narrowly conic (Figs 37–39). Central tooth (Fig. 36d) with 2 or 3 pairs of basal denticles. In fresh or brackish water near South African coast; also in E Zaire ....**Pomatiopsidae: *Tomichia*** (p. 77)

Family **BITHYNIIDAE**

1 A Neritoid (globose, whorls rapidly increasing, spire low); shell may have pigmented pattern. Operculum nucleus is subspiral. Central tooth without basal denticles. Found only in rivers in Sierra Leone and Guinea. 2

B Shell of various other shapes; operculum with definite spiral nucleus; central tooth with basal denticles 3

2 A Shell may reach 10 mm high; usually with pigmented patches or bands, or evenly dark. Found only in Sierra Leone .....***Sierraia*** (p. 91)

B Reaching only 6 mm high, lip oblique (Fig. 4b). Operculum very small and weakly calcified. Found only in Guinea .....***Soapitia*** (p. 94)

3 A Shell ovately conic, reaching 15 mm. Found in only the NW part of Africa .....***Bithynia*** (p. 82)

B Smaller (<10 mm); depressed to ovately conic and narrower. In tropical Africa and Egypt 4

4 A Shell depressed, very small (<2 mm high), with notch in the basal lip (Fig. 4d). Found only in or near the lower Zaire River ....***Funduella*** (p. 91)

B Ovate with conical spire; lip without notch. 5

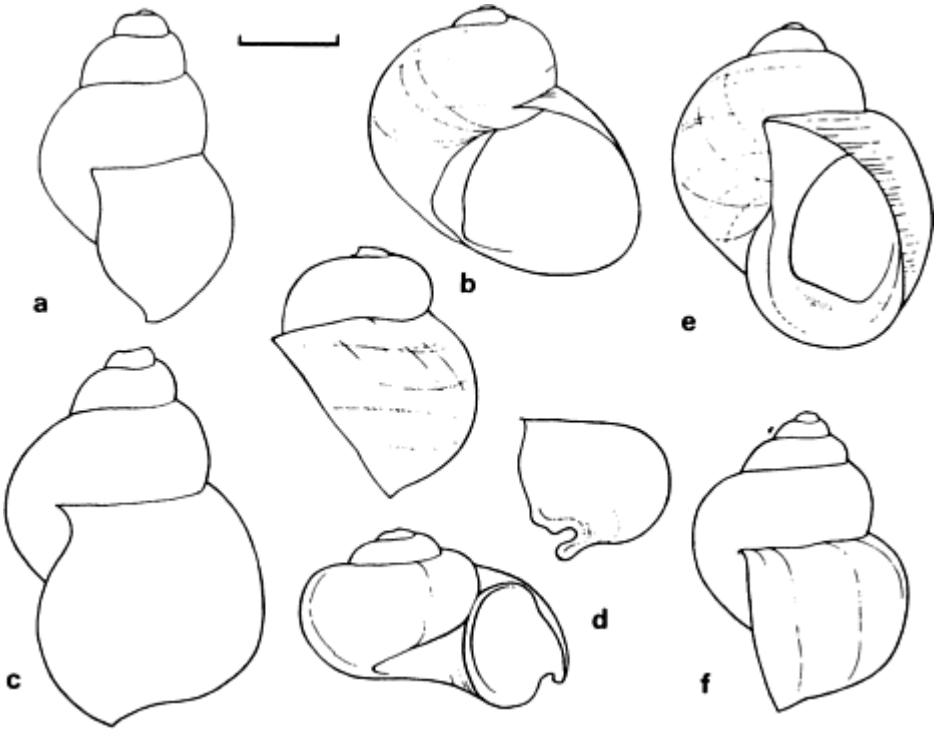


Fig. 4. Hydrobiidae and Bithyniidae. (a) *Lobogenes pusilla.* (b) *Soapitia dageti* (two views), (c) *Congodoma zairensis.* (d) *Funduella incisa* (two views), (e) *Liminitesta sulcata.* (f) *Jubaia excentrica.* Scale line: 1 mm (a,c,d) or 2 mm (b,e,f).

5 A With strong spiral sculpture and a ridge in the base of the aperture (Fig. 4e) against which the operculum lodges. Found only in the lower Zaire River .....***Liminitesta*** (p. 91)

B Shell smooth to the naked eye 6

6 A Lip strongly sinuous (Fig. 4c). Found only in the lower Zaire River.. ....***Congodoma*** (p. 91)

B Lip more straight (Fig. 4f). Various habitats including lakes and small pools 7

7 A Operculum with thin corneous margin (Fig. 9e) and capable of retraction deep within the aperture. Central tooth with only one basal denticle on each side. NE Kenya .....***Incertihydrobia*** (p. 90)

B Operculum calcareous right to its thick margin (Fig. 9b), lodging at or near the apertural lip. Central tooth with 2–5 pairs of basal denticles. 8

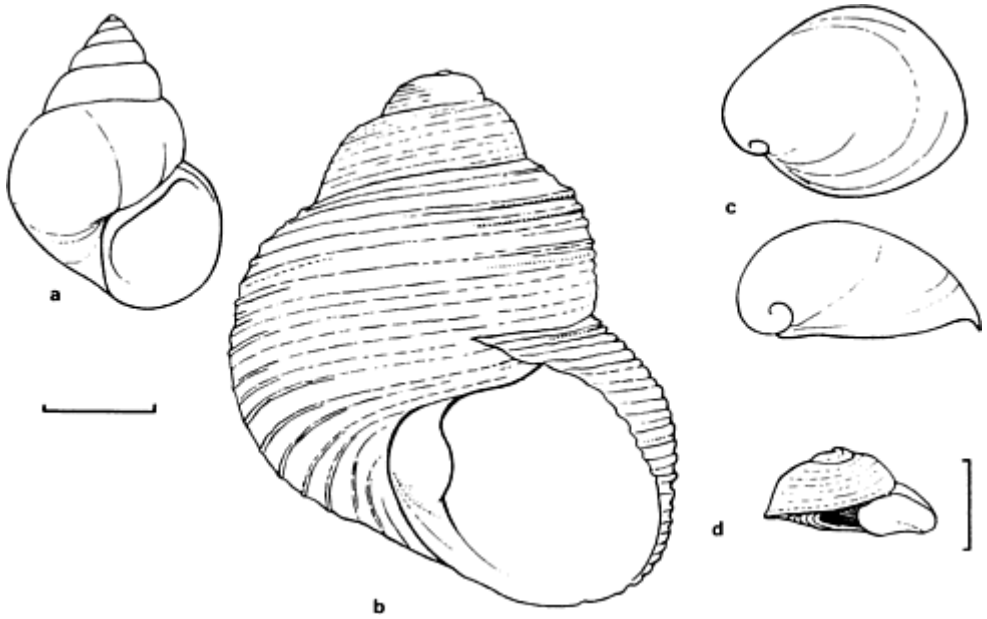


Fig. 5. Assimineidae. (a) *Eussoia inopina.* (b) *Pseudogibbula duponti.* (c) *Septariellina congolensis.* (d) *Valvatorbis mauritii.* Scale lines: 1 mm (d) or 2 mm (a–c).

8 A Spiral nucleus of operculum central (Fig. 9b). Central tooth with 2–5 pairs of basal denticles. Egypt and tropical Africa ..***Gabbiella*** (p. 82)
B Spiral nucleus of operculum nearer the outer margin (Fig. 9a). Central tooth with only 2 pairs of basal denticles. S Somalia and SE Ethiopia. ....***Jubaia*** (p. 90)

Family **ASSIMINEIDAE**

1 A Shell ovately conic (Fig. 5a); in fresh or brackish water, usually near coast. 2
B Shell globose, depressed or cap-like (Figs 5b,c,d); found only in rapids of the lower Zaire River. 3
2 A Central tooth with strong basal lobe. Tentacles reduced to short lobes. In brackish water. .....***Assiminea*** (p. 95)
B Central tooth with weaker basal lobe; outer marginal tooth with more cusps (Fig. 44). Tentacles longer. In fresh water .....***Eussoia*** (p. 97)
3 A Shell globose with strong spiral ridges (Fig. 5b). ***Pseudogibbula*** (p. 98)
B Shell depressed or cap-like 4
4 A Cap-like (Fig. 5c) .....***Septariellina*** (p. 99)
B Depressed, very small, carinate with spiral ridges. ***Valvatorbis*** (p. 99)

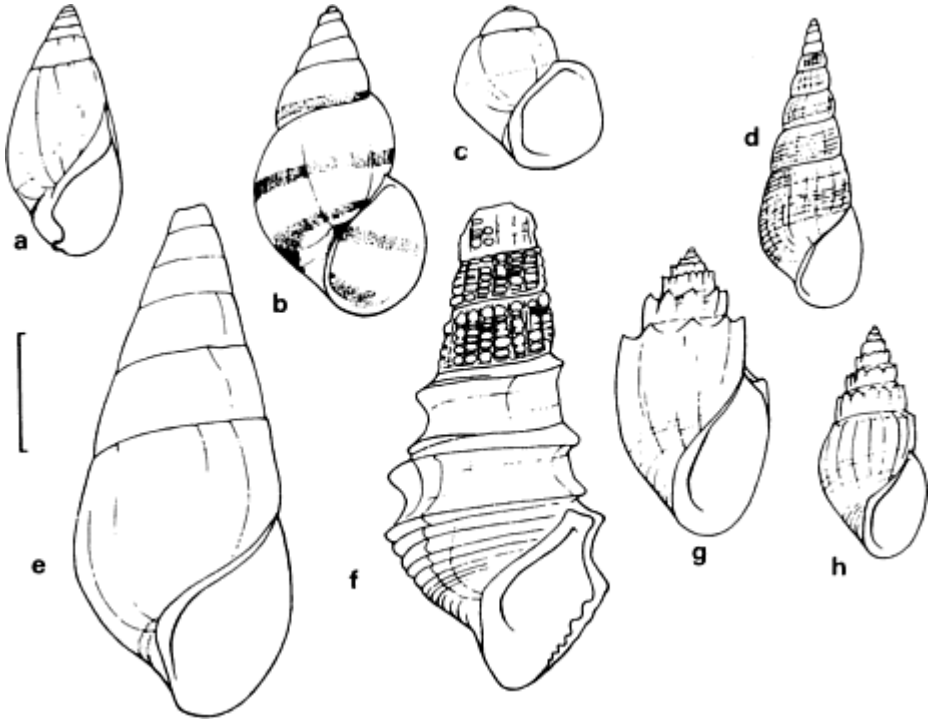


Fig. 6. Thiaridae. (a) *Melanopsis praemorsa.* (b) *Cleopatra ferruginea.* (c) *Pseudocleopatra bennikei.* (d) *Melanoides tuberculata.* (e) *Potadoma freethi.* (f) *Pachymelania fusca.* (g) *Thiara amarula.* (h) *T. scabra.* Scale line: 10 mm.

