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# GASTROPODA

## GENERAL CHARACTERISTICS OF GASTROPODA

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### CONTENTS

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# NAME AND DEFINITION OF CLASS

## THE NAME "GASTROPODA"

CUVIER in 1797 (27[1]) was the first to recognize the essential characters of this class and the close relationship of its shell-bearing and shell-less forms, which LINNÉ had included respectively in his *Vermes testacea* and *Vermes mollusca*. CUVIER assigned to this group the name "mollusques gastéropodes" or simply "gastéropodes" (Greek γαστήρ, stomach; πoύς, ποδός, foot), which appears to have been first rendered in the Latin form "Gastropoda" by DUMÉRIL in 1806 (32). RAFINESQUE (87) gave the name as "Gasteropodia." Early conchologists included the group in their "Univalvia," but this name was gradually abandoned when the heterogeneous composition of the group so designated was recognized. Further synonyms, mostly used only by their authors, are listed on p. I171. The Gastropoda, as restricted by the definition given below, are the Gastropoda Anisopleura of LANKESTER (63). ZITTEL (113) used the name Glossophora, then recently introduced by P. FISCHER, as an inclusive term for the Polyplacophora, Scaphopoda, and Gastropoda. FISCHER (35, p. 8, 519, 529, etc.), however, did not intend to apply this term to a single taxonomic group, but used it repeatedly, in groups of differing taxonomic rank, to distinguish radula-bearing forms from forms (Aglossa) without a radula. Some German authors have followed ZITTEL. LANKESTER (63) included all the molluscan classes except the Pelecypoda in the Glossophora.

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[1] Reference numbers inclosed by parentheses indicate publications cited in the list beginning on p. I165.

### DEFINITION OF CLASS

The class Gastropoda includes Mollusca with a distinct head, which in unspecialized forms has eyes and tentacles and is more or less fused with the foot, typically solelike and adapted for creeping, but much modified in pelagic and some other forms. A radula normally is present. Cerebral and pleural nerve ganglia are distinct. Organs of the pallial complex are re-oriented (in relation to their positions in a conjectural primitive mollusk) as the result of "torsion," which in some forms is a definite episode observable in early ontogeny, and in others in inferred to have taken place in ancestral forms, although omitted in a condensed ontogeny. Bilateral asymmetry is present to a varying degree in all living representatives, although complete symmetry may have existed in the extinct Bellerophontacea. The shell, if present, is single (univalve), calcareous, closed apically, endogastric when spiral, and not divided regularly into chambers.

The definition just given excludes certain groups which have frequently been included among the gastropods, but in which the orientation of the various organs is (or is inferred to have been) unaffected by "torsion" and in which there is bilateral symmetry. These groups are the Polyplacophora, with their 8-valved shells, and the Monoplacophora with their cap-shaped shells. Excluded also are the shell-less Solenogastres (or Aplacophora), which LANKESTER included with the Polyplacophora in his Gastropoda Isopleura. The systematic position of the bellerophontids, with their bilaterally symmetrical, coiled shells, has been much discussed. J. B. KNIGHT (55, p. 48-55) has reviewed the relevant evidence and concluded that they were forms which were affected by torsion and were true prosobranch gastropods. If they underwent torsion in early ontogeny, an asymmetrical arrangement of their organs must have existed during the course of this episode. Whether perfect symmetry of all soft parts existed on completion of the torsion we have no means of knowing, but the presence of two symmetrically arranged columellar muscle scars can be observed.

All gastropods, with the possible exception of this group, are more or less asymmetrical. The asymmetry is obvious in most forms in which the shell is coiled. In *Patella* and similar genera, the simple conical shell is symmetrical, but asymmetry is displayed by the nervous system and the digestive, excretory, and reproductive organs. In *Fissurella,* although the shell is symmetrical when adult, it is coiled and asymmetrical in an early developmental stage. The pteropods, a group of opisthobranchs modified for a pelagic mode of life, include several genera with bilaterally symmetrical shells, but their digestive, circulatory, and reproductive organs lack symmetry.

Description of the foot as "solelike and adapted for creeping" needs qualification. It is not strictly applicable even to all benthonic gastropods. In the swimming pelagic groups (pteropods and heteropods), the foot is much modified for purposes of propulsion. In some species of the parasitic genus *Stilifer* but not all, the foot is much reduced. It has completely atrophied in the endoparasitic family Entoconchidae. A radula is present in the great majority of gastropods but is obsolete in parasitic families, such as the Eulimidae and Pyramidellidae. Families in which tentacles are absent from the head include the Gadiniidae and Siphonariidae, while eyes are absent in most Cocculinacea, a deep-sea group.

The absence of regular internal septa pierced by a siphuncle distinguishes gastropod shells from those of most Cephalopoda, although irregular septa may sometimes seal off the earliest-formed parts of the shell when the viscera move forward to some extent as it grows.

## BIOLOGY

### HABITATS AND FOOD

Gastropods inhabit the sea, fresh water, and land. Most marine forms are benthonic, but some are pelagic, and many benthonic species have pelagic larvae. The benthonic forms live on most types of sea bottom, some creeping on solid rock, others living among seaweed, others sheltering beneath stones, and others burrowing into sediment. Some species live near or even above high-water mark and some may occur at very great depths, but the great majority live in comparatively shallow water. Species dredged from the deepest bottoms include representatives of families such as the Trochidae, Volutidae, and Cassididae, which are common in much shallower seas. One family represented by living forms found only at great depths is the Pleurotomariidae; it is, however, abundantly represented in shallow-water faunas of past eras. In certain cases individual species have a wide depth range. *Natica groenlandica* MØLLER, for example, has been dredged from depths ranging from 2 to 1,290 fathoms. Some marine species, belonging to such genera as *Cerithium* and *Littorina,* can tolerate brackish-water conditions and exist in estuaries, as can also some representatives of typically fresh-water genera, such as *Theodoxus, Melanopsis,* and many Thiaridae. *Hydrobia jenkinsi* SMITH has forsaken brackish water and established itself in fresh water in England within historic times.

Pelagic gastropods are of two types, active swimmers and passive drifters. The pteropods and heteropods are of the first type, while to the second belong *Janthina,* which suspends itself from a raftlike structure or float, to the underside of which its eggs are attached, and *Litiopa,* which lives attached to floating seaweed.

Most gastropods obtain their food direct by means of the mouth and radula, but in a few this mode of feeding is replaced or supplemented by ciliary feeding. Land and fresh-water gastropods are in the main herbivorous, although on occasion slugs and snails will devour animal matter. Of the marine macrophagous forms, some are herbivorous, browsing on seaweed and lichens, and some carnivorous. On the whole, the carnivorous forms are those provided with a long eversible proboscis. Such genera as *Nucella* and *Natica* perforate the shells of other mollusks, particularly pelecypods, in most cases seemingly by the rasping action of the radula, but in the case of *Natica* with the aid also of a chemical secretion; they then extract the soft contents. Parasitic gastropods include species of *Eulima,* which suck the juice of their holothurian or other host by means of a long proboscis. Some Pyramidellidae are parasitic on pelecypods and some on other invertebrates. The living patelliform genus *Thyca* is an ectoparasite, which throughout adult life lives attached to the body of echinoderms. An interesting example of dependence on another organism, although not strictly describable as parasitism or symbiosis, is that of the Paleozoic genus *Platyceras,* which is sometimes found on the calyx of a crinoid in the neighborhood of the anus, suggesting that it derived nourishment from the feces of the crinoid. Comparable among living gastropods is *Hipponyx,* which associates with *Turbo* and other mollusks and feeds on their feces.

A few gastropods are deposit-feeders. Thus *Aporrhais* uses an extensile proboscis to collect detritus of vegetable origin from the muddy sediment in which it lives. Ciliary feeders, which include some Vermetidae, Siliquariidae, Turritellidae, Calyptraeidae, Capulidae, and Struthiolariidae, feed on finely sifted bottom deposits, which are drawn into the mantle cavity with the inhalant current. The food is collected, consolidated with mucus, and conveyed to the mouth by a variety of processes. A process of ciliary feeding, by which the normal means of feeding can be supplemented, has been demonstrated in a fresh-water snail belonging to the genus *Viviparus.* Details of the food of many gastropods are assembled by GRAHAM (45).

## DURATION OF LIFE

The proportion of gastropods that die from old age is probably very small. The majority either become prey to other organisms or perish owing to some external cause such as change in salinity or a falling off in food supply. Some gastropods, particularly among the opisthobranchs and pulmonates, die from exhaustion induced by egg laying. PELSENEER (85, p. 617) and COMFORT (19) have assembled data on the potential duration of life in various species. Some gastropods, especially opisthobranchs and pulmonates, but including certain of the smaller prosobranchs, live only for one year or less. The majority have a longer span of life. Many common land snails live from 5 to 7 years, the maximum recorded age in this group being 9 years (*Helix hortensis* MÜLLER). The maximum recorded longevity of a fresh-water snail, according to data given by PELSENEER, is 10 years, attained by *Viviparus viviparus* (LINNÉ), the usual period for such gastropods being about 5 years. The maximum recorded age for marine prosobranchs is also 10 years, as recorded of *Littorina littorea* (Linné), *Trochus niloticus* Linné, and probably also *Buccinum undatum* Linné, whereas the average span of life in this group seems to be 3 to 5 years. Data on the great majority of species are still wanting.

## MORPHOLOGY OF SOFT PARTS

### PARTS PROTRUSIBLE FROM SHELL

In a gastropod with a coiled shell, part **(visceral mass or visceral hump)** remains permanently within the shell, while part is protruded when the creature is active, but in most forms can be withdrawn when necessary into its shelter. The main and often only protrusible part consists of the single sluglike mass **(head-foot mass** or **cephalopedal mass)** formed by the head and foot (Fig. 51). When this withdraws into the shell the head precedes the foot and if an operculum, borne on the rear dorsal surface of the foot, is present, this completely or partly closes the aperture of the shell.[1] An operculum is present in most prosobranchs, but, with certain exceptions, is absent in pulmonates (which include most land snails) and in opisthobranchs; exceptions are the pulmonate family Amphibolidae and the opisthobranch families Acteonidae and Pyramidellidae. Two tubelike organs, to be discussed later, can also be protruded from the shell in forms in which they are developed. These are the inhalant siphon and the male genital organ **(penis)**. In some gastropods, such as the Cypraeidae and Naticidae, the mantle may extend far beyond the apertural margin, covering the external surface of the shell to a varying extent. Extensions of the foot may also partly cover the shell.

The foot is typically a broad, tough, muscular structure with a flat base applied to the surface over which the mollusk creeps, but in some genera it is greatly modified. In many forms it contains one or more glands. In land snails the **mucous gland** runs longitudinally along the front part of the foot and opens just below the animal's mouth, depositing slime to facilitate its progress over a dry surface. In some marine snails, such as the Cypraeidae, the pedal gland forms a secretion for a similar purpose of lubrication. In many forms the secretion from a pedal gland solidifies to form a thread which is attached to some object and enables the animal to lower itself slowly or ascend again in water or in the air. Species capable of thread-spinning include freshwater snails such as *Lymnaea* and *Planorbis*, many slugs, small marine forms such as *Skeneopsis, Omalogyra, Rissoella, Litiopa,* and *Balcis,* and certain species of prosobranchs belonging to *Cerithidea, Littorina,* and other genera that have half forsaken a marine life and can suspend themselves from mangrove bushes and similar objects. In most Vermetidae long sticky mucous threads from a pedal gland are used to collect plankton for food; *Vermetus gigas* and *V. triqueter* are among the species in which they are best developed. In the female of some advanced Caenogastropoda, such as *Buccinum,* a ventral pedal gland molds and hardens the egg capsules, the material for which has been secreted around the egg mass in the genital ducts. From the oviduct the eggs pass to this gland along a temporary groove along the right side of the foot.

In some gastropods the anterior and posterior parts of the foot, termed respectively the **propodium** and **metapodium** (Fig. 52), are clearly separated by transverse grooves; in some forms it is convenient to term the median region the **mesopodium.** The metapodium bears the operculum, if one is present. In certain genera, such as *Natica, Sinum,* and *Oliva,* which crawl through wet sand, a well-developed, plowlike propodium pushes the sand away to both sides in front of the animal. In many living Archaeogastropoda the foot has a projecting upper border termed the **epipodium;** in some genera, such as *Haliotis* and many Trochidae, this has tentacle-like protrusions. In certain genera of the Thaididae and Muricidae a small **pedal sucker** on the anteroventral part of the foot assists the animal to grip its prey while boring into it. If the foot is examined when the animal is creeping, a series of waves appears to pass along it, the waves being produced by contraction of muscle fibers perpendicular to the creeping surface. Owing to peculiarities in their mode of progression, gastropods of some genera leave very distinctive tracks behind them.

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[1] In some operculate gastropods, however, the operculum is reduced to a vestige which may have secondary functions.

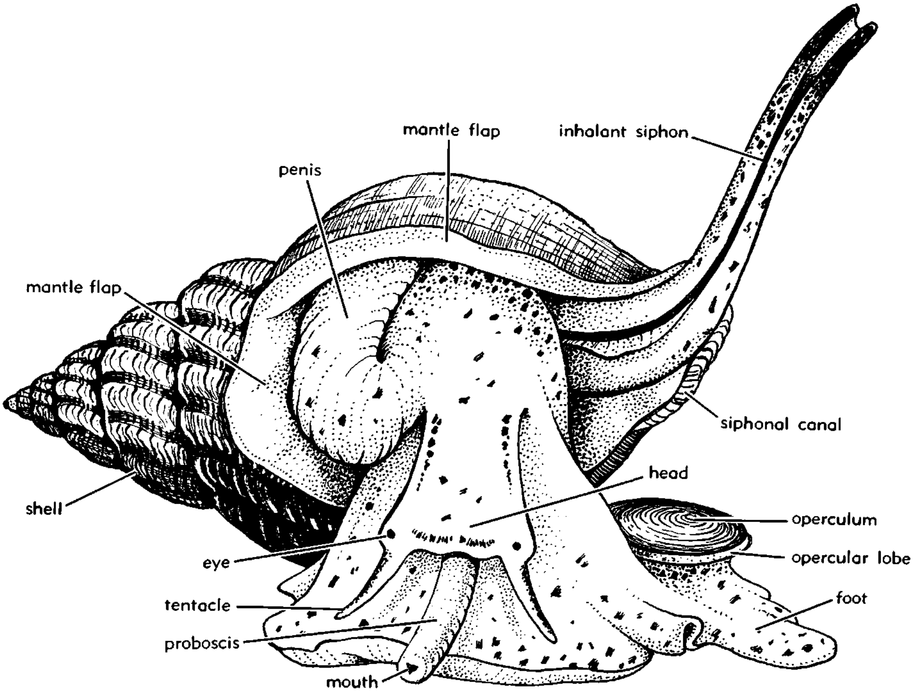


FIG. 51. *Buccinum undatum* LINNÉ (♂) (115n). Shell with protruded head-foot mass; anterior view, ×1.25.

In some opisthobranchs the lateral parts of the foot (termed **parapodia**) form broad extensions which, together with the mantle, tend to fold over and cover the shell (Fig. 88). In the pteropods, pelagic forms now classed with the opisthobranchs, the parapodia are finlike structures, and the animal swims with their aid. In the heteropods, pelagic gastropods classified as prosobranchs, the foot is also much modified, forming a fan-shaped, finlike structure in the family Pterotrachaeidae.

The head-foot mass is drawn into the shell by means of the **columellar** (or **retractor) muscle** or **muscles,** the only attachment of the soft parts to the shell. The muscle is attached most commonly to the columella some distance back from the aperture (Fig. 53) and passes through the foot to a place of insertion beneath the operculum. In the genus *Haliotis,* with its ear-shaped shell, there are two retractor muscles attached to the interior of the shell; one is very large, cylindrical in shape, and almost median in position, whereas the other is very small and situated near the left-hand margin. In *Scissurella* there are two attachment muscles that differ in size only slightly. The Neritacea and certain Caenogastropods also have two unequal muscles. In the bellerophontids of the Paleozoic two equal muscles existed. In patelliform shells there is a symmetrical, horseshoe-shaped muscle, with an anterior gap.

The head of the gastropod (Fig. 51) bears the animal's most obvious sensory organs. Almost all forms, except certain opisthobranchs, have at least one pair of **cephalic tentacles,** which form hornlike projections pointing obliquely forward. Most gastropods have two eyes which, when (as in most prosobranchs) there is a single pair of tentacles, are situated either on the head at or near the base of the tentacles, or some distance up the latter, alhough not at their tip. In the Strombidae the eyes are very large and the tentacles are replaced by

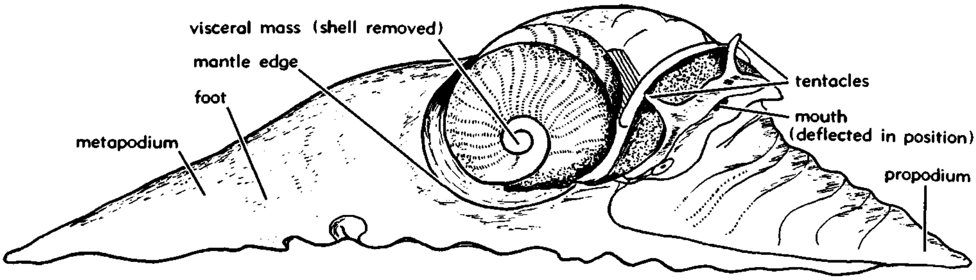


FIG. 52. *Sinum laevigatum* (LAMARCK), showing plowlike propodium and metapodium (a small vestigial operculum is not seen) (132). In this genus the soft parts cannot be fully withdrawn into the shell (not shown in the illustration), ×1.25.

grotesquely enlarged optic peduncles. In the land pulmonates, however, there are two pairs of tentacles, and the eyes are placed at the top of the longer and upper pair, which are capable of retraction by invagination. Two pairs are also present in some opisthobranchs. Apart from their association with the eyes, the tentacles act as tactile organs, while in the case of the pulmonates and opisthobranchs it is believed that the posterior of two pairs are rhinophores (i.e., that they bear olfactory organs). In *Acteon, Scaphander,* and other burrowing opisthobranchs the tentacles form lobes and are used for pushing sand away as the animal moves.

In many gastropods the mouth is a simple opening in the head proper, but in some genera it is placed at the end of a protrusion from the front of the head, ranging from a blunt snout to a long retractible (eversible) **proboscis** (Fig. 54). In some forms, such as *Tonna* and *Mitra,* the proboscis is longer than the rest of the head-foot mass.

## MANTLE AND MANTLE CAVITY

The part of the visceral mass termed the **digestive gland** (Fig. 53) extends almost to the apex of a coiled shell, and has a thin, colorless integument. The front portion of the visceral mass, occupying part, commonly most, of the last whorl of the shell, is covered by a thin fleshy hood, known as the **mantle flap,** which is attached at its rear end to the visceral mass. Under the mantle flap, and least developed on the side near the columella, is a space known as the **mantle cavity** (or **pallial cavity**), which plays an important part in the life of the animal. In many forms the mantle extends forward only as far as the aperture when the animal is extruded from the shell, its margin, which in some forms is a thickened collar, being known as the **mantle edge.** The whole outer surface of the mantle (including that part forming the integument of the visceral mass) contains epithelial cells capable of secreting calcareous shell, but secretion is most active at the mantle edge while forward growth of the shell continues. In gastropods in which the process has been studied, it also has been shown that the periostracum is secreted by the cells along a groove of the mantle edge **(supramarginal groove).** The surmise of some authors that this is the function of a glandular mass found near the mantle edge in *Buccinum* and some other forms is thus probably incorrect. In some groups the mantle flap, as already seen, extends well beyond the aperture, covering part of the outer surface of the shell and depositing a smooth shelly

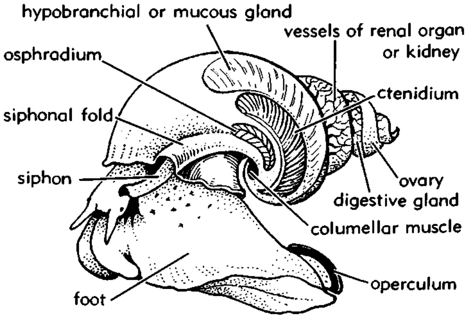


FIG. 53. *Buccinum undatum* LINNÉ (♀), with head-foot mass protruded but with shell treated as transparent to show positions of various organs, ×0.5 (115n).

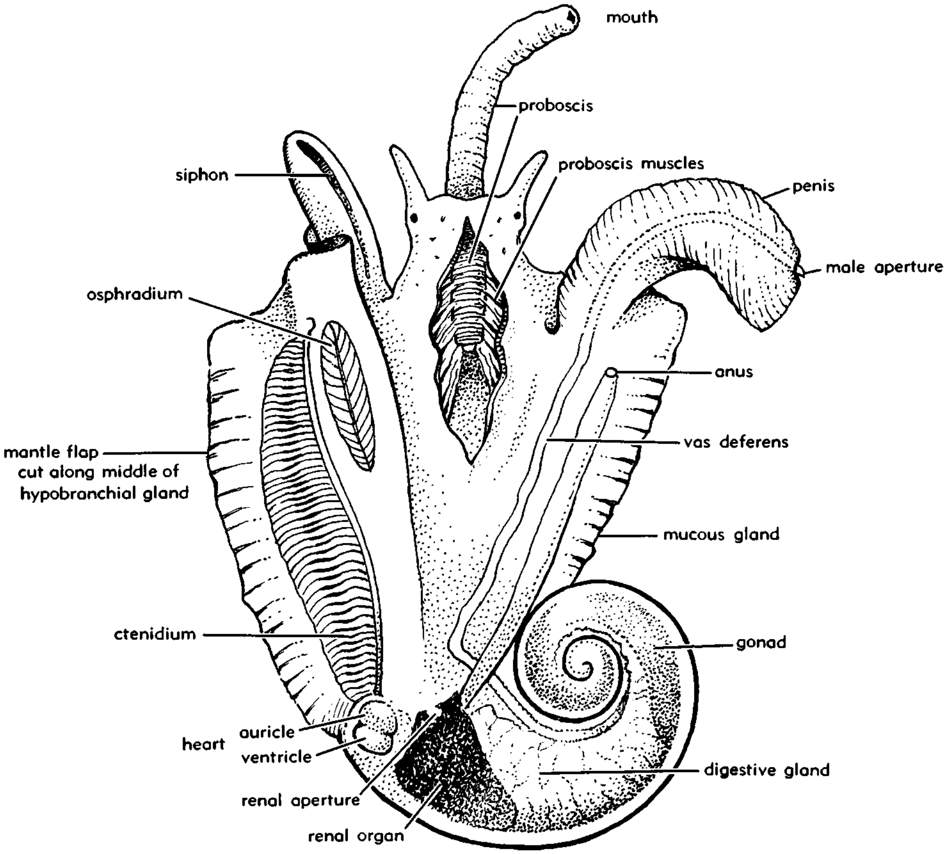


FIG. 54. *Buccinum undatum* LINNÉ (♂) (115n). The organs in the mantle cavity have been exposed by making a median longitudinal incision along the mantle flap and folding the two sides of the latter back; the proximal end of the proboscis and its muscles have been revealed by a further incision, ×1.25.

layer upon it. At sexual maturity it may develop one or more very narrow, shell-secreting protrusions, which give rise to digitations of the outer lip, as in the Aporrhaidae. In *Oliva* there is a long, cordlike appendage of the mantle which coils round the shell, fitting into a groove along the suture. Small tentacles project from the mantle edge in some genera. In *Turritella* and *Vermicularia* a series of pinnately branched tentacles, directed into the mantle cavity from the mantle edge, acts as a screen that prevents detritus from being carried into the cavity with the inhalant current (Fig. 55). In *Valvata* a ciliated pallial tentacle assists in creating a respiratory current.