Family **THIARIDAE** (excluding genera restricted to Lake Tanganyika)

1 A Base of apertural lip narrowed and spout-like (Fig. 6f); sculpture strong. W coast, in brackish water .....***Pachymelania*** (p. 111)

B Basal lip more evenly curved; sculptured to a varying degree or smooth. In fresh water 2

2 A Shell with transverse ribs which project as spines near the suture (Figs 6g,h). E coast, in fresh water but near tidal influence.***Thiara*** (p. 100)

B Shell otherwise 3

3 A Operculum concentric with spiral nucleus (Figs 9g,h). Shell may have brown spiral bands 4

B Operculum entirely paucispiral (Figs 9d,f) 5

4 A Operculum nucleus small (Fig. 9h). Shell often brown-banded. Widely distributed .....***Cleopatra*** (p. 120)
B Operculum nucleus larger (Fig. 9g). Shell rarely brown-banded. Restricted to Volta Basin and lower Zaire River. ***Pseudocleopatra*** (p. 128)

5 A Operculum nucleus near the basal margin (Fig. 9d) ....***Melanoides*** (p. 102)
B Operculum nucleus near centre (Fig. 9f) 6

6 A Larger, shell usually >15 mm high even when decollate; may be smooth or with ridges and spines. Radula very long (about half of the shell height); central tooth distinctively quadrangular. Widespread in W and central Africa .....***Potadoma*** (p. 114)
B Smaller, <15 mm high, variously sculptured. Radula shorter, with narrow central tooth. Restricted to E Zaire and Malagarasi Delta of Lake Tanganyika .....***Potadomoides*** (p. 129)

Family **POTAMIDIDAE**

1 A Smaller shell, rarely reaching 20 mm high, with nodular sculpture (Fig. 7a). In brackish water at or near coasts of NE Africa ....***Pirenella*** (p. 145)
B Larger, >20mm high. Brackish waters in tropical region 2

2 A Less than 40 mm high, strongly ribbed, decollate (Fig. 7b) ....***Cerithidea*** (p. 143)
B Growing over 50mm high; ribs lacking or only weak 3

3 A With strong nodules, tubercles and spines. W coast ....***Tympanotonus*** (p. 143)
B Smoother, spire flat-sided (Fig. 7c). Indo-Pacific coasts 4

4 A With low ribs. E coast. .....***Terebralia*** (p. 145)
B Almost smooth, any sculpture is mainly spiral. In Madagascar but not found in Africa. .....***Telescopium*** (p. 145)

Pulmonate families

1 A Shell cap-like (Figs 10d–f) .....**ANCYLIDAE**
B Shell spirally coiled 2

2 A Spired snails, with a slender aperture having internal lamellae (Figs 10a–c). Confined to brackish water, especially mangrove swamp ....**ELLOBIIDAE**

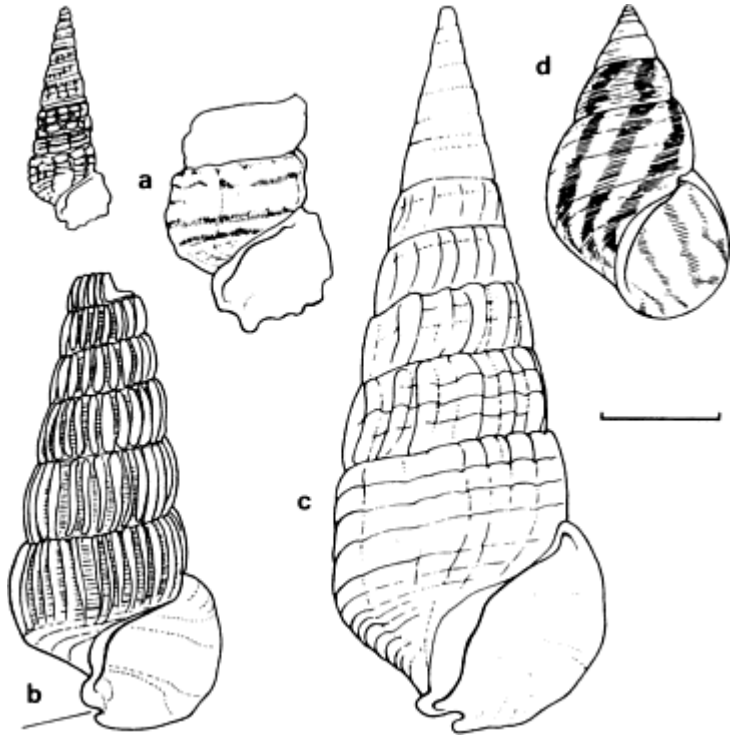


Fig. 7. Potamididae and Littorinidae. (a) *Pirenella conica* (two views), (b) *Cerithidea decollata.* (c) *Terebralia palustris.* (d) *Littoraria (Littorinopsis)* sp. Scale line: 10 mm (lower part of *P. conica* twice this magnification). A guide line indicates the columellar notch in (b).

B With spire or discoid. In fresh water 3

3 A Discoid (Figs 11b–g). **PLANORBIDAE:** subfamily **Planorbinae** in part and ***Indoplanorbis*** of the **Bulininae**

B With distinct spire (Fig. 11a) 4

4 A Shell dextral. Tentacles broadly triangular (Fig. 12a). **LYMNAEIDAE** (Shell similar in the landsnail family Succineidae, of which some species live in marshes; these are recognisable by their tentacles (Fig. 12b) with eyes at the tips and narrower bases).

B Shell sinistral. Tentacles slender (Figs 12c,d) 5

5 A Shell very smooth (glossy), spire sharply pointed. Without pseudobranch; mantle border with finger-like processes (Fig. 12d); blood colourless; radula teeth in V-shaped rows ..... .**PHYSIDAE**

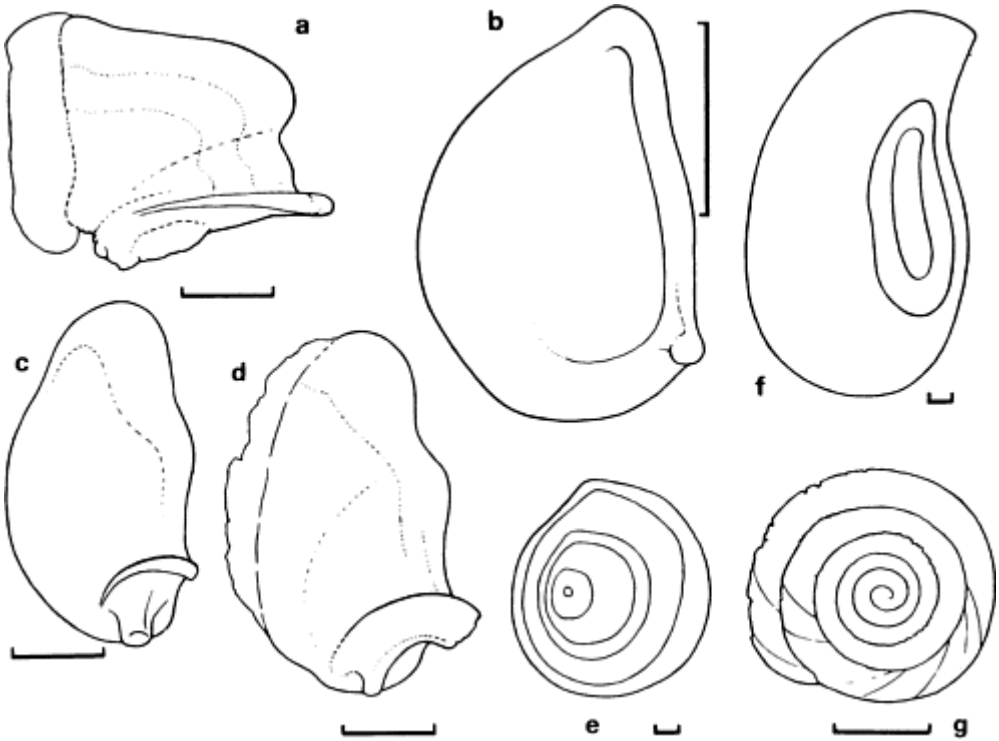


Fig. 8. Opercula: inner surfaces of (a)–(d) and (f), outer surfaces of (e) and (g). (a) *Septaria borbonica.* (b) *Neritilia manoeli.* (c) *Neritina natalensis.* (d) *Clithon longispina.* (e) *Bellamya trochlearis.* (f) *Pila wernei.* (g) *Valvata nilotica.* Scale lines: 1 mm (b,g) or 2 mm (a,c,d–f).

B Shell surface comparatively dull; spire may be low and apex obtuse. With pseudobranch, but not mantle processes (Fig. 12c); blood red; tooth rows nearly straight 6

6 A Whorls rounded, shouldered or carinate; only few if any spiral ridges. Penis of the 'ultrapenis' type, attached at base of preputium (Fig. 14d). Throughout Africa. **PLANORBIDAE:** subfamily **Bulininae** in part.. ....**.(*Bulinus,*** p. 208)

B Whorls sharply shouldered and carinate, flat near the suture; with numerous spiral ridges. Penis of simple type, projecting freely into the sheath. In Africa found only in Nigeria (introduced) ....**PLANORBIDAE: Planorbinae** in part (***Amerianna,*** p. 175)

Family **ELLOBIIDAE**

1 A Shell sinistral .....***Blauneria*** (p. 153)

B Shell dextral 2

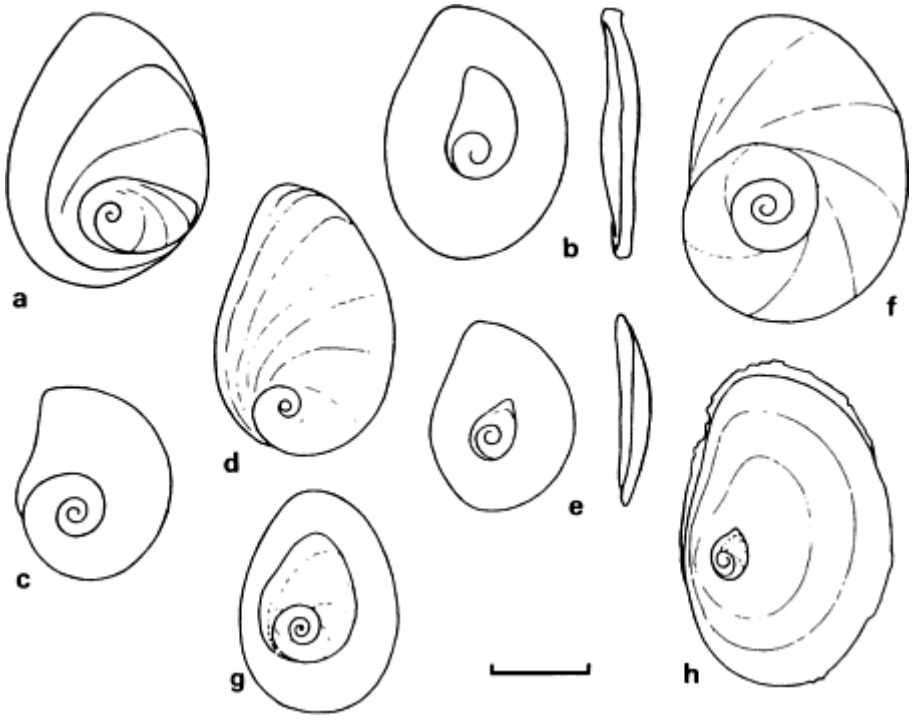


Fig. 9. Opercula: outer surfaces. (a) *Jubaia excentrica.* (b) *Gabbiella adspersa.* (c) *Eussoia inopina.* (d) *Melanoides anomala.* (e) *Incertihydrobia teesdalei.* (f) *Potadoma vogeli.* (g) *Pseudocleopatra togoensis.* (h) *Cleopatra nsendweensis.* Scale line: 1 mm (a–c,e) or 2 mm (d,f–h).