The most important protrusion of the mantle in many species, however, is a narrow fold known as the **inhalant siphon** (usually merely **siphon**), a flexuous, tubelike organ along which the inhalant current of water, containing oxygen necessary for respiration, is drawn into the mantle cavity. The siphon is, on the whole, best developed in carnivorous forms with a long proboscis, and it may be extruded from a notch in the apertural margin or else extend along and be extruded from a narrow extension of the aperture, known as the **siphonal canal.** There are forms, such as *Aporrhais,* in which the siphon is represented only by a very short extension of the mantle, and many others in which no siphon is present, the inhalant current being drawn directly into the mantle cavity. The siphon appears also to have sensory functions in some species. In *Trivia,* a carnivorous genus feeding

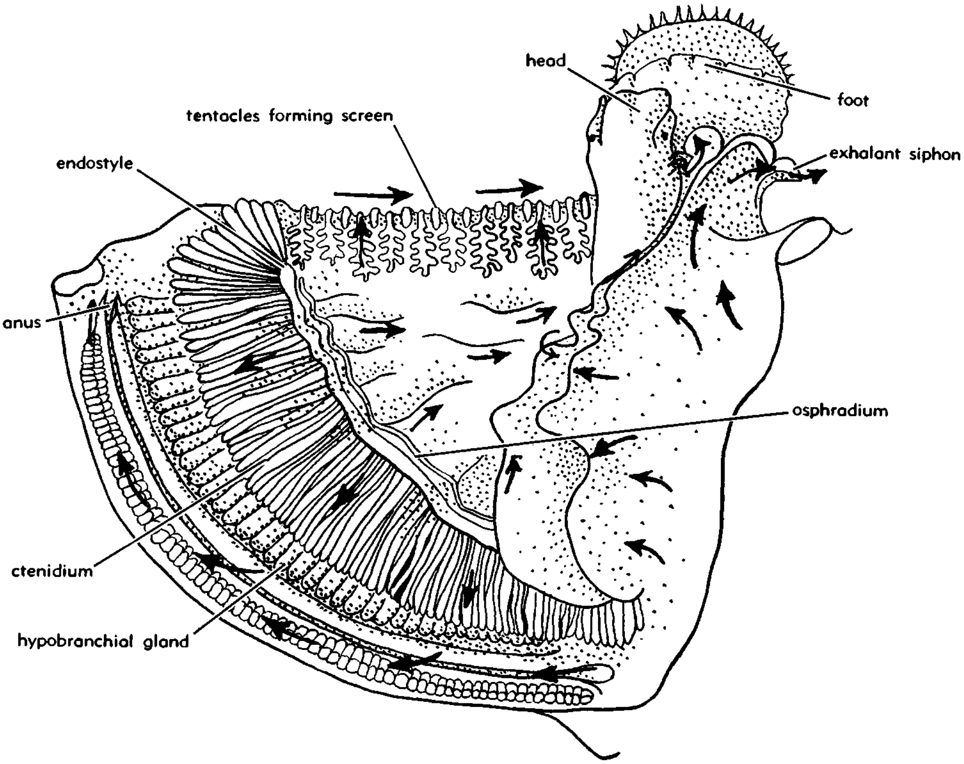


FIG. 55. *Turritella communis* RISSO (42). The organs in the mantle cavity have been exposed by making a longitudinal incision along the right side of the mantle flap and folding the latter back to the left; arrows indicate the course of ciliary currents, ×10.

on zooids, it has been observed to feel round for the mouth of the prey, as if searching for the best spot for the proboscis to start its activities. It has also been suggested that the siphon bears chemoreceptors, organs which test the chemical contents of the water drawn through it.

A short **exhalant siphon,** forming an outlet for the exhalant current, is present in various genera belonging to unrelated groups. In the opisthobranch *Acteon* it is a large mammiform protrusion situated near the mantle edge by the right-hand margin of the foot, and occupies the adapical corner of the aperture when the animal is fully extruded from the shell. In *Turritella* an exhalant siphon is formed by a fold of the skin of the head-foot mass. In *Viviparus* such a fold combines with the adjacent part of the mantle to form an exhalant siphon. In *Fissurella* a short exhalant siphon projects through the apical orifice, and in *Emarginula* through the marginal slit.

The mantle cavity (Figs. 54-56) is primarily a respiratory chamber. Within it, in the majority of gastropods, lie the **ctenidium, osphradium,** and the **hypobranchial** (or **mucous) gland** (these structures are paired in the Zygobranchia, referred to below). Into it are discharged the excreta from the anus and renal opening, while it also contains the female genital opening and houses the male genital organ when this is not protruded.

The inhalant current (Figs. 56*A*), created by the movement of cilia borne by filaments of the ctenidium, enters the mantle cavity, either directly or through a siphon, on the left-hand side of the head-foot mass when there is a single ctenidium. It impinges first upon the osphradium. This organ, situated low on the left side of the mantle flap, is essentially a specialized part of the inner epithelium of the latter. Its size and form vary considerably. It is most complex in the advanced Caenogastropoda,

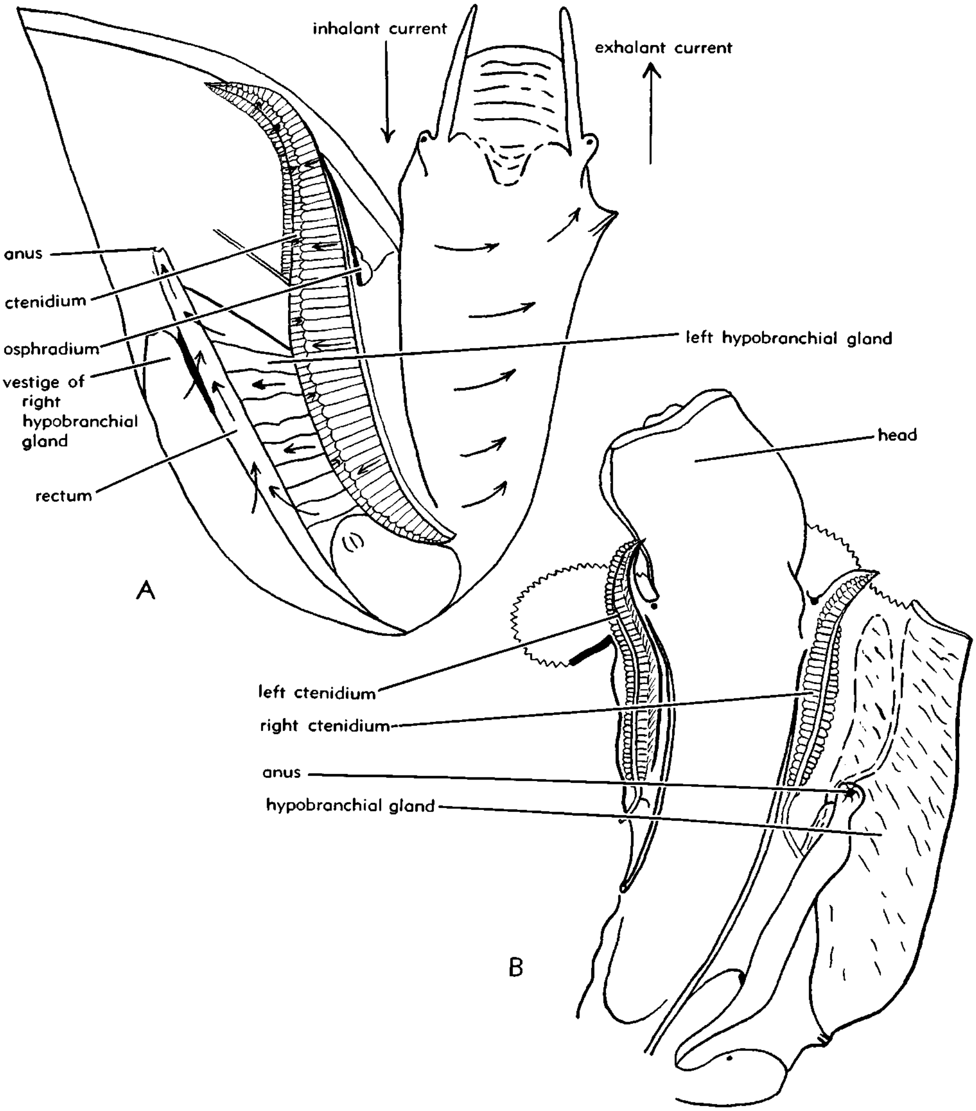


FIG. 56. Mantle cavities of *(A) Calliostoma zizyphinum* (LINNÉ), ×5; *(B) Mikadotrochus beyrichi* (HILGER), ×0.85 (111). As in Figs. 54, 55, the pallial organs have been exposed by appropriate longitudinal incisions along the mantle flap; arrows in *(A)* indicate the course of ciliary currents and in *(B)* attention may be called to the presence of paired ctenidia.

and in *Buccinum,* for example, is a conspicuous plumelike structure superficially resembling a bipectinate gill. In many genera it is a long, narrow, longitudinal ridge. An osphradium has its own nerve, connected with one of the parietal ganglia, and its function is generally considered to be to test the amount of fine sediment in the inhalant current, although, since it is most complex in carnivorous forms, the suggestion has also been made that it may serve to detect live prey.

In most prosobranchs there is a single respiratory organ, the ctenidium, which lies entirely or for the greater part on the left-hand side of the mantle cavity, usually within the last half-whorl of the shell; it is **monopectinate,** that is, its flexible leaflets are arranged on one side only of a main axis. The direction of the latter is usually more or less longitudinal, but is oblique or even transverse in some forms. Two ctenidia, left and right, each accompanied by an osphradium, are, however, present in the most primitive living suborder of the prosobranchs, the Pleurotomariina, the Recent species of which belong to the families Pleurotomariidae (Fig. 56*B*), Haliotidae, Scissurellidae, and Fissurellidae. With one exception (the right-hand one in the Scissurellidae), moreover, paired ctenidia are **bipectinate,** that is, they have two rows of leaflets diverging from a median axis. In the Fissurellidae, in which the shell is patelliform and symmetrical, the two ctenidia are equal and symmetrically disposed. In the conispiral Pleurotomariidae and in the Scissurellidae the left-hand ctenidium is slightly the larger. In the Haliotidae, which are depressed and auriform, the inequality of the ctenidia is more marked, the left-hand one being again the larger. The single ctenidium present in species of the Trochacea, Neritacea, and Turbinidae and in the genus *Valvata* is also bipectinate. In all other forms a single ctenidium is monopectinate. In *Valvata* the ctenidium projects from the mantle cavity and shell.

The ctenidium, upon which the inhalant current impinges after testing by the osphradium, serves to aerate the animal's blood. The deoxygenated water then passes (in most prosobranchs) along the right-hand side of the mantle cavity, to form the exhalant current, which is discharged to the right of the animal's head.

The hypobranchial gland, which is a conspicuous organ in many prosobranchs, occupies the middle part of the roof of the mantle cavity, lying on the right-hand side of the ctenidium. It consists of deep transverse folds of the inner wall of the mantle, containing gland cells that produce a very adhesive secretion, by which fine sediment brought into the mantle cavity with the ininhalant current is consolidated ready for rejection. Another mucus-secreting organ, concerned with the consolidation of phytoplankton in ciliary feeders such as the Calyptraeidae and some species of *Turritella,* is the **endostyle,** which extends on the wall of the mantle cavity along the entire base of the ctenidium, that is, on the opposite side of the latter to the hypobranchial gland.

Yonge (112) showed that in most prosobranchs three distinct sets of ciliary currents are concerned with the disposal of suspended matter in the inhalant current. The largest particles, which tend to settle at once, are dealt with by cilia on the margin of the inhalant region and ejected by way of the inhalant opening. Medium-sized particles, which settle farther within the mantle cavity, are carried by cilia on its floor to its right-hand side, where they are caught up in the exhalant current. The lightest particles are carried by a current produced by frontal cilia on the ctenidium across the roof of the mantle cavity to the hypobranchial gland, where they become entangled in mucus and consolidated; they are then carried to the right-hand side to be removed by the exhalant current. The exhalant current also serves to convey away the excreta discharged into the mantle cavity from the anus and the renal aperture. The former is situated near the front of the cavity on the right-hand side, while the renal aperture is a pore at the rear of the cavity.

In the Pleurotomariina, which, as already noted, have two ctenidia, the courses taken by the respiratory currents differ somewhat from those described above. Thus, the exhalant current, instead of emerging to the right-hand side of the animal's head, passes out either through a slit in the apertural margin situated at or near the periphery of the shell *(Pleurotomaria, Emarginula),* or through one or more orifices (or tremata) in the shell wall at its periphery *(Haliotis),* or, in the case of the patelliform *Fissurella,* through an orifice at the apex of the shell. In these forms the anus lies well back from the aperture, in such a position that excreta are also discharged through the slit or orifices. In this way fouling of the inhalant current is avoided. The respiratory currents in these genera are described by Yonge (112). The inferred paths of the currents in the bellerophontid genus *Knightites* are shown in Figure 57. Although primitive in some respects, the Trochacea and Neritacea possess the mechanism, normal in the higher prosobranchs, for discharge of the exhalant current to the right-hand side of the animal's head.

An entirely different type of respiratory apparatus is found in the family Patellidae,

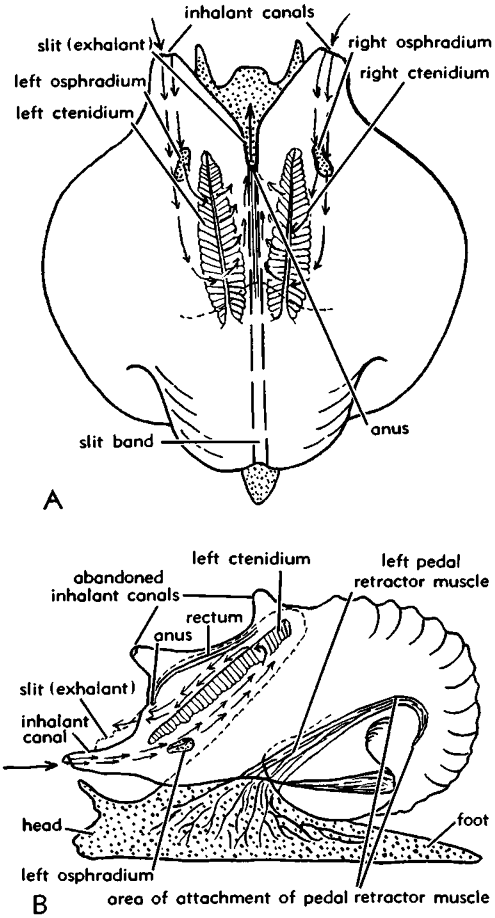


FIG. 57. *Knightites multicornutus* MOORE, restoration of pallial organs, arrows indicating the inferred courses of ciliary respiratory currents, *(A)* dorsal and *(B)* left lateral views, ×2.5 (55).

referred to the suborder Patellina of the Prosobranchia. The whole mantle edge, which adjoins the margin of the conical shell, is here fringed with a circlet of gill-lamellae. These are of secondary origin and not homologous with the ctenidia of normal prosobranchs. Two small osphradia, situated on the neck of the animal, probably indicate the presence of paired ctenidia in its ancestors. In *Patella* itself gentle inhalant and exhalant currents cross the mantle margin all around its circumference, and solid matter is ejected by muscle contractions at the middle of the right-hand side of the margin. The mechanism differs somewhat in other genera of the family. In the Acmaeidae, patelliform gastropods also included in the Patellina, a true ctenidium is developed on the left-hand side and secondary gill-lamellae are absent. In some of the smaller prosobranchs a tendency toward simplification of the organs of respiration appears. Thus, in the marine genera *Omalogyra* and *Rissoella* both osphradium and ctenidium, and in *Caecum* the ctenidium only, have been lost, respiration taking place through the epithelium of the mantle itself. The exhalant current is created by strips of ciliated epithelium and the inhalant current enters to compensate for the outflowing water. In the land prosobranch families Helicinidae and Pomatiasidae the ctenidium is absent or reduced to a few folds of epithelium, the mantle itself acting as the main respiratory organ. In the amphibious prosobranch family Ampullariidae the mantle cavity is divided by an incomplete fleshy partition into two compartments, the left-hand one containing a normally functioning ctenidium and the right serving as a lung for air-breathing. On the left-hand side is a long siphon which can be extended so as to reach above the surface of the water when the animal is immersed and admit air to the pulmonary chamber. In *Siphonaria,* now classified as a pulmonate, there is also a ctenidium as well as a pulmonary chamber.

These forms are intermediate between normal gill-breathing gastropods and the air-breathing pulmonates proper, and show how gastropods may have succeeded in adapting themselves to a terrestrial habitat. In the great majority of pulmonates a ctenidium is absent and the mantle cavity is no longer freely open to the exterior, but is converted into a respiratory chamber (or **pulmonary sac**) by fusion of the mantle edge with the integument of the head-foot mass. The chamber can be enlarged by the contraction of muscles on its floor, and air is admitted by a narrow aperture (**pneumostome** or **pulmonary orifice**) on the right-hand side. The roof of the chamber is lined with a network of blood vessels and it is here that the blood is oxygenated. Many aquatic pulmonates rise periodically to the surface to admit air into the pulmonary sac, but it is probable that such forms are also capable of respiration through their skin. Secondary or adaptive branchiae are, however, present in some aquatic pulmonates. They consist of a simple supra-anal lobe in the Ellobiidae, but are intricately folded structures outside the mantle cavity in the Planorbidae and Ancylidae.

Among the opisthobranchs a ctenidium is present in the tectibranchs, lying on the right-hand side and partly projecting from the mantle cavity. The organ is absent in the Pyramidellidae, as also in some other small shell-bearing groups, circulation in and out of the mantle cavity being effected by an exhalant current produced by ridges of ciliated epithelium near the hypobranchial gland. Some nudibranchs have no special breathing organs and respire through the integument, but the majority have developed secondary leaflike gills carried on the back in an exposed position. Few pteropods have a ctenidium of the normal type, but in some an accessory posterior gill is developed. Others respire only through the integument. In the opisthobranch genera *Acteon, Scaphander,* and *Akera,* there is a narrow cordlike extension of the mantle cavity, termed the **pallial caecum,** which is wound around the whorls of the visceral hump on the interior of the shell almost to the tip of the spire. It is thought to be part of a highly developed pallial cleansing apparatus.

## CIRCULATORY SYSTEM

In most gastropods the blood is colorless or else faintly blue, owing to presence of the oxygen-carrier haemocyanin. The heart lies within a chamber known as the **pericardial cavity,** situated to the right of the median line in the majority of forms, between the kidney and the digestive gland, and close to the ctenidium. It consists of a ventricle and either one or two auricles. There are two auricles in all gastropods included in the Archaeogastropoda except the Patellina and the Helicinidae; that is, in all forms with bipectinate ctenidia. In other gastropods only the left auricle is present. The auricle adjoins the ctenidium if this is present, and receives from it the efferent branchial vessel (Fig. 58); in the pulmonates, such as *Helix,* it faces the network of blood vessels in the roof of the mantle cavity, and receives the pulmonary vein to which the vessels converge. The ctenidium lies in front of the heart in the Prosobranchia and behind it in most of those Opisthobranchia in which it is developed, as the names for these subclasses imply. In the pulmonates the respiratory chamber is in front of the heart.

Details of the circulatory system differ in various gastropods. The ventricle gives off

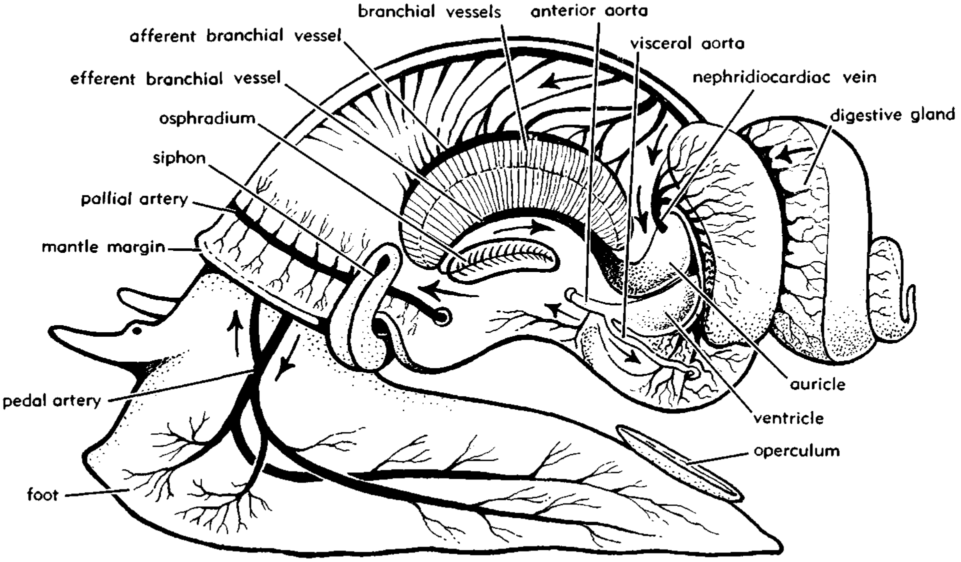


FIG. 58. *Buccinum undatum* LINNÉ, diagrammatic representation of respiratory system, slightly enlarged (115n).

the main aorta, which then subdivides to supply the arterial systems of various parts of the body. In some genera *(Haliotis, Fissurella)* it also gives off directly an artery supplying the mantle. The arteries, which in some forms cannot be traced far from the pericardium, lead to irregular spaces or **lacunae** in the connective tissue of all parts of the body, and the blood from these, when de-oxygenated, collects in other blood spaces, the **venous sinuses.** From these it returns by veins or a series of sinuses to the auricle by way either of the kidney and ctenidium, of the kidney alone, or of the ctenidium alone.

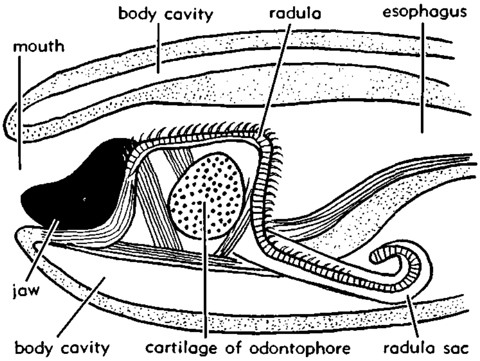


FIG. 59. *Charonia opis* (RÖDING), diagrammatic longitudinal (but not quite median) vertical section of buccal cavity, the buccal mass or odontophore forming the median elevation supporting the radula, much enlarged (129).

## DIGESTIVE AND EXCRETORY ORGANS

The mouth of the gastropod lies at the end of the proboscis or of the snout, if either is present, or else on the lower part of the head proper, and it opens into the **pharynx** or **buccal cavity** (Fig. 59). Thickenings around the aperture form **lips.** Within the pharynx are characteristic structures formed of horny material, for the rasping and trituration of food. These are the jaw or jaws (absent in carnivorous genera, in many opisthobranchs, and in the heteropods), and the radula. Most land pulmonates, such as *Helix,* have a single jaw, often arched, placed in the roof of the mouth. Most prosobranchs except carnivorous ones have two jaws, placed dorsolaterally just within the mouth, and these may have an elaborate sculpture of small ridges resembling the teeth of a file. Just beyond the jaws, its front part working against them, is the **radula,** a ribbon-like band, bearing transverse rows of minute teeth, which is borne longutudinally by a bulging, tonguelike object (the **odontophore** or **buccal mass**) that projects into the buccal cavity from its posterior end, is composed partly of cartilage and partly of muscle, and is covered by a layer of cuticular material. The radula is produced continuously in the **radular sac** at its rear end, and works forward as its frontal part, on the projecting surface of the odontophore, is worn away. Its relative length and breadth vary in different genera. In *Littorina* it is several times the length of the animal, in *Buccinum* about 30 mm. long, and in other genera relatively much shorter. The structure of the radula differs considerably in various groups of the Gastropoda and is an important aid in classification, unfortunately not available to the paleontologist. The different types of radula are described subsequently. **Salivary ducts** also open into the pharynx near the radular sac. In some carnivorous genera their secretion is acid, and this may help the radula in piercing the shell of their prey.

From the pharynx the masticated food passes in to the **esophagus** (Fig. 60), a tube which in many genera is the longest section of the alimentary canal. The salivary ducts, already mentioned, originate in one or two pairs of **salivary glands** lying to the side of the pharynx or of the esophagus, and in the latter case the ducts run for part of the way along the sides of the esophagus. In many pulmonates and opisthobranchs and a few prosobranchs there is a widened part of the esophagus termed the **crop,** in which food can be stored temporarily before it is passed on to the stomach for digestion. In carnivorous forms, such as *Buccinum,* various glands, such as the one known as "Leiblein's gland," open into the esophagus and give rise to secretions aiding digestion. In many Archaeogastropoda the middle part of the esophagus bears lateral glandular pouches in which digestive enzymes are secreted. In many tectibranchs (but not *Acteon*) the esophagus has two dilated portions (anterior and posterior crops), separated by a **triturating gizzard** in which are

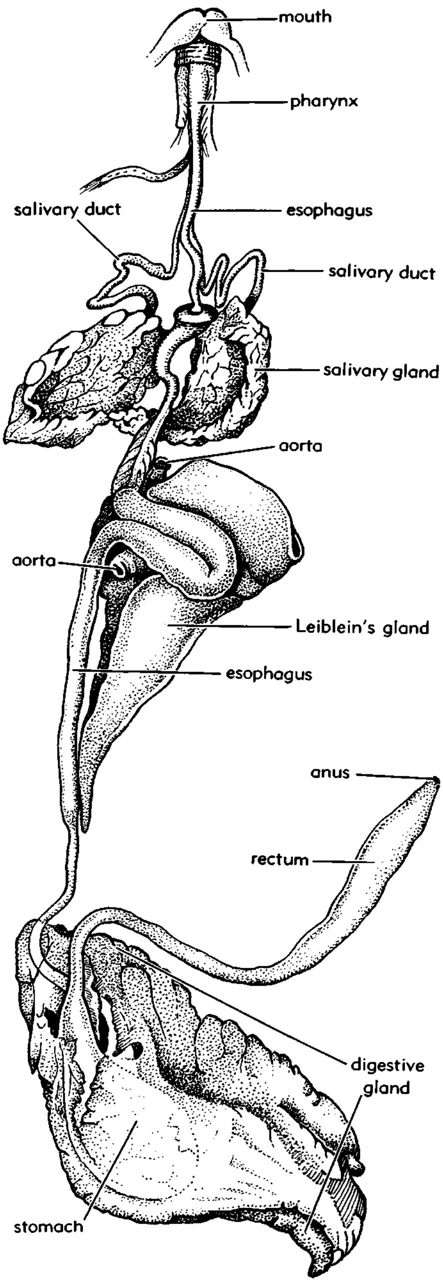


FIG. 60. *Concholepas peruviana* LAMARCK, with dissected alimentary canal and associated organs (119).

three calcareous plates. By the action of these the food is thoroughly triturated and masticated before passing to the stomach.