2 A Shell more than twice as high as wide (Fig. 10a). Living subterraneanly. .....***Auriculastra*** and ***Auriculodes*** (p. 152–3)

B Shell less than twice as high as wide. Surface-dwelling on shaded mud. 3

3 A Outer lip with strong internal rib (Fig. 10b) .....***Cassidula*** (p. 153)

B Outer lip without rib, but may have spiral ridges (Fig. 10c) ....***Melampus*** (p. 155)

Family **ANCYLIDAE**

1 A Apex with radial rows of small pits (Figs 10d; 79e) ....***Burnupia*** (p. 163)

B Apex with radial ridges 2

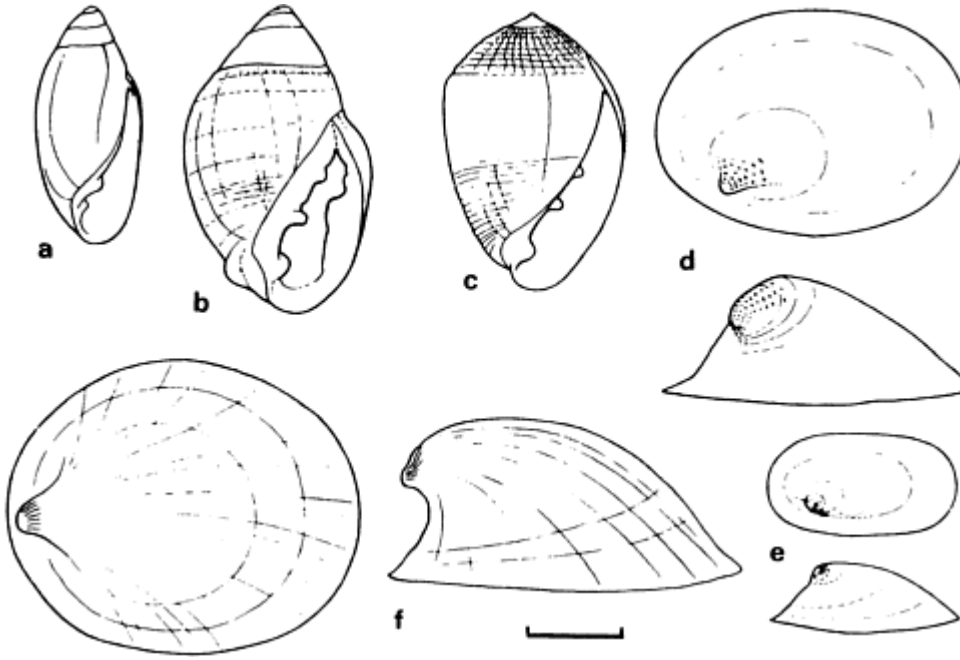


Fig. 10. Ellobiidae and Ancylidae (viewed from above and side), (a) *Auriculastra radiolata*. (b) *Cassidula labrella*. (c) *Melampus semiaratus*. (d) *Burnupia* sp. (e) *Ferrissia* sp. (f) *Ancylus fluviatilis*. Scale line: 2 mm (d–f) or 4 mm (a–c).

2 A Shell smaller, <5 mm long, apical ridges very fine (Figs 10e; 79f) ....***Ferrissia*** (p. 169)

B Larger, reaching 6–10 mm long, apical ridges coarser (Figs 10f; 79c,d). Restricted to NW Africa and Ethiopian highlands ..***Ancylus*** (p. 161)

Family **PLANORBIDAE:** subfamily **Planorbinae**

(excluding the few palaearctic genera reported rarely from NW Africa).

This key includes *Indoplanorbis* of the Bulininae, which has a large discoid shell similar to *Biomphalaria* and *Helisoma*.

1 A Shell with pointed spire, sinistral; whorls sharply shouldered. In Africa found only in Nigeria .....***Amerianna*** (p. 175)

B Shell discoid 2

2 A Shell very small (up to 3 mm diameter); whorls flat, with widely-spaced ribs (Fig. 11f). In Africa found only in Algeria and highland Ethiopia .....***Armiger*** (p. 179)

B Shell may be larger (10–20 mm diameter) or if small then without wide-spaced ribs (Fig. 11g) 3

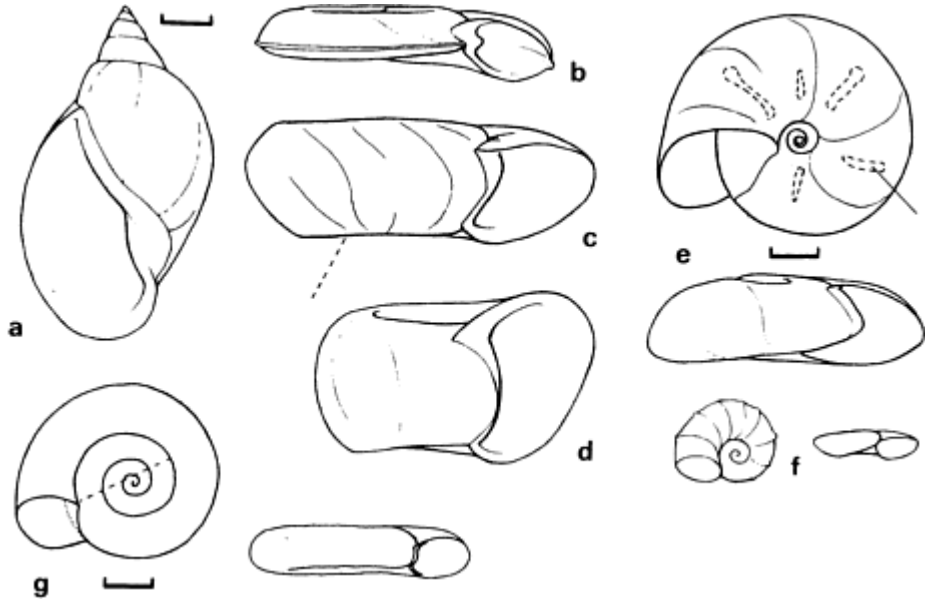


Fig. 11. Physidae and Planorbidae. (a) *Physa acuta.* (b) *Planorbis planorbis.* (c) *Biomphalaria angulosa,* (d) *Helisoma duryi.* (e) *Segmentorbis angustus* (guide line indicates internal lamellae), (f) *Armiger crista.* (g) *Ceratophallus natalensis.* Scale lines: 1 mm (e–g) or 2 mm (a–d). A broken line indicates the underside in (c) and the diameter of the umbilicus in (g).

3 A Shell small, <8 mm diameter; distinctly convex on one side (the 'upper') and flat on the other (the 'underside'); whorls rapidly increasing, umbilicus (on underside) very small; internal lamellae may be visible through the shell wall (Fig. 11e) 4

B Shell larger (10–20 mm diameter) or if small then upper and under sides are more similarly shaped; whorls increase less rapidly, umbilicus larger; without lamellae (Fig. 11g) 5

4 A Shell usually without lamellae. Copulatory organ without flagellum. .....***Lentorbis*** (p. 188)

B With 3 or more lamellae. Copulatory organ may have a flagellum. .. ..***Segmentorbis*** (p. 190)

5 A Shell large, >2 mm high 6

B Shell smaller, <2 mm high 9

6 A Shell up to 3 mm high, usually with carina below (Fig. 11b). In Africa found only in Egypt, Algeria and Morocco .....***Planorbis*** (p. 176)

B Shell >3 mm high, periphery evenly convex although there may be angles on the upper and lower surfaces of the whorls 7

7 A Shell only rarely reaching 7 mm high; whorls not flattened within the umbilicus. Copulatory organ without preputial gland. Prostatic lobes arranged in a row. Widely distributed .....***Biomphalaria*** (p. 194)

B Shell commonly over 7 mm high; whorls may be flat within the umbilicus. Introduced species of restricted occurrence 8

8 A Whorls commonly angular on the underside and flat within the umbilicus. Copulatory organ with an external preputial gland. Prostatic lobes in a bunch. Many scattered localities .....***Helisoma*** (p. 205)

B Whorls strongly convex above and below, not flat within the umbilicus. Copulatory organ with 'ultrapenis' (see Bulininae). Prostatic lobes in a compact organ. In Africa found only in Nigeria and Niger ....***Indoplanorbis*** (p. 208)

9 A Penis with distal part sclerotised; opening terminal (Fig. 14a) ....***Ceratophallus*** (p. 180)

B Penis tissues not sclerotised, though there is a separate stylet or cuticular cap; opening subterminal 10

10 A Penis with large dagger-like stylet (Fig. 14b) .....***Gyraulus*** (p. 185)

B Penis with small cap-like stylet (Fig. 14c) .....***Afrogyrus*** (p. 176)

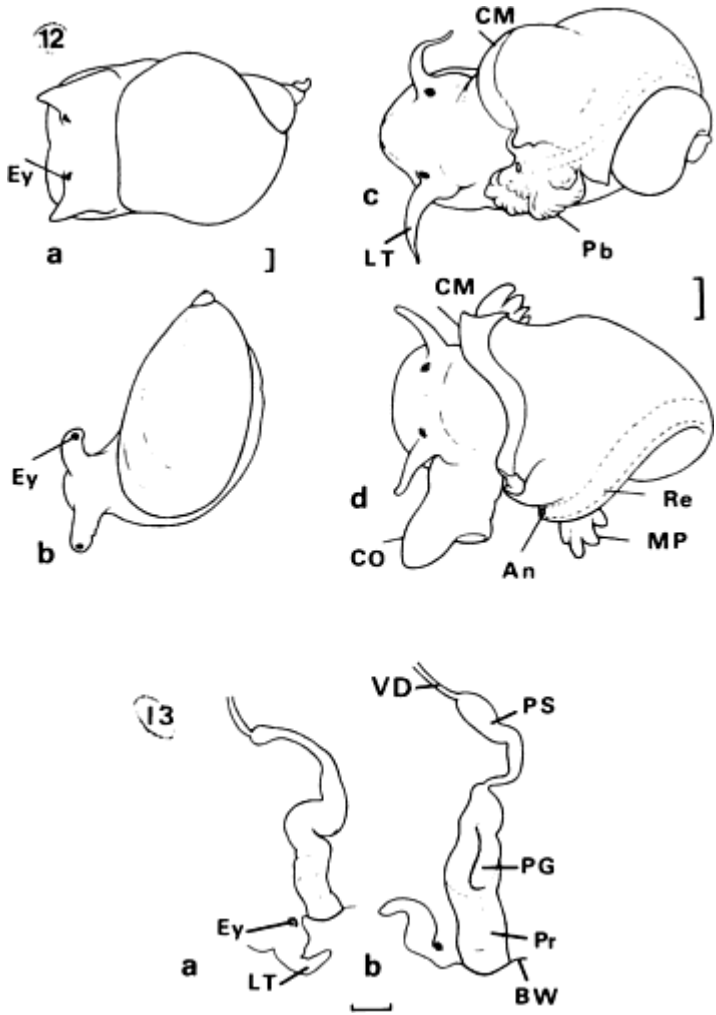
Family **PHYSIDAE**

A Shell broad. Copulatory organ with large preputial gland, visible externally (Fig. 13b). Widely distributed .....***Physa*** (p. 248)

B Shell more slender, fusiform. Copulatory organ without an externally visible gland. W Africa and SE Africa .....***Aplexa*** (p. 249)

Checklist of gastropod molluscs found in the fresh and brackish waters of the African continent

These are species recognised in the present account which can be only provisional. Increases in number of species are likely to arise from further taxonomic study in several groups, especially the endemic prosobranchs of Lake Tanganyika and the hydrobioid snails of northern Africa (the latter excluded entirely from this list because comprehensive revision is needed). Species found only in neighbouring islands are listed separately later. Some authors' names are abbreviated: Bgt (Bourguignat), Linn. (Linnaeus), M.-B. (Mandahl-Barth), Mor. (Morelet). The order of species is as in the present systematic synopsis. The term 'aggregate' is used when it appears likely that a taxon includes more than one



Figs 12, 13. Fig. 12. (a) *Lymnaea natalensis,* animal removed from shell to show tentacles, (b) *Succinea* sp., narcotised whole snail, (c) *Bulinus tropicus,* narcotised animal, mantle removed, (d) *Physa acuta,* narcotised animal with copulatory organ everted, mantle removed. Fig. 13. Copulatory organs of (a) *Aplexa waterloti* and (b) *Physa acuta* viewed from the left side. An, anus. BW, body wall. Ey, eye. CM, cut edge of mantle. CO, copulatory organ. LT, left tentacle. MP, mantle processes. Pb, pseudobranch. PG, preputial gland. Pr, preputium. PS, penis sheath. Re, rectum. VD, vas deferens. Scale lines: 1 mm.

biologically distinct species. Brackets enclose the names of species believed to have been introduced in recent historical time.