The **stomach,** which may be merely a dilation of the alimentary canal, but more frequently is a well-marked bag, lies at the posterior end of the esophagus. Its position is more or less at the base of the visceral hump, and it abuts against or is even more or less surrounded by the brownish **digestive gland,** forming most of the coiled hump in spiral gastropods. Ducts (hepatic), usually two in number, open into the stomach from the digestive gland. The latter consists essentially of repeated ramifications of the ducts, ending ultimately in blind caeca. It is primarily an organ of intercellular digestion, but in many carnivorous forms it produces an enzyme-bearing fluid that aids digestion of food in the stomach. In tectibranchs the digestive gland is also an organ of excretion, performing a function similar to that of the kidney in taking up waste matter from the blood. This matter is compacted and leaves the body with the feces.

The two main openings of the stomach are those of the intestine and esophagus. As a result of torsion the former is anterior and the latter posterior in the more primitively organized gastropods (such as *Diodora* and *Scutum*). In more advanced forms, the position of the esophageal opening becomes nearer to that of the intestine, until in the pulmonates and tectibranch opisthobranchs the two are in close proximity. At the posterior end of the stomach, except in more advanced gastropods (in a few of which it is vestigial) is the **style sac.** In Archaeogastropoda this is a gradually contracted part of the stomach leading directly to the intestine. In such forms it contains a rod of loosely compacted feces (the protostyle of MORTON), which, by rotation, stirs up the contents of the stomach to assist their complete digestion. This rod is continuous, on the one hand, with fecal matter in the intestine, and, on the other hand, with the string of food from the esophagus. In some Caenogastropoda, belonging mainly to the superfamilies Rissoacea, Cerithiacea, Calyptraeacea, and Strombacea, and in one group of pteropods, the protostyle is replaced by the **crystalline style,** a cylindrical hyaline rod, which, besides functioning mechanically in the manner described, contains an enzyme which further aids digestion. Gastropods in which a crystalline style is present are all microphagous herbivores, which feed in such a manner that there is an almost continuous stream of food along the alimentary canal. The structure is thus absent in carnivorous forms and in herbivores that feed only at intervals. In some gastropods, including those with a crystalline style, the wall of the stomach bears a cuticular structure **(gastric shield)** against which the style rotates. A further appendage to the stomach, situated at the opposite end to the style sac, is the **posterior caecum,** developed in most Archaeogastropoda (but not in Fissurellidae) and in a few opisthobranchs and pulmonates, but not in higher prosobranchs. It is commonly more or less coiled and its function is to assist in the sorting of the contents of the stomach by means of the cilia with which it is lined.

From the stomach the intestine takes an anterodorsal course, passing under the kidney and enlarging to some extent to form the **rectum,** which runs along the right side of the roof of the mantle cavity, to terminate, usually not far from the mantle's edge, in the **anus.** In the Archaeogastropoda, apart from the Patellina and the Helicinidae, the rectum passes through the ventricle of the heart. In some prosobranch and tectibranch genera **anal glands** open into the rectum close to the anus, and are concerned with preparation of the feces. An interesting exception to the general absence of remains or traces of the soft parts in fossil gastropods is Dr. R. CASEY's (13) discovery of the mold of the intestine preserved in a Lower Cretaceous specimen.

The **kidneys** (alternatively termed **renal organs** or **nephridia**) are the main organs for excretion of the waste products of metabolism. Two are present in gastropods in which the heart has two auricles, except those belonging to the Neritacea, that is, in all Archaeogastropoda except the Patellina and the Neritacea. Otherwise, only one is present. When two are present, the left one is much reduced in size and only the right one functions. When a single one is present, however, it appears to be the homologue of the left one in forms in which there are two. The kidney, reddish or dark brown in color, lies just behind the mantle cavity and adjoins both the digestive gland and the pericardial cavity. It communicates with the latter by a narrow ciliated passage (**renopericardial canal**) and with the mantle cavity either through simple apertures or by a duct (**ureter**). It is a sac with a spongy internal structure, due to the presence of numerous intricate folds of the epithelium of its outer wall, which are covered by cells containing uric acid. The venous blood flows through the organ past these structures, which serve to extract waste products from it before it passes to the ctenidia. The excreta from the kidney pass into the mantle cavity. In the Archaeogastropoda (except the Neritacea) the right kidney also serves as a duct for the passage of genital products to the mantle cavity (Fig. 8).

## REPRODUCTIVE ORGANS

In most prosobranch gastropods the sexes are distinct, but there are a few exceptions. Except in most Archaeogastropoda and certain genera of other groups, a male organ (**penis**) or, as the case may be, the series of female genital organs described below, is present, and sexual union precedes fertilization. In both sexes the gonad is embedded in or lies upon the digestive gland. Spermatozoa from the male gonad, or **testis,** collect in the greatly coiled proximal part of the genital duct, which thus acts as a **vesicula seminalis.** They then pass through a shorter, ciliated, part of the genital duct, the **vas deferens,** to the **prostate gland,** which runs along the floor of the mantle cavity on the right-hand side, parallel with the rectum. From the prostate a narrow duct runs along the right side of the neck to the penis, the proximal end of which lies on the head or neck behind the right tentacle; the penis may be an organ of considerable size.

The female genital organs are more complicated in the higher prosobranchs. The duct serving to conduct the ova from the female gonad (**ovary**) is termed the **oviduct.** Its proximal part, in which the ova collect, leads to two successive glandular regions, the **albumen gland** (which produces the albuminous fluid by which the eggs are surrounded) and either a **jelly gland** or a **capsule gland** (producing either the jelly in which masses of eggs are deposited or the material of their capsules). Between the albumen and capsule glands lies the **spermatheca** or **receptaculum seminis,** a lateral pouch in which incoming sperm can be stored until required. From the capsule gland the ova pass through the **vestibule** and **vagina** to the female aperture, which lies close to the anus just within the mantle cavity. Adjoining the distal end of the capsule gland is the **bursa copulatrix** or **uterus,** which receives the male organ during sexual union. Fertilization of the ova takes place at the anterior end of the albumen gland.

In all Archaeogastropoda except the Neritacea, however, the genital products are discharged by both sexes, by way of the kidney, ureter, mantle cavity, and exhalant current, into the sea. Fertilization of the ova, which are usually shed singly, depends on their being encountered by spermatozoa. In such forms the prostate and penis are absent in the male, as are all genital organs that normally lie anterior to the proximal part of the oviduct in the female. In the males of certain other prosobranch genera, such as *Vermetus* and *Magilus,* in which the animal is sessile and sexual union impossible, and in *Turritella,* in which a screen of pinnate tentacles virtually closes the mantle cavity, a penis is also absent and the spermatozoa are discharged into the sea. In these groups they enter the female with the inhalant current and the ova are fertilized internally.

All the Opisthobranchia and Pulmonata, and a few prosobranchs, including *Crepidula, Capulus,* some *Acmaea, Valvata,* and *Trichotropis,* Scalidae and Janthinidae, are hermaphrodite, each individual having both male and female sexual organs and being capable of producing both ova and spermatozoa. Most hermaphrodite gastropods are **protandrous,** that is, in any individual a period of male maturity, during which spermatozoa are produced, precedes one of female maturity. Copulation is usual, free shedding of genital products, as in the Archaeogastropoda, being unknown. Hermaphrodite gastropods may be divided into two groups (not corresponding with accepted taxonomic groups), namely, "Digonopora," in which the male and female orifices are separate, and "Monogonopora," in which they are united. In the first group sexual union may be unilateral (each individual functioning only as a male or as a female in one mating episode), or reciprocal but not simultaneous (each individual acting first as one sex and then as the other in such an episode). In the second group reciprocal sexual union is simultaneous. The spermatozoa may remain stored after union for a period, before fertilization occurs. Parthenogenesis (reproduction without fertilization) occurs in the prosobranchs *Hydrobia jenkinsi* and *Campeloma rufini,* in which species males are unknown. Self-fertilization has been recorded under experimental conditions in a number of pulmonates, both land and aquatic, but whether it takes place in nature to any extent is difficult to determine.

In hermaphrodite forms both ova and spermatozoa are produced in one gonad, termed the **hermaphrodite gland,** which lies embedded in the spiral digestive gland. From the gonad they pass at first along the same duct (**little hermaphrodite duct**), which is much convoluted, but towards its distal end they have begun to follow two distinct channels. This duct opens into, or close to the mouth of, the albumen gland or glands, and fertilization of the ova by incoming spermatozoa following sexual union takes place not far from this point, in some forms in a distinct **fertilization chamber.** A small receptaculum seminis adjoins the place of fertilization. From here the ova and outgoing sperms enter the **great hermaphrodite duct,** in which their paths become separated by longitudinal folds or by a partition. The female portion of this duct (oviduct) is dilated and puckered, its major, posterior, part constituting a mucous gland or a capsule gland, or both in succession. The ventral, male, portion of the great hermaphrodite duct (vas deferens) is relatively narrow and not puckered.

The details of the anterior part of the genital system in hermaphrodite gastropods differ considerably in different groups. In forms in which the male and female genital openings are distinct, the vas deferens diverges completely from the oviduct, usually becomes dilated to form a prostate gland, and then becomes narrow and tubelike until it leads into the penis sac behind the male genital opening. The penis, which is retractile, lies within this sac. In some forms (e.g., *Aplysia*) in which there is a common genital aperture the oviduct and vas deferens remain contiguous for the whole of their course. In *Helix* the male and female ducts diverge completely and then converge again, so that the penis sac and vagina continuing the oviduct meet behind the common genital aperture, an additional mucous

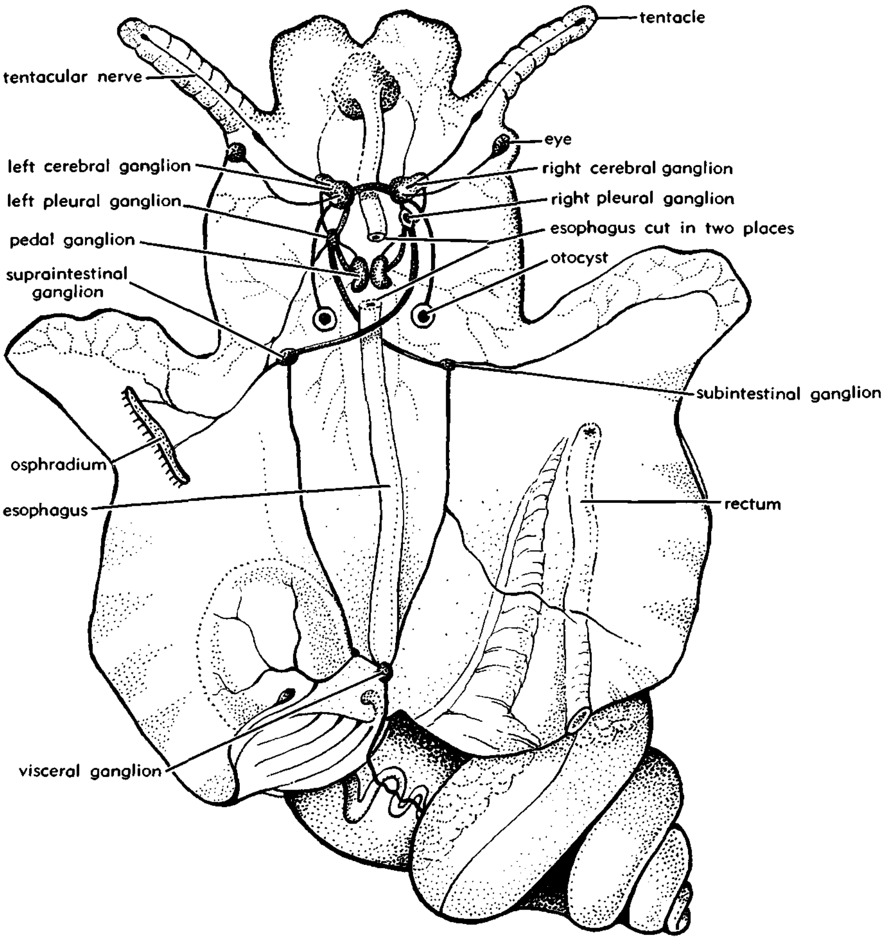


FIG. 61. Nervous system a caenogastropod, *Pomatias elegans* (MÜLLER) (58).

gland opening into the vagina not far from the aperture. A bursa copulatrix or sac homologous to it opens out of the vagina in most forms, but is absent in some. A remarkable sac which opens into the vagina near the genital aperture in many Helicidae is the **dart sac.** The dart, which is produced in this, is a small, sharply pointed, dagger-like, calcareous structure which is extruded and becomes embedded in the flesh of the partner just before sexual union. The genital openings usually lie just behind the right tentacle. When they are separate the male opening lies in a slightly more anterior position.

## NERVOUS SYSTEM

The nervous system in the Gastropoda consists of a number of nerve centers or **ganglia,** which are joined by nerve cords (**commissures** or **connectives**), and communicate by means of threadlike nerves with various parts of the animal. The most important ganglia, which are paired but not quite symmetrically disposed, are the **cerebral** (receiving nerves from the eyes and tentacles, and also from the otocysts or hearing organs, in forms where these exist), the **pleural** (innervating the walls of the body cavity, the siphon, etc.), and the **pedal** (from which arise the nerves of the foot). The cerebral and pleural ganglia are always in fairly close proximity, arranged around the esophagus in the animal's cephalic region. The pedal ganglia are close to the pleural ganglia in many gastropods, but in some are more removed. Several other ganglia usually occur, their identity and positions varying according to the particular group.

In the less advanced Caenogastropoda (Fig. 61) a **visceral** (or **abdominal**) **ganglion** is situated a considerable distance posterior to these three pairs of ganglia, in the region between the rear of the pallial cavity and the visceral mass. Some forms have two such ganglia. Between the visceral ganglion and the three anteriorly situated pairs are two other ganglia, the **subintestinal ganglion** on the right side of the animal and the **supraintestinal** one on the left. From these originate the pallial nerves, which divide up to form a network around the mantle edge. The supraintestinal ganglion also innervates the ctenidium and osphradium, while smaller nerves from the subintestinal ganglion innervate the columellar muscle and walls of the body cavity. Posteriorly, each of these two ganglia is joined by a nerve cord to the visceral ganglion or ganglia, and anteriorly each is joined to one of the pleural ganglia. The supraintestinal ganglion, however, although it lies on the left side, is joined to the right pleural ganglion and the subintestinal ganglion to the left, the respective nerve commissures crossing so that the one from the right pleural ganglion passes over that from the left. The so-called **visceral loop,** formed by the circuit of nerve cords joining the pleural ganglia to the visceral ganglion and passing through the intermediate ganglia mentioned, thus forms a figure 8. This condition is described as "streptoneurous" and is clearly the result of the "torsion" undergone by the animal in early ontogeny. In the more advanced prosobranchs there is a marked tendency to concentration of the ganglia (apart from the visceral ones) in the anterior region; in *Buccinum,* for example, the subintestinal and supraintestinal ganglia are situated in the collar of ganglia surrounding the esophagus. In such a case the nerve cords of the visceral loop cross close to these two ganglia on their posterior side.

In the Archaeogastropoda (Fig. 62*A*), the most primitive order of prosobranchs, there is a marked absence of concentration of nerve centers, the ganglia being elongated or the commissures including a series of ganglion cells. The pleural and pedal ganglia are fused into a single mass. The foot is innervated by a conspicuous pair of almost parallel, elongated, ganglionated nerve cords joined by numerous cross-connectives to form a structure recalling a rope-ladder. This last condition is also found in some less advanced Caenogastropoda (e.g., Pomatiasidae). In some gastropods the anterior series of ganglia includes, in addition to those already mentioned, a pair of **buccal ganglia** which are connected by a short loop with the cerebral ganglia and innervate the buccal mass.

In most Opisthobranchia (Fig. 62*B*) and Pulmonata the nerve cords of the visceral loop do not cross in the manner described above, and these subclasses have, therefore, been grouped together under the name Euthyneura. Exceptions are members of the family Acteonidae, which are streptoneurous, although classified as opisthobranchs; *Chilina* is streptoneurous, although a pulmonate. In some opisthobranchs the visceral loop is well extended, with the visceral ganglion or ganglia remote from the pleural ganglia; subintestinal and supraintestinal ganglia are not developed. In other opisthobranchs the visceral loop is much shortened or altogether absent, all the ganglia being in close proximity and united by short commissures to form a ring at the posterior end of the esophagus. A similar concentration is found in the pulmonates, the visceral loop being close to the main group of ganglia and formed by two visceral ganglia separated by an abdominal one, all joined by very short commissures. The osphradial nerve, when present, communicates with the supraintestinal ganglion. A small **osphradial ganglion** may be present near the osphradium.

## RADULA

A few notes on the radula (Fig. 63), already referred to, may appropriately follow the foregoing account of the soft parts, since it also is not found fossil. It is a rasplike structure consisting of numerous similar, symmetrical, transverse rows of **teeth,** or **unci,** borne on a supporting band. The horny material of which it is formed is usually alluded to as chitin, a term originally applied to the material forming the integument of arthropods. Its composition is complex and variable; basically protein, it also contains sodium, iron, phosphorus and several other elements (93). The teeth vary greatly in number in different genera, tending to be largest and fewest in carnivorous forms. They also vary considerably in shape, some being broad and comblike, with a number of cutting points (**cusps** or **cones**), and others narrow and pointed. The total number of teeth in a gastropod radula ranges from one to about 750,000, the latter being the number present in *Umbrella.* The number of rows present may be very few or as many as several hundred. The structure of the radula is constant in any one species and all the transverse rows of teeth are alike, or almost so. The radula is added to continuously in the radula sac at its rear end, and at the same time the worn teeth in front are discarded. In the opisthobranch group, Sacoglossa, there is a small pouch for their reception.

The term **median, central,** or **rachidian tooth** is applied to a single tooth present at the middle of each row in the majority of radulae. On either side of this, in the most fully developed radulae, other teeth, termed **marginals** or **uncini,** are present in most herbivorous prosobranchs. When there are two or perhaps several very similar teeth at the middle of each row, all are sometimes

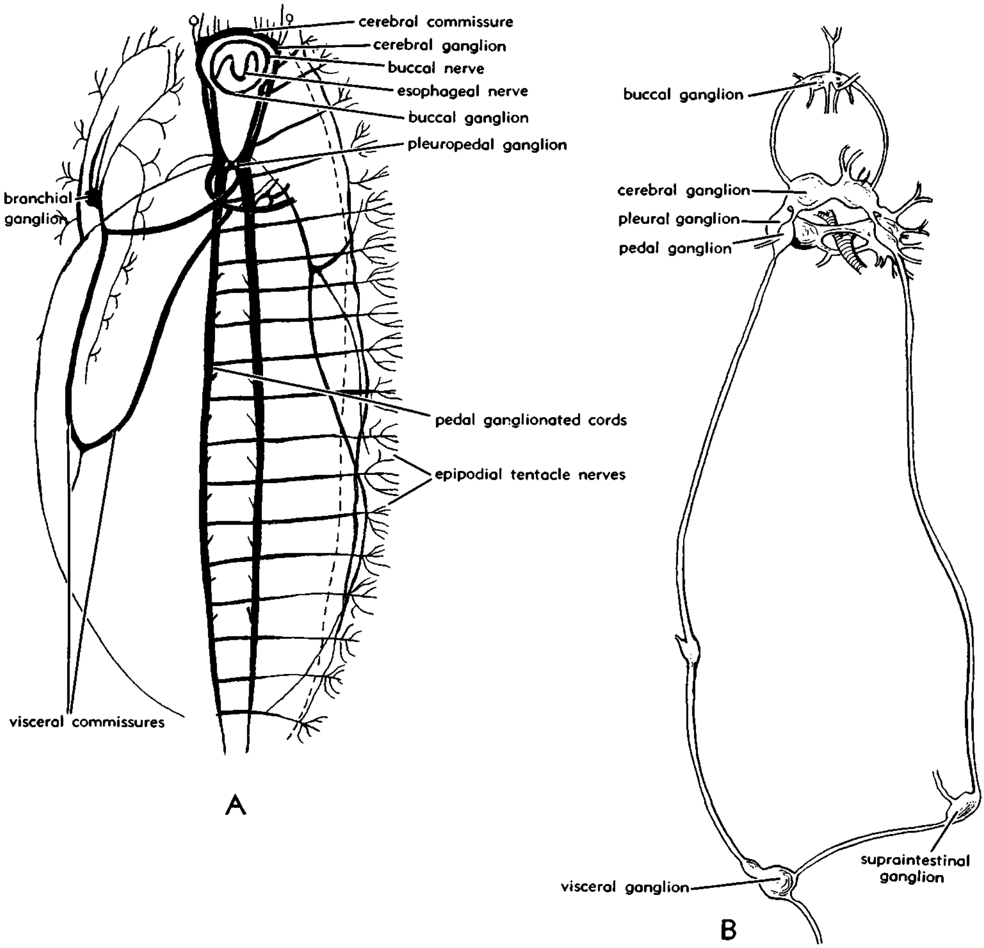


FIG. 62. Nervous system of *(A)* an archaeogastropod, *Haliotis tuberculata* LINNÉ (121) and *(B)* an opisthobranch, *Akera bullata* MÜLLER (80).

regarded as medians; if the number is even, no tooth lies absolutely in the middle. The part of the radula which includes the median and admedian teeth is termed the **rachis** and the parts with the marginal teeth are the **pleurae.** Special terms may be used for individual teeth in various types of radula. Teeth of any of the series mentioned may be absent. The radula formula is a series of numbers (usually 5) referring to the teeth of each series present in the appropriate place in every row, a 0 being included if those of any series are absent, and the "infinity" symbol (∞) if they are too numerous to count, as is sometimes the case with the marginals. Thus, 1:1:1:1:1 denotes the presence of one median tooth, with one admedian on each side of it and one marginal at each end of the row, but 1:0:1:0:1 denotes the presence of a median and marginals only, with admedians absent. There may be several admedians on each side, but the number is never very large. If marginals are absent, the "0" on each side may be omitted from the formula, which is thus reduced to three numbers. The average number of rows of teeth present in the radula of any species may be added at the end of the formula, preceded by a multiplication sign, for example 1:1:1:1:1 (×42).

The prosobranchs have been divided by GRAY, TROSCHEL, and others into a number of groups which take their names from the prevalent type of radula, a classification based on the radula separating to a considerable extent the same groups as one based on the general characters of the soft parts and shell; in most groups, however, there are species in which the radula shows abnormalities. The most important of these groups are as follows.

### RHIPIDOGLOSSA

The formula is ∞:ca.5:1:ca.5:∞. The very numerous marginals are long, narrow, hooked and arranged in a somewhat fanlike manner. The admedians, of which there are several (most frequently about 5) on each side, are not always very different from the median one. In the Neritidae the outermost admedian on each side, termed a **capituliform tooth,** is broad and flat-topped. All the Archaeogastropoda except the limpets have a rhipidoglossan radula.

### DOCOGLOSSA

The number of teeth, which are lancelike or clawlike in shape, is small, and two or more teeth may be regarded as medians. Marginals or admedians, or uncommonly both sets, may be absent. There is thus no constant formula. That of *Patella* is 3:1:(2+0+2):1:3, the medians (indicated in parentheses) numbering 4, grouped as indicated. The limpets (Acmaeidae, Patellidae, Lepetidae) constitute this group.

### TAENIOGLOSSA

The usual formula is 2:1:1:1:2, but there are variations. The median tooth most frequently has a number of cusps, with the middle one the largest. The admedians are broad and commonly cuspidate. The two marginals on each side are narrow and hooklike or cuspidate. Many of the less advanced Caenogastropoda have a radula of this type.

### PTENOGLOSSA

The radula has an indefinite number of long, hooked teeth, of which the outermost are the largest. Two families of Caenogastropoda, Scalidae and Janthinidae, have this type of radula, but in the former the teeth are small and in the latter they are large and there is a smooth band along the middle of the radula.