CLASS GASTROPODA

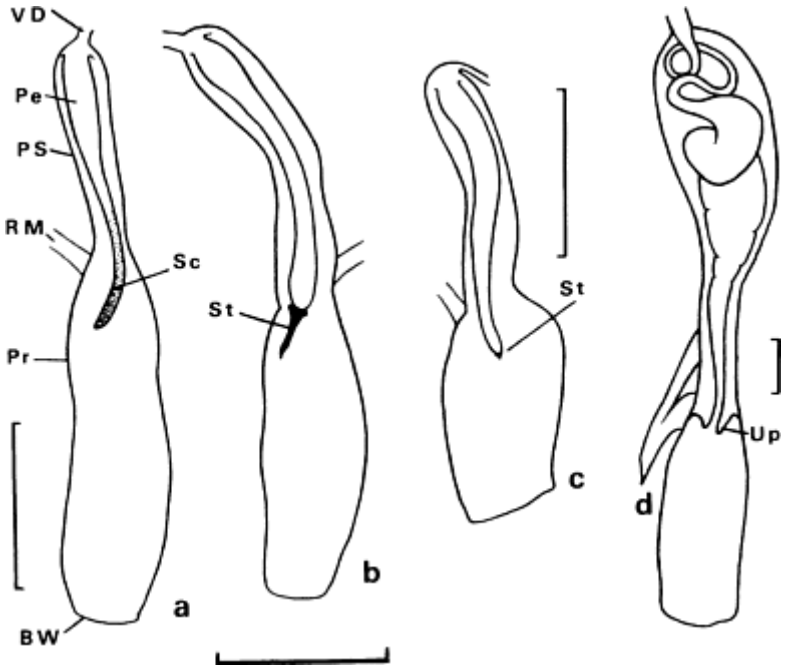


Fig. 14. Planorbidae: diagrams of copulatory organs, (a) *Ceratophallus.* (b) *Gyraulus.* (c) *Afrogyrus.* (d) *Bulinus.* Scale lines: 0.5 mm. BW, position of attachment to body wall. Pe, penis. Pr, preputium. PS, penis sheath. RM, retractor muscle. Sc, sclerotisation. St, stylet. Up, attachment of 'ultrapenis' to base of preputium. VD, vas deferens.

SUBCLASS STREPTONEURA (PROSOBRANCHS)

Family Neritidae

Theodoxus numidicus (Récluz)
T. maresi (Bgt)
T. meridionalis (Philippi)
T. niloticus (Reeve)
Neritina pulligera (Linn.)
N. natalensis Reeve

N. gagates Lamarck
N. oweniana (Wood)
N. tiassalensis Binder
N. rubricata Mor.
N. cristata Mor.
N. adansoniana (Récluz)
N. glabrata Sowerby
N. kuramoensis Yoloye & Adegoke
N. afra Sowerby
Septaria borbonica (Bory de St Vincent)
Neritilia manoeli (Dohrn)

Family Viviparidae

Bellamya unicolor (Olivier)
B. crawshayi (Smith)

B. capillata (Frauenfeld)
B. monardi (Haas)
B. phthinotropis (Martens)
B. costulata (Martens)
B. jucunda (Smith)
B. constricta (Martens)
B. trochlearis (Martens)
B. rubicunda (Martens)
B. mweruensis (Smith)
B. pagodiformis (Smith)
B. ecclesi (Crowley & Pain)
B. jeffreysi (Frauenfeld)
B. robertsoni (Frauenfeld)
B. leopoldvillensis (Putzeys)
B. contracta (Haas)
(?)B. liberiana (Schepman)
Neothauma tanganyicense Smith

Family Ampullariidae

Pila ovata (Olivier)
P. occidentalis (Mousson)
P. africana (Martens)
P. speciosa (Philippi)
P. wernei (Philippi)
Lanistes carinatus (Olivier)
L. intortus Martens
L. bicarinatus Germain
L. neritoides Brown & Berthold
L. congicus O.Boettger
L. nsendweensis (Dupuis & Putzeys)
L. neavei Melvill & Standen
L. varicus (Müller)
L. libycus (Mor.)
L. ciliatus Martens
L. alexandri (Bgt)
L. nyassanus Dohrn
L. nasutus Mandahl-Barth
L. solidus Smith
L. ovum Peters
L. purpureus (Jonas)
L. ellipticus Martens
L. farleri Craven
L. stuhlmanni Martens
L. graueri Thiele
Afropomus balanoidea (Gould)
Saulea vitrea (Born)
(*Marisa cornuarietis* (Linn.))

Family Valvatidae

Valvata nilotica Jickeli

Family Littorinidae

Littoraria (Littorinopsis) spp.

Family Hydrobiidae (of tropical Africa only)

Hydrobia accrensis Connolly
H. gabonensis Mor.
H. guyenoti Binder
H. lineata Binder
H. luvilana M.-B
H. plena Bequaert & Clench
H. schoutedeni Bequaert & Clench
(?)*H. alabastrina* Mor.
(?)*Potamopyrgus ciliatus* (Gould)
Lobogenes michaelis Pilsbry & Bequaert
L. spiralis Pilsbry & Bequaert
L. pusilla M.-B.

H. rheophila Bequaert & Clench

Family Pomatiopsidae

Tomichia ventricosa (Reeve)
T. zwellendamensis (Küster)
T. tristis (Mor.)
T. rogersi (Connolly)
T. natalensis Connolly
T. differens Connolly
T. cawstoni Connolly
T. hendrickxi (Verdcourt)
T. kivuensis M.-B.
(?)*T. guillemei* Leloup

Family Bithyniidae

Bithynia tentaculata (Linn.)
Gabbiella humerosa (Martens)
G. kichwambae (M.-B.)
G. matadina M.-B.
G. neothaumaeformis (Germain)
G. kisalensis (Pilsbry & Bequaert)
G. parva (M.-B.)
G. parvipila (Verdcourt)
G. verdcourti M.-B.
G. spiralis M.-B.
G. tchadiensis M.-B.
G. stanleyi (Smith)
G. neumanni (Martens)
G. senaariensis (Küster)
G. schweinfurthi (Jickeli)
G. africana (Frauenfeld)
G. adspersa (Jickeli)
G. zambica M.-B.
G. balovalensis M.-B.
G. candida M.-B.
G. rosea M.-B.
G. depressa M.-B.
G. barthi Brown
G. walleri (Smith)
Incertihydrobia teesdalei Verdcourt
Jubaia excentrica M.-B.
J. aethiopica (Verdcourt)
Congodoma zairensis (Bequaert & Clench)
Funduella incisa M.-B.
Liminitesta sulcata M.-B.
Sierraia leonensis Connolly
S. expansilabrum Brown
S. outambensis Brown
S. whitei Brown
Soapitia dageti Binder

Family Assimineidae

Assiminea bifasciata Nevill
A. hessei O.Boettger
A. keniana Brown
Eussoia inopina Preston
E. aethiopica (Thiele)
E. leptodonta (Connolly)
E. oblonga M.-B.
Pseudogibbula duponti Dautzenberg
(?)*P. cara* (Pilsbry & Bequaert)
Septariellina congolensis Bequaert & Clench
Valvatorbis mauritii Bequaert & Clench

Family Thiaridae

Thiara amarula (Linn.)
T. scabra (Müller)
Melanoides admirabilis (Smith)
M. crawshayi (Smith)
M. magnifica (Bgt)
M. mweruensis (Smith)
M. nodicincta (Dohrn)
M. nyassana (Smith)
M. pergracilis (Martens)
M. polymorpha (Smith)
M. pupiformis (Smith)
M. turritispira (Smith)
M. agglutinans (Bequaert & Clench)
M. anomala (Dautzenberg & Germain)
M. bavayi (Dautzenberg & Germain)
M. depravata (Dupuis & Putzeys)
M. dupuisi (Spence)
M. kisangani Pilsbry & Bequaert
M. kinshassaensis (Dupuis & Putzeys)
M. langi Pilsbry & Bequaert
M. liebrechtsi (Dautzenberg)
M. nsendweensis (Dupuis & Putzeys)
M. nyangweensis (Dupuis & Putzeys)
M. wagenia Pilsbry & Bequaert
M. angolensis M.-B.
M. manguensis (Thiele)
M. recticosta (Martens)
M. tuberculata (Müller)
M. victoriae (Dohrn)
M. voltae (Thiele)
Pachymelania byronensis (Wood)
P. aurita (Müller)

P. fusca (Gmelin)
Potadoma freethi (Gray)
P. schoutedeni Pilsbry & Bequaert
P. moerchi (Reeve)
P. togoensis Thiele
P. vogeli Binder
P. liricincta (Smith)
P. bicarinata M.-B.
P. alutacea Pilsbry & Bequaert
P. ignobilis (Thiele)
P. wansoni Bequaert & Clench
P. liberiensis (Schepman)
P. ponthiervillensis (Dupuis & Putzeys)
(?)*P. buttikoferi* (Schepman)
P. zenkeri (Martens)
P. nyongensis Spence
P. trochiformis (Clench)
P. angulata Thiele
P. kadeii Samé-Ekobo & Kristensen
P. riperti Samé-Ekobo & Kristensen

Cleopatra bulimoides (Olivier)
C. ferruginea (I. & H.C.Lea)

C. africana (Martens)
C. obscura M.-B.
C. exarata (Martens)
C. elata Dautzenberg & Germain
C. cridlandi M.-B.
C. langi Pilsbry & Bequaert
C. johnstoni Smith
C. mweruensis Smith
C. smithi Ancey
C. nsendweensis Dupuis & Putzeys
C. pilula M.-B.
C. guillemei Bgt
C. athiensis Verdcourt
C. hemmingi Verdcourt

C. rugosa Connolly
Pseudocleopatra togoensis Thiele
P. voltana M.-B.
P. dartevellei M.-B.
P. bennikei M.-B.
Potadomoides pelseneeri Leloup
Pot. bequaerti (Dautzenberg & Germain)
Pot. hirta (Dautzenberg & Germain)
Pot. schoutedeni (Dautzenberg & Germain)
(?)*Pot. broecki* (Putzeys)

Thalassoid prosobranchs of Lake Tanganyika

Syrnolopsis lacustris Smith
S. minuta Bgt
S. gracilis Pilsbry & Bequaert
Anceya giraudi Bgt
A. terebriformis (Smith)
Martelia tanganyicensis Dautzenberg
Lavigeria nassa (Woodward) aggregate
L. grandis (Smith)
Mysorelloides multisulcata (Bgt)

Hirthia globosa Ancey
H. littorina Ancey
Spekia zonata (Woodward)
Tanganyicia rufofilosa (Smith)
Stanleya neritinoides (Smith)
Reymondia horei (Smith)
R. pyramidalis Bgt
R. tanganyicensis Smith
Bridouxia giraudi Bgt
B. praeclara (Bgt)
B. leucoraphe (Ancey)
B. smithiana (Bgt)
B. ponsonbyi (Smith)
B. rotundata (Smith)

Stormsia minima (Smith)
Paramelania damoni (Smith) aggregate
P. iridescens (Moore)
Bathanalia howesi Moore
B. straeleni Leloup
Tiphobia horei Smith
Limnotrochus thomsoni Smith
Chytra kirki (Smith)

Family Melanopsidae

Melanopsis praemorsa (Linn.)