### RACHIGLOSSA

The radula formula is 1:1:1 or 0:1:0. The median tooth has one to about 14 sharp cusps and the admedians, if present, are usually broad and rakelike, with numerous cusps, but in some genera they have only two large cusps. In some of the advanced Caenogastropoda that have been classed as Rachiglossa, however, the typical rachiglossate radula has degenerated. Thus, some species, belonging to different families, have lost the admedians, and in the genus *Harpa* the radula has completely atrophied in the adult.

### TOXOGLOSSA

In most genera of the three families (Conidae, Turridae, Cancellariidae) classified under this heading, the radula consists only of long teeth, which there is evidence for regarding as marginals. The formula is thus 1:0:0:0:1, or 1:0:1, as usually given.

In *Conus* the teeth are very large and a poison gland is associated with them.

### STENOGLOSSA

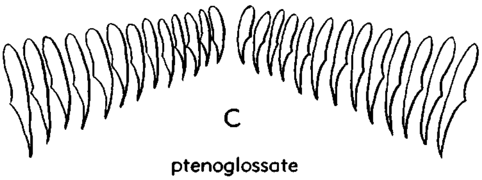
The Rachiglossa and Toxoglossa have been combined under the name Stenoglossa, this name referring to the relative narrowness of the radula, although there is little resemblance between the two constituent groups in other respects.

### GYMNOGLOSSA

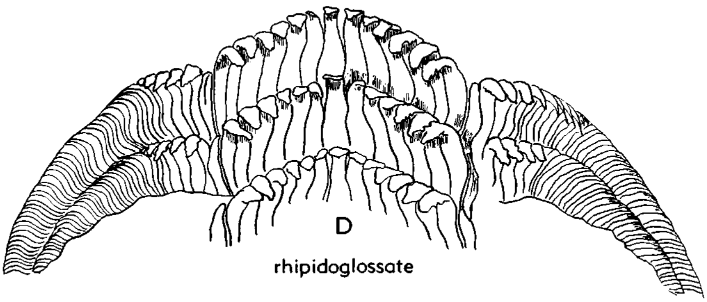
This name is applied to the Eulimidae and Pyramidellidae, and denotes the absence of a radula, which is not needed owing to a parasitic mode of life.

docoglossate

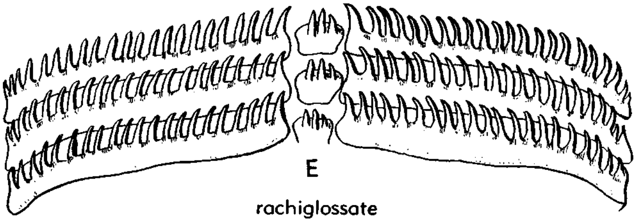
taenioglossate



ptenoglossate



rhipidoglossate



rachiglossate

FIG. 63. Gastropod radulae. Docoglossate, *Patella (Ancistromesus) pica* REEVE (97); taenioglossate, *Vermetus grandis* GRAY (20); ptenoglossate, *Janthina fragilis* LAMARCK (67); rhipidoglossate, *Margarita umbilicalis* BRODERIP & SOWERBY (20); rachiglossate, *Fasciolaria trapezium* LAMARCK (20).

### OTHER GROUPS

In the Pulmonata and Opisthobranchia there is also great diversity in the structure of the radula, but in these groups it has not been used in classification. An extensive literature exists on the radulae in both subclasses.

# MORPHOLOGY OF HARD PARTS

## OCCURRENCE OF SHELL IN GASTROPODA

A shell is present in the great majority of the gastropods and in most forms is completely external when the head-foot mass is withdrawn. This is the case even in some families, such as the Cypraeidae, Marginellidae, Olividae, and Hydatinidae, in which the shell is almost enveloped by the mantle or the foot is much enlarged when these organs are protruded. In some genera, such as *Sinum, Harpa,* and many opisthobranchs, however, the soft parts cannot be entirely withdrawn into the shell. The latter may even be completely internal, as in some opisthobranchs and in the slugs. In such cases it has frequently suffered degradation, being reduced to a small calcareous plate in the case of the slugs. It is absent in a few groups.

Among the prosobranchs the shell-less condition is associated with a parasitic life in the case of genera such as *Paedophoropus, Entoconcha, Pseudosacculus, Asterophila,* and *Ctenoscalum,* and with a pelagic life in the case of *Pterotrachea,* but the marine, sluglike *Titiscania* leads a crawling existence. The opisthobranchs include the shell-less nudibranchs, which are widely distributed in present-day seas.

## GENERAL FEATURES OF SHELL

The gastropod shell is essentially a protective structure that permanently covers the visceral mass and provides a retreat for the head-foot mass, which is extruded from it when active. Typically, it may be regarded as a conelike tube (showing much diversity, however, in cross-sectional shape), which is closed at its apical end, formed first during growth, and open at the other end, where growth increments are added, while at the same time there is usually a progressive increase in diameter. It is convenient to allude to this tube as the **helicocone,** the opening at its extremity being termed the **aperture** (Fig. 64). In most gastropods the shell assumes a spiral form as the helicocone, during growth, coils repeatedly about an imaginary **axis** passing through its apex. If the direction of growth of the helicocone is constantly perpendicular to the axis as coiling takes place, the outermost point on the edge of the apertural margin will trace a plane spiral and the resulting shell may be described as **planispiral,** or as **isostrophic** when the cross-section of the helicocone is such that there is symmetry about a median plane (e.g., Bellerophontidae, Fig. 65*J*). With most gastropod shells, however, the direction of growth of the helicocone has a component parallel with the axis and, except when this component is relatively small, the spiral body formed will have a protruding apex, and may even be considerably drawn out like a corkscrew. Spiral shells with a distinctly protruding apex are described as **conispiral.**

Each complete coil of the helicocone is termed a **whorl.** In most shells each coil conceals part of the preceding one, and then the term whorl commonly refers only to the visible part of each coil. Each coil embraces the preceding one up to a line of contact known as the **suture,** which itself forms a spiral when the shell is considered as a whole. As only one side of the shell can be viewed at a time, it is customary to regard any whorl as bounded by two sutures, notwithstanding their essential continuity. They are best referred to as the **adapical** and **abapical** sutures of the whorl in question, according to whether they are nearer to or farther from the apex.

The helicocone may be coiled so broadly with respect to the axis that a conical cavity, known as an **umbilicus,** remains surrounding the axis. In this case, in addition to the usual suture on the outer surface of the shell, a second suture (**umbilical suture**) may be visible within the umbilicus. If the shell has no protruding apex, but a depressed adapical surface, this surface will constitute a second umbilicus, known as the **adapical umbilicus.** A shell with an adapical umbilicus is described as **involute** (Fig. 65*I*), and one in which the last whorl completely envelops and obscures the preceding ones as **convolute** (Fig. 65*A*). Planispiral and isostrophic shells may be either involute or convolute.

The **columella** of a shell is the pillar, surrounding the axis, formed by the **adaxial** wall of the coiled helicocone. A solid columella is produced by the complete fusion of successive parts of this wall as the shell grows. The term **spire** denotes, collectively, the adapical visible part of all the whorls except the last. The **periphery** of the shell (or of any particular whorl) is the part farthest from the axis, while the **base** of the shell is the abapically facing part of the surface, delimited in most shells by the periphery, but in certain genera, when so defined, by a spiral carina or angulation serving as an obvious boundary.

In some gastropod shells, such as the limpets, the helicocone is not coiled in a spiral, but has the form of a simple depressed cone. The terminology relevant to such shells is correspondingly simple.

The direction of coiling of an adult gastropod in relation to the head-foot mass is described as **endogastric.** This means that, when the shell rests on the crawling head-foot mass, it is so coiled that the body of the shell extends backwards, away from the head. The result is that the head withdraws into the shell before the foot, the operculum on the latter (if present) closing the aperture. The opposite condition, in which the body of the shell tends to extend forward over the head, and the foot withdraws into the shell before the head, is termed **exogastric,** and is found in gastropods only in a very early developmental stage, prior to torsion. It is the normal condition in the cephalopod *Nautilus.*

## VARIETY IN SHELL FORM

The general form of a coiled gastropod shell depends on a number of interrelated factors, chief among which are the cross-sectional shape of the helicocone, the degree of overlap of successive coils, and the openness of coiling of the whole spiral with respect to the axis. Not in every genus, moreover, are the mode of coiling and the rate of increase in the cross-sectional area of the helicocone constant during growth.

In some shells the helicocone is so loosely coiled that the whorls remain **disjunct,** not touching one another. In other forms the earlier whorls form a close coil, but the later ones, or perhaps only part of the last whorl, become disjunct (Fig. 65*D*). In some species of the land prosobranch genus *Opisthostoma* and also in the Paleozoic marine genera *Scoliostoma* and *Brilonella* the terminal part of the last whorl bends up towards the apex. In the family Vermetidae, while the helicocone is at first spirally coiled in some species, in later growth stages it becomes very irregularly contorted and often

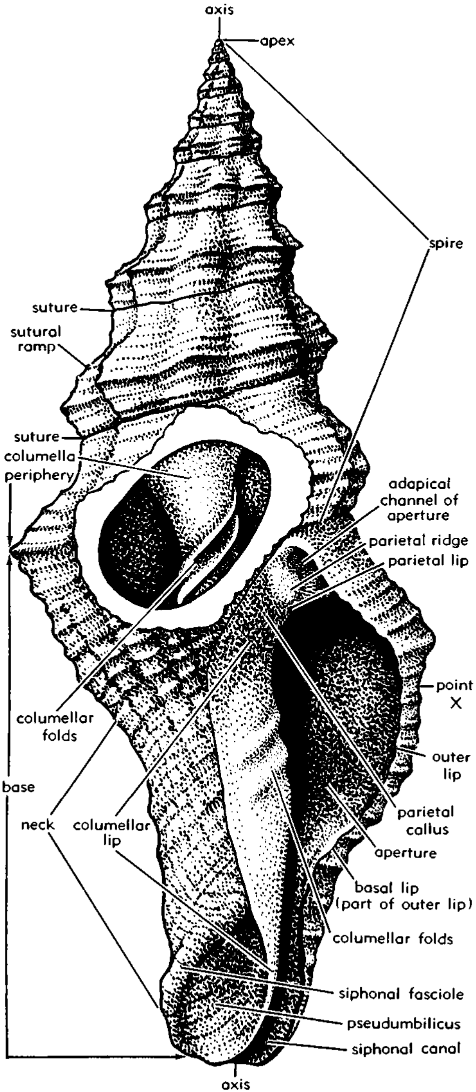


FIG. 64. Typical gastropod shell, *Latirus lynchi* (BASTEROT), Mio., Fr., showing terminology of its various parts. The columella is seen through a "window" in the last whorl (115n).