Family Potamididae

Cerithidea decollata (Bruguière)
Tympanotonus fuscatus (Linn.)
Terebralia palustris (Linn.)
Pirenella conica (de Blainville)

SUBCLASS EUTHYNEURA (INCLUDES THE PULMONATES)

Family Ellobiidae

Auriculastra radiolata (Mor.)
Auriculodes gaziensis (Preston)
Blauneria exsilium Preston
Cassidula labrella (Deshayes)
C. mustelina (Deshayes)
Melampus semiaratus Connolly
M. liberianus H. & A.Adams

Family Lymnaeidae

Lymnaea natalensis Krauss
(*L. columella* Say)
L. truncatula (Müller)
L. stagnalis (Linn.)
L. palustris (Müller)
L. peregra (Müller)

Family Ancylidae

Ancylus fluviatilis Müller
A. regularis Brown
A. ashangiensis Brown
Burnupia caffra (Krauss) aggregate
Ferrissia isseli (Bgt) aggregate

Family Planorbidae

Subfamily Planorbinae

(*Amerianna carinata* (H.Adams))
Planorbis planorbis (Linn.)
Afrogyrus coretus (de Blainville)
Armiger crista (Linn.)
Ceratophallus natalensis (Krauss)
C. blanfordi Brown
C. kigeziensis (Preston)
C. kisumiensis (Preston)
C. bicarinatus (M.-B.)
C. subtilis (M.-B.)
C. concavus (M.-B)
C. crassus (M.-B.)
C. pelecystoma Brown
(?)*C. apertus* (Martens)
(?)*C. faini* (Adam)
Gyraulus ehrenbergi (Beck)
G. costulatus (Krauss)
G. connollyi Brown & Van Eeden
Lentorbis benguelensis (Dunker)
L. junodi (Connolly)
L. carringtoni (de Azevedo *et al.*)
Segmentorbis angustus (Jickeli)
S. planodiscus (Melvill & Ponsonby)
S. eussoensis (Preston)
S. excavatus M.-B.
S. kanisaensis (Preston)
Biomphalaria pfeifferi (Krauss)
B. rhodesiensis M.-B.
B. choanomphala (Martens)
B. smithi Preston
B. stanleyi (Smith)
B. barthi Brown
B. alexandrina (Ehrenberg)
B. angulosa M.-B.
B. tchadiensis (Germain)
B. camerunensis (C.R.Boettger)
B. salinarum (Mor.)
B. sudanica (Martens)
(*Helisoma duryi* (Wetherby))
Planorbarius metidjensis (Forbes)

Subfamily Bulininae

(*Indoplanorbis exustus* (Deshayes))

***Bulinus africanus* group**

B. africanus (Krauss)
B. nasutus (Martens)
B. abyssinicus (Martens)
B. globosus (Mor.)
B. jousseaumei (Dautzenberg)

B. ugandae M.-B.
B. obtusus M.-B.
B. umbilicatus M.-B.
B. hightoni Brown & Wright

***B. truncatus/tropicus* complex**

B. angolensis (Mor.)
B. permembranaceus (Preston)

B. depressus Haas
B. hexaploidus Burch
B. natalensis (Küster)
B. nyassanus (Smith)
B. octoploidus Burch
B. succinoides (Smith)
B. transversalis (Martens)
B. trigonus (Martens)
B. tropicus (Krauss)
B. truncatus (Audouin)

B. forskalii group

B. forskalii (Ehrenberg)
B. scalaris (Dunker)
B. canescens (Mor.)
B. senegalensis (Müller)
B. camerunensis M.-B.
B. crystallinus (Mor.)
B. barthi Jelnes
B. browni Jelnes

B. reticulatus group

B. reticulatus M.-B.
B. wrighti M.-B. is closely related but found only in Arabia

Family Physidae

(*Physa acuta* Draparnaud) (*Aplexa waterloti* (Germain))

Species found in islands of the western Indian Ocean but not in Africa

This list is primarily of the freshwater species that seem to be distinct from African species, though probably not all are different. There are likely to be additional brackish-water species not found in Africa, especially in the Neritidae, Assimineidae, Thiaridae, Potamididae and Ellobiidae.

Abbreviations: Com. (Comoro Islands), Mad. (Madagascar), Mau. (Mauritius).

Family Neritidae
Clithon spp. Com., Mad., Mau.
Neritilia consimilis (Dohrn) Com., Mad., Mau., Réunion, Seychelles

Family Viviparidae

Bellamya bengalensis (Lamarck) Mau.

Family Ampullariidae

Pila cecillei (Philippi) Mad.
Lanistes grasseti (Mor.) Mad.

Family Thiaridae

Thiara datura (Dohrn) Com., Réunion
Melanoides psorica (Mor.) Mad.
Melanatria fluminea (Gmelin) Mad.
M. madagascariensis (Grateloup) Mad.
Cleopatra colbeaui (Craven) Mad.
C. madagascariensis (Crosse) Mad.
C. grandidieri (Crosse & Fischer) Mad.
Paludomus ajanensis Mor. Seychelles

Family Lymnaeidae

Lymnaea mauritiana Mor. Mau.
Lantzia carinata Jousseaume Réunion

Family Ancylidae

Ferrissia modesta (Crosse) Mad.

Family Planorbidae

Afrogyrus rodriguezensis (Crosse) Rodriguez
A. starmuehlneri Brown Mad.
A. crassilabrum (Mor.) Mad.
(?)*Ceratophallus socotrensis* (Godwin-Austen) Socotra
Gyraulus cockburni (Godwin-Austen) Socotra
G. mauritianus (Mor.) Mau.
Bulinus obtusispira (Smith) Mad.
B. liratus (Tristram) Mad.
B. cernicus (Mor.) Mau.
B. bavayi (Dautzenberg) Mad., Aldabra

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Chapter 3.
Systematic Synopsis: Prosobranchs

The classification of gastropod molluscs is in a continuing state of revision and it will be some time before a system comes to be generally agreed for the groups of higher rank (Haszprunar, 1988; Ponder, 1988a). Gastropods have been divided commonly into two major groups, the Streptoneura (including those known as the Prosobranchia or prosobranchs) and the Euthyneura (pulmonates and opisthobranchs). The freshwater gastropods of Africa are either prosobranchs (so-called because they have a comb-like gill, the ctenidium, situated within the mantle cavity and in front of the heart) or pulmonates (lacking a gill, the mantle cavity serving as an air-breathing organ; treated in Chapter 4).

Almost all African freshwater prosobranchs have an operculum of horny or calcareous material attached to the foot and closing the aperture to a varying degree (the operculum is much reduced in *Soapitia* and apparently lacking in *Valvatorbis*). The sexes are separate in all African genera apart from *Valvata*. The radula is either rhipidoglossate (Neritidae only; many teeth in a transverse row but only few are conspicuous) or taenioglossate (the other families; only 7 teeth per transverse row, all clearly distinct). Of the families considered here the Neritidae have been classified traditionally in the order Archaeogastropoda and the rest in the Mesogastropoda.

Family ***Neritidae***

Shell small to medium-sized and typically ‘neritiform’; whorls few and rapidly expanding, spire low; lip oblique, aperture D-shaped, its straight side forming a columellar plate, which may be toothed. Shell commonly with a pattern of dark markings on a variously coloured background. Operculum paucispiral, calcified, with one or two internal projections or apophyses (the ‘rib’ and ‘peg’) on its inner columellar side. Radula rhipidoglossate (with many small marginal teeth).

Many neritids are marine and various lineages have adapted to brackish and fresh waters, particularly in the tropics; in tropical Africa no species penetrates far above the limit of tidal influence. Because of the obliquity of the neritid apertural lip it is difficult to make standard measurements; those given here are for height or width, according to whichever is the greater.

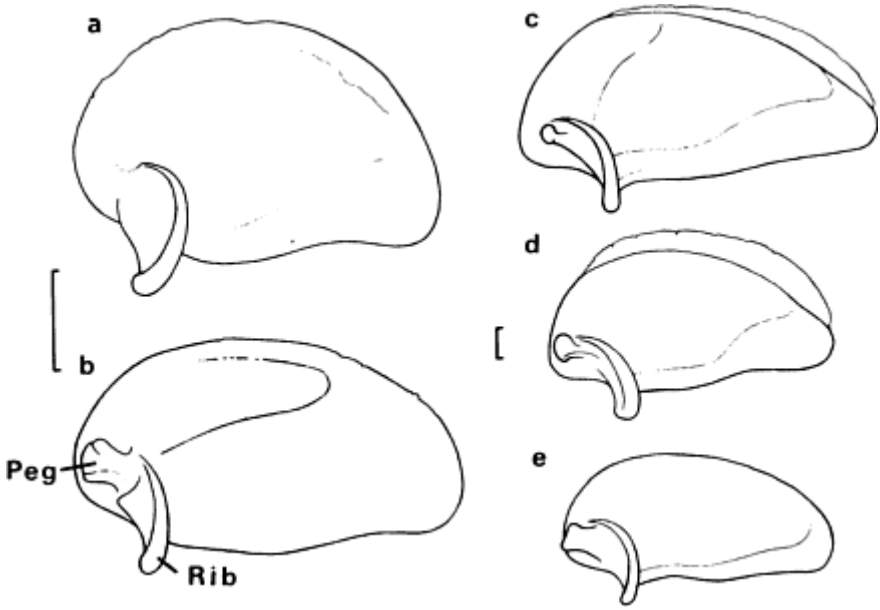

Fig. 15. Neritidae, opercula. (a) *Theodoxus fluviatilis* (England), (b) *T. jordani* (Jordan, Azrak). (c) *Neritina tiassalensis* (shell Fig. 17c). (d) *N. oweniana* (shell Fig. 17a). (e) *N. cristata* (syntype, BMNH). Scale lines: 1 mm.

Genus *Theodoxus* Montfort, 1810

Shell small, neritiform; columellar plate not toothed. Operculum with one or two apophyses (Fig. 15). Two groups of species were recognised (Baker, 1923), section *Theodoxus* with the peg on the operculum reduced or lacking, and section *Neritaea* with the peg clearly visible; this division was rejected by Kristensen (1986a) who observed one or two apophyses present in different individuals of the same species. Yet there seems to be a geographical pattern of variation, the single-apophysis form (Fig. 15a) being common in a western area, whereas the double-apophysis form (Fig. 15b) alone is found in the Near East (Dagan, 1971; Roth, 1984; Burch, 1985) and Egypt (my own observations). Further investigation is desirable of variation in the opercular apophyses and their value in taxonomy.

In lakes, spring-pools and perennial streams, usually attached to stones; tolerant of low salinity.

Europe, North West Africa, Egypt and the Near East (but not found in Sinai or Arabia). Only the one species *T. fluviatilis* of Europe was recognised to occur in North West Africa by Brown (1980a), but Kristensen (1986a) concluded that this species probably does not occur in the area and recognised the 3 other species that follow. Type species: *Nerita fluviatilis* Linnaeus, 1758, Europe.

Theodoxus numidicus (Récluz, 1841, *Neritina*). Type locality: NW Algeria, Oran. **Fig. 16a**.

7 mm. Shell small, may be white-spotted though often all black, with flat columellar plate. Operculum with a single apophysis. Central radular tooth with the 'wings' narrow and as long as the base; first lateral tooth with the posterior lobe prominent and rounded.

DISTRIBUTION. Algeria and Morocco (Kristensen, 1986a).

Theodoxus maresi (Bourguignat, 1864, *Neritina*). Type locality: NE Algeria, Ain Khadra near Zerguin in NE Algeria.

8 mm. Shell dark brown or black, with a convex columellar plate. Operculum commonly with one apophysis, though some individuals have two. Base of central tooth clearly longer than the 'wings'; first lateral tooth with a weak posterior lobe.

DISTRIBUTION. Algeria and Morocco (Kristensen, 1986a).

Theodoxus meridionalis (Philippi, 1836, *Neritina*). Type locality; Sicily, Syracuse.

8 mm. Shell purplish to brown with light spots, last whorl strongly convex. Operculum with two strong apophyses. Central tooth with broad lateral wings; first lateral tooth with a pointed posterior lobe.

DISTRIBUTION. Tunisia (Kristensen, 1986a).

Theodoxus niloticus (Reeve, 1856, *Neritina*). Type locality: Egypt, the Nile. **Figs 16b,c**.

8 mm. Shell may have a prominent spire; colour and patterns highly variable (Gardner, 1932), commonly with purplish-brown zig-zag bands. Operculum with 2 apophyses. *T. africanus* (Reeve, 1856; of 'Africa') is very likely a synonym. *T. niloticus* is perhaps the same species as *T. jordani* (Sowerby, 1836) of the Near East (Tchernov, 1975a; Dagan, 1971; Roth, 1984; Burch, 1985); this has a similar Operculum (Fig. 15b).

HABITAT. Slowly flowing water in lower Egypt; tolerant of some salinity and abundant in the extinct fauna of aquatic molluscs in the Faiyum Depression (Gardner, 1932).

DISTRIBUTION. Egypt; lower Nile and canals. Sudan: 'modern' shells below the second Nile Cataract (Martin, 1968). Ethiopia: reports of *T. africanus* from the Blue Nile below Lake Tana (Bourguignat, 1883) and near Massawa (Bacci, 1951) have not been substantiated.

Genus *Neritina* Lamarck, 1816

Shell small to medium-sized, neritiform, edge of columellar plate smooth or toothed, outer lip smooth (not serrate or toothed as it is in *Nerita,* a mostly marine genus). Operculum with the rib and peg well separated (compare with *Clithon,* Figs 8c,d). Egg capsules oval, 1 or 2 mm long, often attached to the shell.

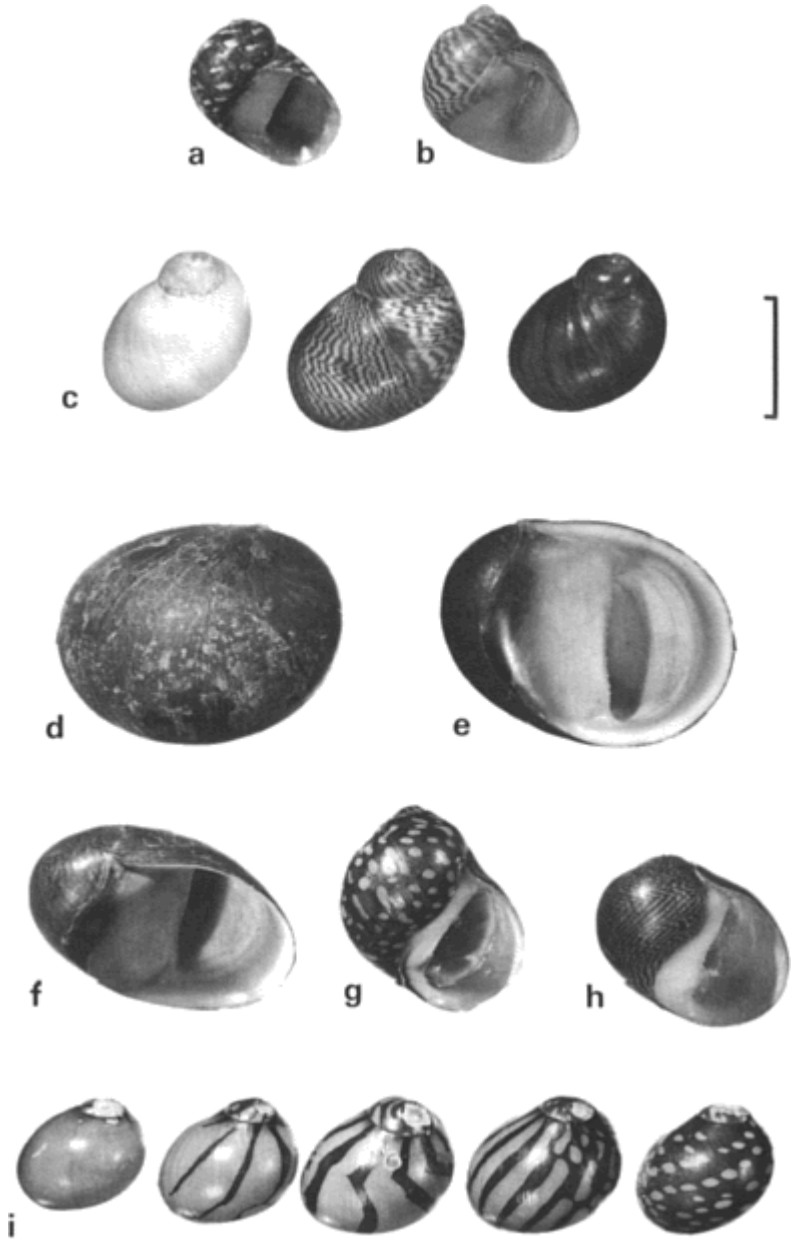

Fig. 16. Neritidae. (a) *Theodoxus numidicus;* Morocco, Ain Fekan. (b) *T. niloticus;* Egypt, Nile, (c) *T. niloticus;* Egypt, Maadi, drain, (d–f) *Neritina pulligera;* Mayotte Island, (g) *N. natalensis;* South Africa, Durban, (h) *N. gagates;* Zanzibar. (i) *N. natalensis;* Kenya, Gazi (range of colour pattern). Scale line: 5 mm (a–c) or 10 mm (d–i).

Neritina was subdivided by Baker (1923) according to radular characters; he

examined some African species but their shells were not illustrated and the identifications need confirmation. Comments by Binder (1957) on variation in the radulae of West African species add to doubts about the validity of Baker's groups, which are not employed here.

In brackish and fresh water near coasts, circumtropical and subtropical; 13 or more species in Africa and Madagascar, treated here in 3 geographical areas: eastern, Madagascar and western. Type species: *Nerita pulligera* Linnaeus, 1767.

1) *Neritina* in eastern Africa

Neritina pulligera (Linnaeus, 1767, *Nerita*). Type locality: not given. **Figs 16d–f**.

23 mm. Last whorl greatly expanded, almost entirely enclosing the earlier whorls; appearing black, though with a fine reticulate pattern; lip usually orange within. The name *N. knorri* (Récluz, 1841; Philippine Islands) has been used for African snails but is a synonym of *N. pulligera* according to Starmühlner (1969).

HABITAT. Rivers and streams, near tidal influence; on stones in currents up to 0.5 m sec^{-1} (Starmühlner, 1969). Found by myself on mud near streams flowing into mangrove swamps in South Africa and Kenya.

DISTRIBUTION. Pemba (Mozley, 1939, *N. knorri*); Kenya (Gazi, BME); Mozambique (Azevedo *et al.,* 1961, *N. knorri*); South Africa, Durban (Brown, 1967a, *N. gagates*). Comoro Islands (Starmühlner, 1983; Backeljau *et al.,* 1986); Madagascar, Mascarene Islands and Seychelles (Starmühlner, 1969, 1983; Fischer-Piette & Vukadinovic, 1973); Far East (Brandt, 1974).

Neritina natalensis Reeve, 1855. Type locality: South Africa, Umgeni River (near Durban). **Figs 16 g,i**.

20 mm. Shell with obviously projecting spire; yellowish-brown with variable black bands, sometimes reducing the light areas to small spots (Fig. 16i).

HABITAT AND DISTRIBUTION. Mangrove swamp (Brown, 1971). Somalia, Giuba River (Connolly, 1928a) and southwards to Mozambique (Azevedo *et al.,* 1961) and South Africa, Natal: Durban, (Brown, 1971), Umzimkulu River (Connolly, 1939).

Neritina gagates Lamarck, 1822. Type locality: not given. Fig. 16h.

22 mm. Like *N. natalensis* but generally more depressed and darker coloured.

HABITAT AND DISTRIBUTION. Streams near tidal influence, on stones in currents up to 0.75 m sec^{-1} (Starmühlner, 1969, 1983). South Africa: Natal (Connolly, 1939). Comoro Islands, Madagascar, Mascarene Islands and Seychelles (Germain, 1921a; Starmühlner, 1969, 1983; Fischer-Piette & Vukadinovic, 1973; Backeljau *et al.,* 1986).

2) *Neritina* present in Madagascar but not found in Africa. *N. auriculata* Lamarck, 1816 (Starmühlner, 1969, 1983) has a rapidly increasing last whorl like *N. pulligera,* but the lip is distinctively expanded. *N. turrita* (Chemnitz, 1786) is large and high-spired; reported without precise localities (Fischer-Piette & Vukadinovic, 1973).

3) *Neritina* in West Africa. Among the 8 species recognised here, *N. oweniana* and *N. tiassalensis* are comparatively large and there is a distinct group of smaller species with strongly patterned shells *(adansoniana, glabrata, kuramoensis)*. Binder (1957) gave a comparative account of 6 species found in Ivory Coast.

Neritina oweniana (Wood, 1828, *Nerita*). Type locality: Africa. **Figs 17a,b**.

28 mm (including the 'wings'). Last whorl expanded enclosing earlier whorls almost completely; lip commonly expanded above and below forming two wing-like projections; columellar edge smooth in large shells but toothed in some juveniles; highly varied black markings on a yellowish-brown background. Operculum with a well developed peg (Fig. 15d).

HABITAT. The wings were most fully developed in nearly fresh water above the mangrove zone (Pilsbry & Bequaert, 1927). Living in a salinity range of 0.3–1.1‰ (Binder, 1968) and found by myself commonly on *Vallisneria* plants in apparently fresh water in the lower Volta River.

DISTRIBUTION. Liberia to Angola (Pilsbry & Bequaert, 1927); furthest inland at Bator, Volta River (McCullough, 1965a) and Zambi, Zaire River (Pilsbry & Bequaert, 1927).

Neritina tiassalensis Binder, 1955, 1957. Type locality: Ivory Coast, rapids of the Bandama River at Tiassalé (80 km inland). **Figs 15c, 17c**.

26 mm. Like a large darkly-pigmented *N. oweniana* but lacking the wing-like expansions of the lip (Fig. 17c). Peg of operculum comparatively small (Fig. 15c). Distinguished from *N. aequinoxialis* (see *N. afra*) by the smooth columellar edge and the finer microsculpture on the shell (Binder, 1955).

HABITAT AND DISTRIBUTION. Rocks in the full current of a river in Ivory Coast.

Neritina rubricata Morelet, 1858. Type locality: Senegambia (although syntypes from Morelet's collection (BMNH) are labelled from Calabar, Gabon and Congo). **Figs 17d–f**.

13 mm. Spire prominent, columellar edge toothed; similar to *N. oweniana* in the yellowish-brown colour and dark patterns (Binder, 1957). DISTRIBUTION. Gambia to Cameroon (DBL) and Gabon (BMNH, Fig. 17d).

Neritina cristata Morelet, 1864. Type locality: Gabon, Como River. **Fig. 17g**.

16 mm. Like *N. oweniana* but spire more prominent and columellar edge always toothed (Binder, 1957). Mature shell usually with an expansion of the upper lip forming a subsutural ridge, to which the species owes its name. Operculum with a large peg (Fig. 15e).

DISTRIBUTION. Sierra Leone (DBL), Ivory Coast (Binder, 1957), Cameroon (DBL) and Gabon.

Neritina adansoniana (Récluz, 1841, *Nerita*). Type locality: Senegal River estuary. **Fig. 18a**.

12 mm (to 16 mm; Binder, 1957). Spire prominent and whorls somewhat angular, being flattened above the periphery; colour ranges from grey to pink with varied markings. It is likely that *N. kuramoensis* is the same species.

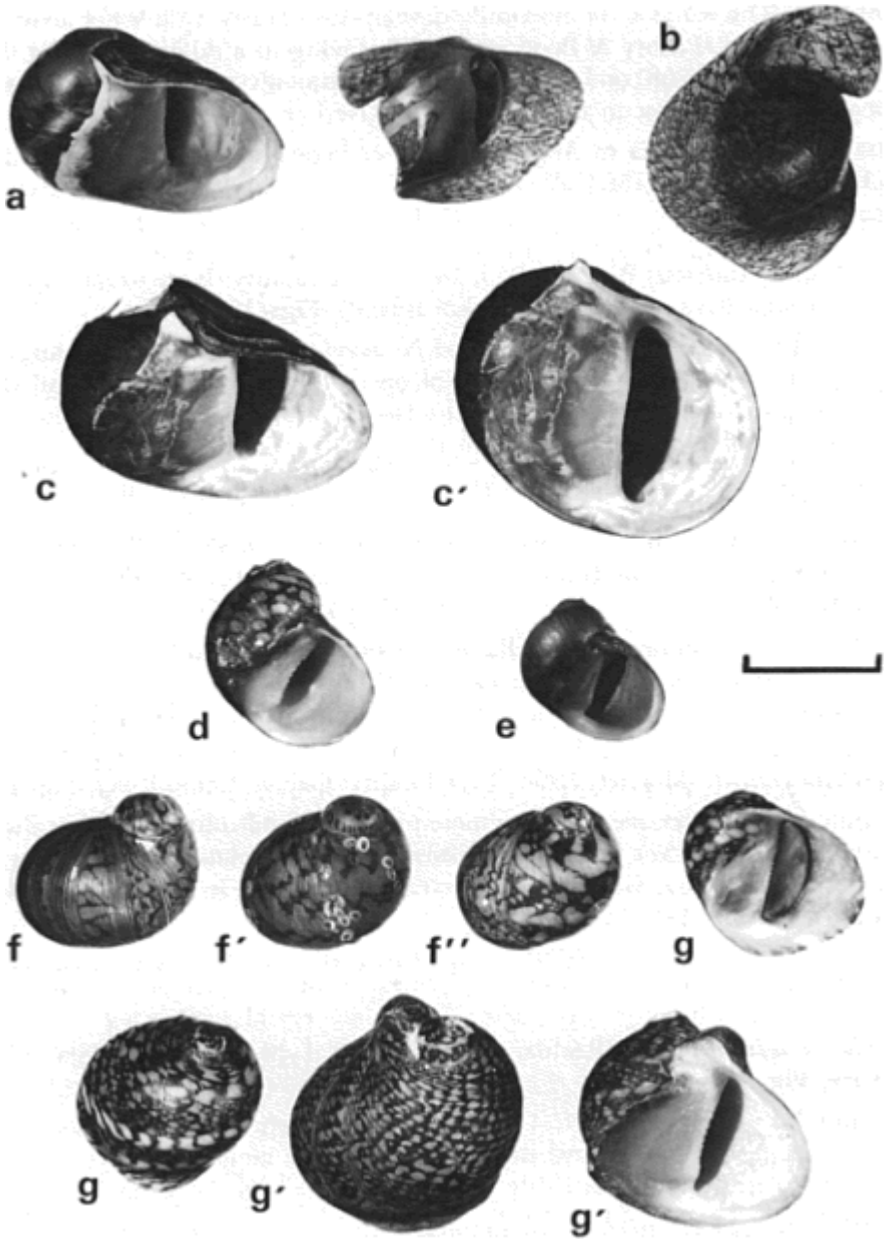

Fig. 17. *Neritina.* (a) *N. oweniana;* Sierra Leone, Kambia. (b) *N. oweniana;* Ghana, Volta River. (c,c′) *N. tiassalensis;* Ivory Coast (collected from the type locality in 1964 by E.Binder), (d–f′′) *N. rubricata,* from the collection of Morelet in BMNH: d,f (same shell), f′ and f′′, all from Gabon; e, from Nigeria, Old Calabar. (g,g′) *N. cristata;* syntypes (BMNH1893.2.4.1829–34). Scale line: 10 mm.

HABITAT AND DISTRIBUTION. More tolerant than *N. glabrata* of varying salinity and strong wave-action according to Pilsbry & Bequaert (1927), although both species were found in a wide salinity range in Ivory Coast (Binder, 1968). Senegal to Angola.

Neritina glabrata Sowerby, 1849. Type locality: not given. **Figs 18b,c**.

8.5 mm. Generally smaller than *N. adansoniana,* with a smoother and glossy surface; spire lower and last whorl more evenly rounded. The beautiful varied colouration was illustrated in colour by Pilsbry & Bequaert (1927); ground colour commonly yellowish, patterned with black, brown or red.

HABITAT AND DISTRIBUTION. Sheltered coves, in brackish water (Pilsbry & Bequaert, 1927); estuaries and lagoons, living usually at depths of less than 1 m, on sand, rocks and vegetation (Binder, 1957). In a moderate range of salinity in Lagos Lagoon (Yoloye & Adegoke, 1977); most common on sand (Ajao & Fagade, 1990a). Gambia to Angola (Pilsbry & Bequaert, 1927).

Neritina kuramoensis Yoloye & Adegoke, 1977. Type locality: Nigeria, Kuramo Water (a branch of Lagos Lagoon).

12 (to 15 mm). The authors distinguished this species from *N. glabrata* by the larger, thicker shell with a higher spire and duller colour; it seems likely to be a synonym of *N. adansoniana*.

HABITAT AND DISTRIBUTION. Nigeria: localities mostly associated with Lagos Lagoon. On mangrove rhizophores, other vegetation and mud, but not sand (Adegoke *et al.,* 1969; *Neritina* sp.); in a wide range of salinity.

Neritina afra Sowerby, 1841. Type locality: Fernando Po. **Figs 18d,e**.

14 mm. Spire low though distinct, edge of columella with coarse teeth; colour generally dark greenish-brown with yellowish spots; columellar plate white with a faint orange tint towards the outer margin. Placed incorrectly in *Theodoxus* by Pilsbry & Bequaert (1927) following Baker (1923). *N. aequinoxialis* Morelet (1848; Ile du Prince) is founded on shells that seem to be large *N. afra* (Fig. 18d) and resemble *N. tiassalensis* (see also Binder, 1955).

HABITAT. Torrential streams at 200–300 m altitude (Germain, 1912a), but otherwise found only in coastal localities.

DISTRIBUTION. Fernando Po, Ile du Prince (Germain, 1912a), São Tomé (Brown, 1991), Cameroon (Germain, 1912a; Victoria, DBL), Angola (Morelet, 1868).

Genus *Clithon* Montfort, 1810

Shell small to medium-sized, neritiform, with spines in some species (Fig. 18g). Operculum with a high ridge between the peg and the rib, unlike *Neritina* (Figs 8c,d). In the lower courses of rapid streams in the Indo-Pacific region, but not found in Africa. Three species reported from the Comoro Islands (Starmühlner, 1983; Backeljau *et al.,* 1986) and 3 or more found in Madagascar and the Mascarene Islands (Starmühlner, 1969, 1979, 1983; Fischer-Piette & Vukadinovic, 1973), including *C. longispina* (Récluz, 1841) (Fig. 18g).

Genus *Septaria* Ferussac, 1807

Shell medium to large, with its last whorl greatly expanded and cap-like. Operculum reduced to a small angular plate (Fig. 8a). In the lower courses of streams in the Indo-Pacific region, but rarely found in Africa. Type species: *Patella borbonica* Bory de St Vincent, 1803, Réunion Island.

Septaria borbonica (Bory de St Vincent, 1803, *Patella*). Type locality: Réunion Island. **Figs 18h,i**.

27 mm long (large South African shell). Taxonomy revised and reproduction described by Haynes (1992); a widespread species, reported under many different names.

HABITAT. The only known African localities are streams on the Natal coast (Connolly, 1939); probably now extinct as the result of habitat disturbance.

DISTRIBUTION. South Africa, Natal coast (Connolly, 1939, as *S. tessellaria*) and Indian Ocean Islands (Starmühlner, 1969, 1983; Fischer-Piette & Vukadinovic, 1973, as *S. lineata;* Backeljau *et al.,* 1986).

Genus *Neritilia* Martens, 1879

Shell small, neritiform, lacking colour and pattern; columellar edge smooth. Operculum with single apophysis (Fig. 8b). Radula lacking central tooth. In fresh water near coasts; West Africa, Caribbean and Indo-Pacific regions. Few species; possible synonymies discussed by Starmühlner (1983). One species in Africa. Type species: *Neritina rubida* Pease, 1865, Tahiti (Brandt, 1974).

Neritilia manoeli (Dohrn, 1866, *Neritina*). Type locality: Principe Island, in stony streams. **Fig. 18f**.

4 mm wide. Easily recognised from the small, pale (when clean), unpatterned shell. *N. succinea* (Récluz, 1841) of the Caribbean region is more depressed with a relatively larger aperture (Brown, 1980b).

DISTRIBUTION. Principe Island, São Tomé Island (collected by C.Ripert, 1992) and Cameroon: Bibundi (Boettger, 1905) and Victoria, on aquatic plants (DBL).

Neritilia consimilis Martens, 1897a. Type locality: Mauritius, Creole River.

5 mm wide. Shell so like that of *N. manoeli* that it could be the same species; examples from Mauritius and Anjouan Island described by Brown (1980b), taxonomic relationships discussed by Starmühlner (1983).

HABITAT AND DISTRIBUTION. On rocks in streams up to 120 m altitude in Anjouan (Starmühlner, 1976a). Comoro Islands: Anjouan (Starmühlner, 1976a; Backeljau *et al.,* 1986); Madagascar (Fischer-Piette & Vukadinovic, 1973); Mauritius, Réunion and Seychelles (Starmühlner, 1976b, 1983).

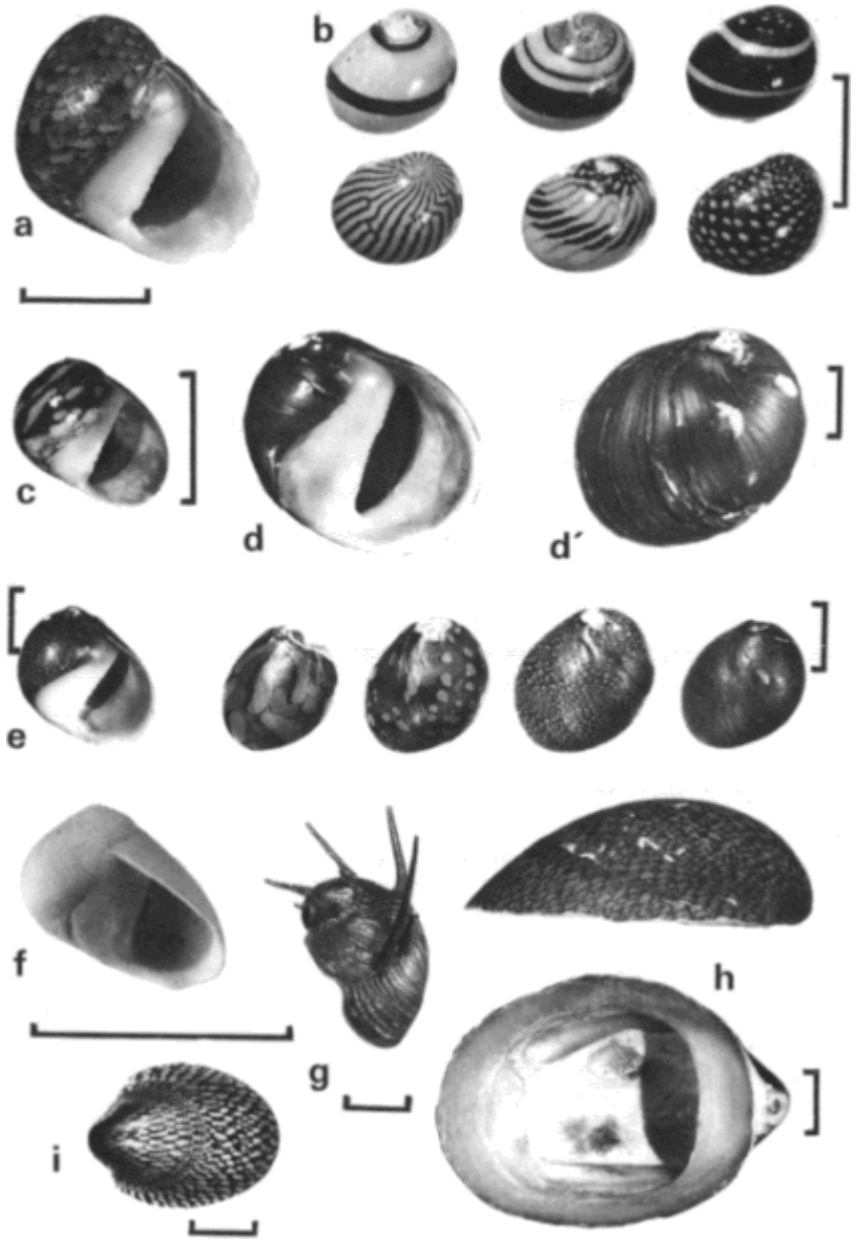

Fig. 18. Neritidae. (a) *Neritina adansoniana;* Ivory Coast, lagune d'Ebrié. (b) *N. glabrata;* Nigeria, Lagos (6 shells), (c) *N. glabrata;* Lagos. (d,d′) *N. afra;* Principe Island (syntype of *N. aequinoxialis*, BMNH1893.2.4.1842–44). (e) *N. afra;* Cameroon, Victoria (5 shells). (f) *Neritita manoeli;* Cameroon, Victoria, (g) *Clithon longispina;* Mauritius, (h) *Septaria borbonica;* South Africa, Widenham. (i) *S. borbonica;* Mauritius. Scale lines: 5 mm.

Family ***Hydrocenidae***

A single genus of small snails, with the operculum bearing an internal apophysis, living on land in moist places in the Indo-Pacific region. *Hydrocena noticola* Benson is recorded from South Africa (Connolly, 1939) and was classified in *Assiminia* by Thiele (1927). Three species are listed for Madagascar by Starmühlner (1969); one reported from a freshwater lake (Germain, 1935a).

Family ***Viviparidae***

Shell medium to large, dextral; spire conical, whorls varying from evenly convex to angular or carinate. Operculum corneous and concentric (Fig. 8e). Viviparous; young develop in the lower oviduct. Male with right tentacle modified as a copulatory organ. Radula taenioglossate; central tooth wide and lacking basal denticles. Nearly cosmopolitan in fresh water, but absent from South America. Two genera in Africa.

Genus *Bellamya* Jousseaume, 1886

Characters as for the family. Distinguished from *Viviparus* of Europe by anatomical characters including a differently positioned testis (Rohrbach, 1937). Shell apex (Fig. 2c) sharply pointed, with a ridge and bristles (whereas it is blunt and smooth in *Neothauma* of Lake Tanganyika).

In rivers, lakes and smaller permanent waterbodies of Africa and S Asia, but apparently not Arabia or the Near East, although viviparid shells of uncertain generic position are known from Yemen (Ayad, 1956), the Jordan Valley (Tchernov, 1975b) and Syria (Pallary, 1939).

In Africa from Egypt southwards into Zululand and N Namibia (Fig. 69). The species were reviewed according to shell characters by Dartevelle (1952a) and taxonomic use of the arrangement of embryos was introduced by Mandahl-Barth (1973a); improved understanding of species is expected from chromosome studies (Kat, 1986). Of the 18 species recognised here, only *unicolor* and *capillata* are widely distributed, and most are restricted to large lakes. Species will be treated in 3 groups: those found in smaller habitats, those restricted to lakes and lastly a few of uncertain status.

Type species: *Vivipara duponti* De Rochebrune, 1882, Senegal.

1) Species found in smaller waterbodies

Bellamya unicolor (Olivier, 1804, *Cyclostoma*). Type locality: Egypt, Alexandria. **Figs 19a–c**.

30×20 mm. Aperture usually about half of the total shell height; last whorl slightly flattened at the periphery, producing two blunt angles; umbilicus narrow or closed; spiral rows of small bristles may occur. Embryos small and numerous (Mandahl-Barth, 1973a). To the same species apparently belong populations living in lakes and having a higher spire; named forms include *B. abyssinica*

(Martens, 1866) of Lake Tana, Ethiopia (Fig. 19b), *unicolor variety elatior* Martens (1897) of Lake Victoria (Fig. 19c) and *B. gracilior* (Martens, 1903) of Lake Chad. *B. duponti* (the genus-type) appears to be conspecific, although it is little known.

HABITAT. Lakes, rivers and perennial streams. Especially abundant on bottom sediments in Lake Chad (Chapters 10, 11) and Lake Victoria (down to 64 m depth; Mandahl-Barth, 1954a).

DISTRIBUTION (Fig. 69). Range large, but localities widely scattered. Lower Egypt, Sudan and southwards into Kenya and perhaps Tanzania; westwards through a narrow zone into Senegambia. Subfossil shells in the Rift Valley of Ethiopia (Brown, 1965); late Pleistocene-Holocene distribution in the Sahara included southern Libya, Chad and Niger (Van Damme, 1984). Doubtful record for Madagascar (Fischer-Piette & Vukadinovic, 1973, *Vivipara*).

Bellamya capillata (Frauenfeld, 1865, *Vivipara*). Type locality: Lake Nyasa (Malawi). **Figs 19d–g**.

20×15 mm (syntype); to 35 mm high (Brown *et al.,* 1992). Shell like *B. unicolor,* although the eggs are larger according to Mandahl-Barth (1973a), variation in shell and embryos described for NE Namibia (Brown *et al.,* 1992). Mandahl-Barth (1968a) treated as two subspecies, *B. aethiops* (Reeve, 1864; central Africa) and *B. kalingwisiensis* (Smith, 1908; Kalungwisi River) (Figs 19e,f). *B. passargei* (Martens, 1904; Botletle area) was named from a subfossil shell found near the south-western limit of distribution. Revision is needed, including chromosome studies, to clarify the taxonomic status of *B. capillata* and of the many named forms now supposed to be synonyms.

HABITAT. Lakes, rivers and smaller waterbodies if permanent. On the coastal plain of Natal, *B. capillata* lives in shallow pans as well as on the bottom of Lake Sibaya (Appleton, 1977c; Hart, 1979).

DISTRIBUTION (Fig. 69). Range large, but localities scattered. From Tanzania southwards into north-eastern Natal; westwards into lower Zaire, Angola and the Okavango River (Brown *et al.,* 1992).

Bellamya monardi (Haas, 1934, *Viviparus*). Type locality: S Angola, Kilui stream, a tributary of the Cunene River. **Figs 19g; 21a**.

33×27 mm. Last whorl large, shouldered near the suture and rather flattened above the periphery; umbilicus sometimes surrounded by a low angle; surface with many fine spiral ridges, less smooth than in *B. capillata* and yellowish-brown rather than greenish (Brown *et al.,* 1992). Two earlier named forms seem probably conspecific: *Vivipara unicolor* variety *sambesiensis* Sturany, 1898 and V. *densestriata* Preston, 1905 (Fig. 19g). A shell of *B. monardi* was illustrated by Connolly (1939) as an example of *V. leopoldvillensis* (Putzeys) from Namibia.

DISTRIBUTION. S Angola and N Namibia; Cunene River and tributaries, Okavango River from Rundu to Popa Falls (Brown *et al.,* 1992).

2) Species restricted to large lakes

Bellamya phthinotropis (Martens, 1892, *Vivipara*). Type locality; SW shore of Lake Victoria at Nyamgotso. **Fig. 19h**.

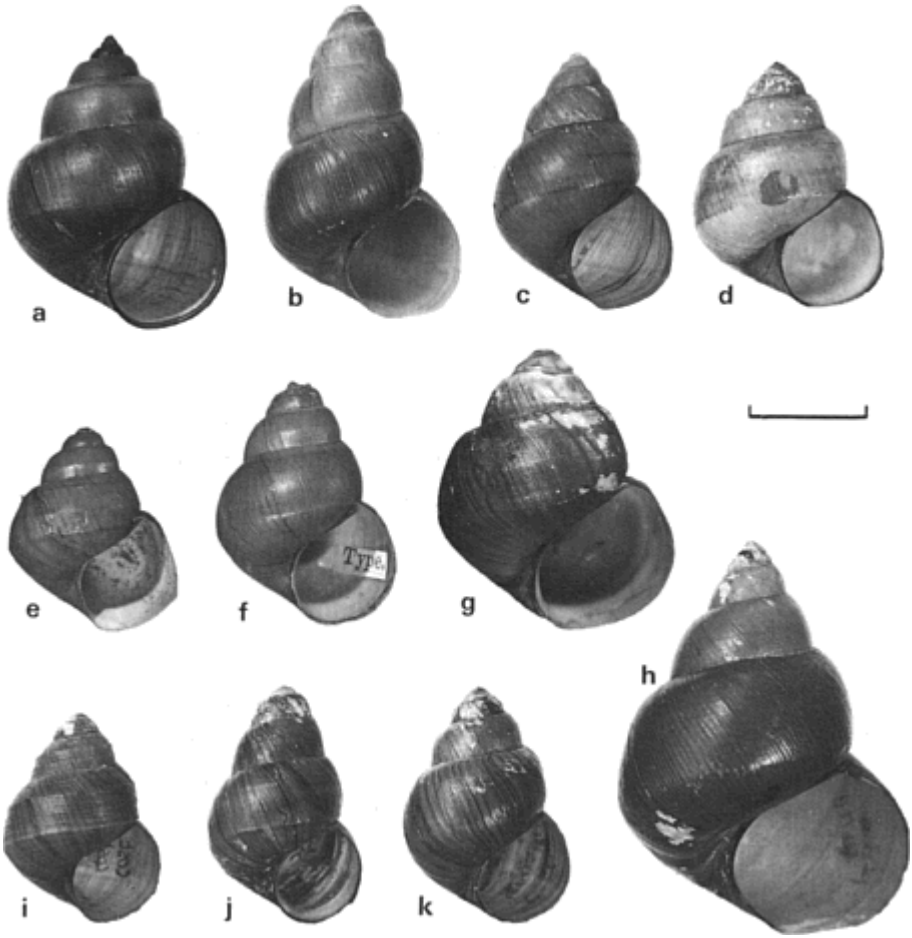

Fig. 19. Viviparidae. (a) *Bellamya unicolor;* Kenya, Lake Jipe. (b) *B. unicolor* (form *abyssinica*); Ethiopia, Lake Tana, (c) *B. unicolor* (form *elatior*); Lake Victoria, Kisumu. (d) *B. capillata;* Lake Malawi (syntype, BMNH). (e,f) *B. capillata;* Zambia, Kalingwisi River (syntypes) of *B. kalingwisiensis,* BMNH1907.11.11.56–62). (g) *B. densestriata;* Zambezi River, above Victoria Falls (syntype, BMNH1905.8.29.2; see under *B. monarch*), (h) *B. phthinotropis;* Lake Victoria, Buvuma Channel at 33 m depth, (i–k) *B. costulata;* Lake Victoria, (i) typical form from Bukoba, (j) form *dagusiae* from north of Dagusi Island at 9–12 m depth and (k) form *ugandae* from Jinja Bay. Scale line: 10 mm.

44×30 mm. Large, with a broad body whorl and sharply tapered spire.

HABITAT AND DISTRIBUTION. Lake Victoria; in deep water, to 33 m (108 feet) (Mandahl-Barth, 1954a).

Bellamya costulata (Martens, 1892, *Vivipara*). Type locality: Kassarassi Island, SW Lake Victoria. **Figs 19i–k**.