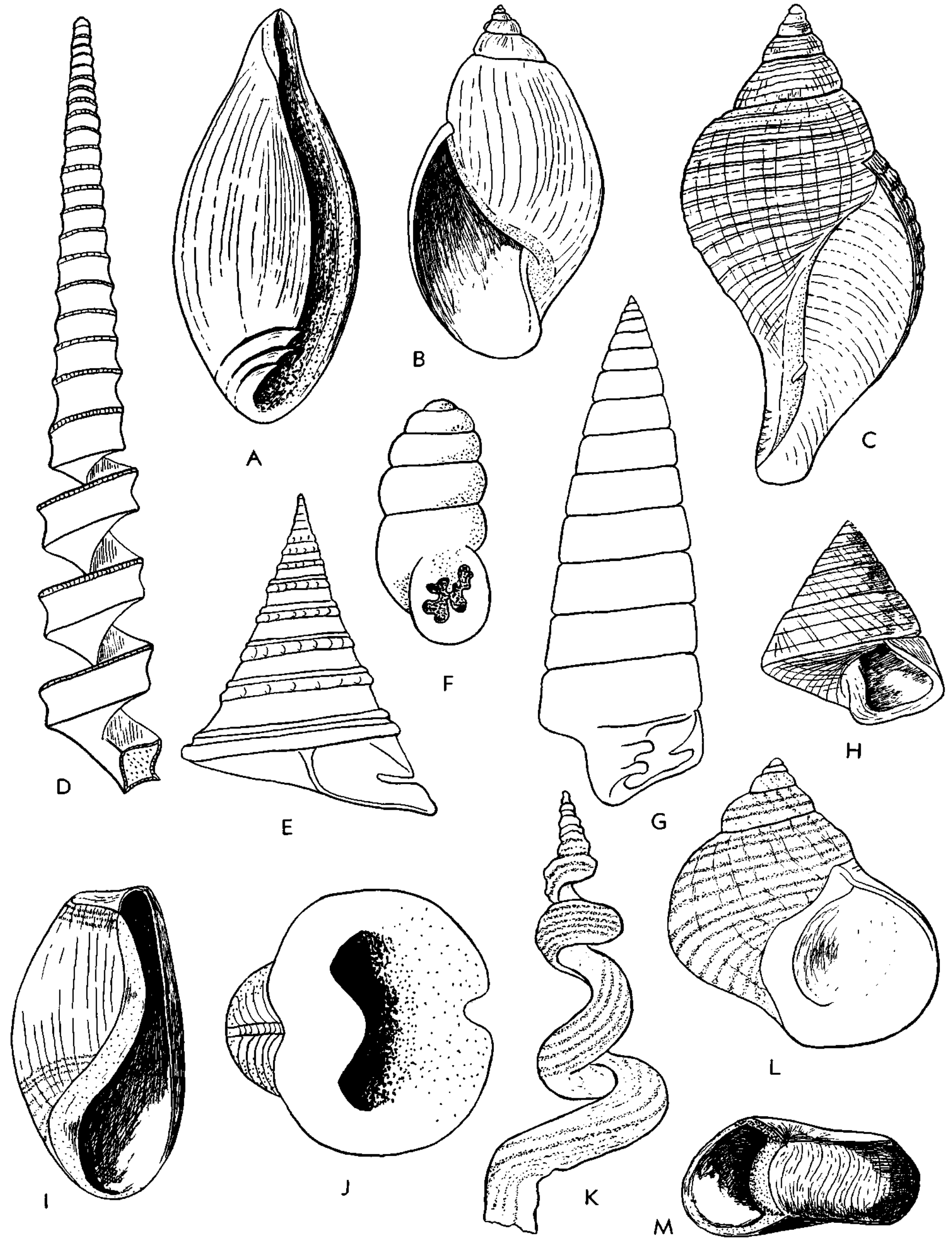


FIG. 65. Variety in gastropod shell form.——*A*. Convolute, *Acteonella gigantea* D'ORBIGNY, Cret., Fr., ×0.7 (78).——*B*. Sinistral, *Physa meigsi* DALL, Plio., Fla., ×1.2 (116).——*C*. Fusiform, *Fasciolaria tulipa* (LINNÉ), Plio., Fla., ×3 (116).——*D*. Turriculate (with later whorls disjunct), *Nerinella libanotica* DELPEY, L.Cret., Syria, ×1.3 (117).——*E*. Coeloconoid, *Pyrgotrochus luciensis* (D'ORBIGNY), M.Jur., Fr., ×0.5 (127).——*F*. Pupiform, *Gastrocopta baudoni* (MICHAUD), Plio., Fr., ×16 (130).——*G*. Cyrtoconoid, *Nerinea requieniana* D'ORBIGNY, U.Cret., Fr., ×0.67 (78).——*H*. Trochiform, *Calliostoma erosum* DALL, Plio., N.Car., ×2.7 (116).——*I*. Involute, *Bulla striata* BRUGUIÈRE, Plio., Fla., ×1.7 (116).——*J*. Isostrophic, *Bellerophon vasulites* MONTFORT, M.Dev., Ger., ×1 (115n).——*K*. Irregularly coiled, *Vermetus spiratus* PHILIPPI, Rec., Carib., ×1 (135).——*L*. Turbiniform, *Turbo militaris* REEVE, Rec., IndoPac., ×0.7 (135).——*M*. Discoidal and sinistral, *Helisoma disstoni* (DALL), Plio., Fla., ×1.3 (116).

disjunct (Fig. 65*K*). The irregular form is correlated with the fact that the shell becomes partly cemented to the substratum. In the Caecidae the initial coiled stage is often lost and the shell then consists of a small, hornlike tube. Irregularity in coiling may arise as a pathological condition. Shells in which the whorls are slightly disjunct owing to this cause are described as **scalariform.** There has been confusion in the past between irregularly coiled gastropods and the tests of coiled serpulid worms, but study of the shell structure enables the two groups to be distinguished.

The genus *Xenophora* is able to cement extraneous objects, such as small pebbles, shells of Foraminifera, and other shells, to its test. The Paleozoic euomphalids *Lytospira* and *Straparollus (Philoxene)* had the same habit.

Terms used commonly to describe the general form of a gastropod shell are defined in the Glossary. Some need little explanation in view of their etymology, whereas others (e.g., bucciniform, naticiform, patelliform) are derived from the names of common genera having the form that they denote. If the whole shell (or only its spire) approaches a cone in shape but has convex sides, it (or the spire) may be described as **cyrtoconoid** (Fig. 65*G*), and, if its sides are concave, as **coeloconoid** (Fig. 65*E*). MOSELEY (229) long ago showed that, when a coiled gastropod shell retains the same shape and proportions at all stages of growth, any particular point on the growing edge of the helicocone traces a logarithmic spiral. Certain mathematical properties result from this fact; for example, the heights of successive whorls measured along any plane passing through the axis form a geometrical progression. The whole subject is admirably discussed by THOMPSON (99). MOSELEY himself showed how the surface area and volume of a shell ideally regular in form can be calculated mathematically. In practice, however, there is seldom more than an approximation to this ideal condition.[1]

## DIRECTIONAL TERMINOLOGY OF GASTROPOD SHELL

There are two conventional methods of posing a gastropod shell for illustration. Most authors place it with the axis vertical and apex uppermost, but in France and a few other countries the shell is placed with its apex lowermost. The second method has the advantage that the aperture is more clearly illuminated when (as is conventional in illustration) the specimen is lighted from the top left-hand side. Exponents of either method are apt to use such terms as "upper" and "lower" according to the way in which they are accustomed to view specimens, and French authors use the term *"plafond"* for the part of the marginal region of the aperture farthest from the apex. To avoid confusion it is thus advisable not to use terms suggested by conventional orientation of the shell, although "apex" and "base" are too firmly established to be discarded.

D'ORBIGNY (78), who made a great advance in gastropod descriptive terminology, referred already to these differing practices and decided to establish two directional terms "anterior" and "posterior." "Je désignerai toujours comme *antérieure* la partie de la coquille d'où sort l'animal, et *postérieure* le côté de la spire où l'extrémité du pied se montre dans les coquilles allongées." Thus originated the practice, adopted by many subsequent authors, of describing the direction from the apex to the base parallel with the axis as "anterior" and the opposite direction as "posterior." If, now, we consider how coiled gastropods carry their shell when crawling (Figs. 51, 67, 68), it is evident that D'ORBIGNY's anterior direction (in the shell) approximates to the true anterior direction (as defined by the direction in which the animal normally progresses when active) when the shell has a high spire (as mentioned by him), or when (as in the Cypraeidae and Conidae) the aperture is narrow and elongate. When, however, the aperture is relatively broad, it may be said that, the lower the spire of the shell, the more does the true anterior direction differ from that defined by D'ORBIGNY, until in planispiral shells it is outward (toward the outer lip) from the axis and not parallel with it. The terms "anterior" and "posterior," defined by reference to the living animal, cannot, therefore, be applied consistently to coiled shells regarded as

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[1] A recent mathematical treatment of the form of the gastropod shell is that of CINTRA & DE SOUZA LOPES (14), who disagree with THOMPSON's conclusions.

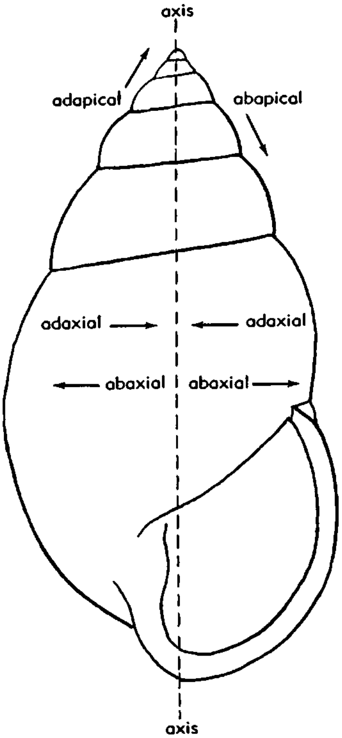

FIG. 66. Directional terminology for a gastropod shell (115n). For high-spired but not all other shells, abapical=anterior, adapical=posterior, and the left and right sides are as viewed in the figure.

geometrical structures. Their replacement by "abapical" and "adapical" (Fig. 66) is advocated. Since, moreover, the directions to be described as "left" and "right" depend on those which are regarded as "anterior" and "posterior" (to which they are perpendicular), it follows that these terms also can be applied satisfactorily to coiled gastropod shells only when the apex points straight to the rear when the animal is crawling. The left side of the shell in such a case is the side on the observers' left when the shell is viewed with its apex uppermost and its aperture facing him. The side of the shell on which the aperture lies may be called the "apertural" side and the opposite side the "abapertural" side. Application of the terms "ventral" and "dorsal" to gastropod shells is not recommended.

In the case of patelliform shells like the limpets, symmetrically poised on the soft parts of the animal and having little play in relation to them, the terms "anterior" and "posterior," defined from the soft parts, are applicable accurately to the shell.

## DEXTRAL, SINISTRAL, AND HYPERSTROPHIC SHELLS

In the apertural view of most coiled gastropod shells the aperture lies on the observer's right when the apex is uppermost; in other words, the shell, viewed from above the apex, coils in a clockwise direction as it grows. Such shells, provided that (as is most commonly the condition) the genitalia of the animal lie on the right-hand side of the head-foot mass or of the pallial cavity, are termed **dextral.** A **sinistral** gastropod is one that is the mirror image of a dextral form in every respect. The aperture appears on the observer's left when viewed as described first above (Fig. 65*B*), and the genitalia are on the left-hand side of the head-foot mass or pallial cavity. Sinistrality may be a family character (Triphoridae), a character only of certain genera of families in which most genera are dextral, or a specific character in genera in which most species are dextral, for example, the well-known English Pleistocene (Red Crag) species *Neptunea contraria* (LINNÉ). Very rarely it may arise as an individual abnormality.

A further case, however, is when an apparently sinistral shell belongs to a dextrally organized animal (i.e., one with its genitalia on the right-hand side) or *vice versa.* Such a shell may be regarded as a dextral one in which the spire side is deeply umbilicate and the basal side less deeply umbilicate or even protruding. Gastropods in which such conditions obtain are described as **hyperstrophic (ultradextral** and **ultrasinistral** are also used in this connection). Planispiral shells constitute an intermediate type between such shells and those with a normal protruding spire. Thus in the family Ampullariidae (Fig. 67), *Pila, Ampullaria,* and *Ampullarius* are normal dextral genera; *Marisa* and *Pseudoceratodes* are involute and almost planispiral; and *Lanistes,* apparently sinistral, in fact is hyperstrophic. The Planorbidae (Fig. 65*M*) are sinistral and hyperstrophic-discoidal. It should be noted that, following the convention of most authors who have dealt with them, dextral and sinistral hyperstrophic shells of Paleozoic age are illustrated in this work with the aperture to the right or left respectively.

Usually, hyperstrophy can be detected only when the soft parts are available for anatomical study. The Macluritacea, an important group of Lower Paleozoic gastropods, are, however, known to have been hyperstrophic because of the direction of coiling of the operculum. Figure 68 shows a restoration of a representative of this family, indicating how the hyperstrophic shell was probably carried by the crawling gastropod. The term **orthostrophic** may be used as the converse of hyperstrophic, denoting normality in coiling.

## APICAL WHORLS

The majority of gastropod shells that have escaped abrasion or corrosion preserve in their successive whorls a record of their development from the time when the primitive shell-gland began to secrete a calcareous test. Exceptions are those genera, such as *Patella,* in which the earliest-formed shell is cast off when the shell begins to acquire its adult shape. In some families, moreover, notably the Thiaridae, the apical whorls are discarded following the withdrawal of the tip of the visceral spiral from them and the secretion of a septum above it; this process is known as "**decollation.**" The earliest formed test is horny in some genera, such as *Scaphella,* and is soon lost; in such cases its former presence may be indicated by a scar on the apex of the calcareous shell, culminating in a point.

In land and fresh-water gastropods and many marine species the earliest whorls are succeeded by the later ones with no evidence of any discontinuity, the mode of coiling being constant and the ornament of the adult shell appearing gradually. In others, however, certain whorls at the apex are clearly demarcated from those that follow (Fig. 69). The demarcation may consist only of a small swelling (or **varix**) parallel to the axis, or it may be indicated by a sudden incoming of ornament or change in ornament, or by a change in shell texture. At times, however, the axis of the early whorls forms a distinct angle, in some species even exceeding 90 degrees, with that

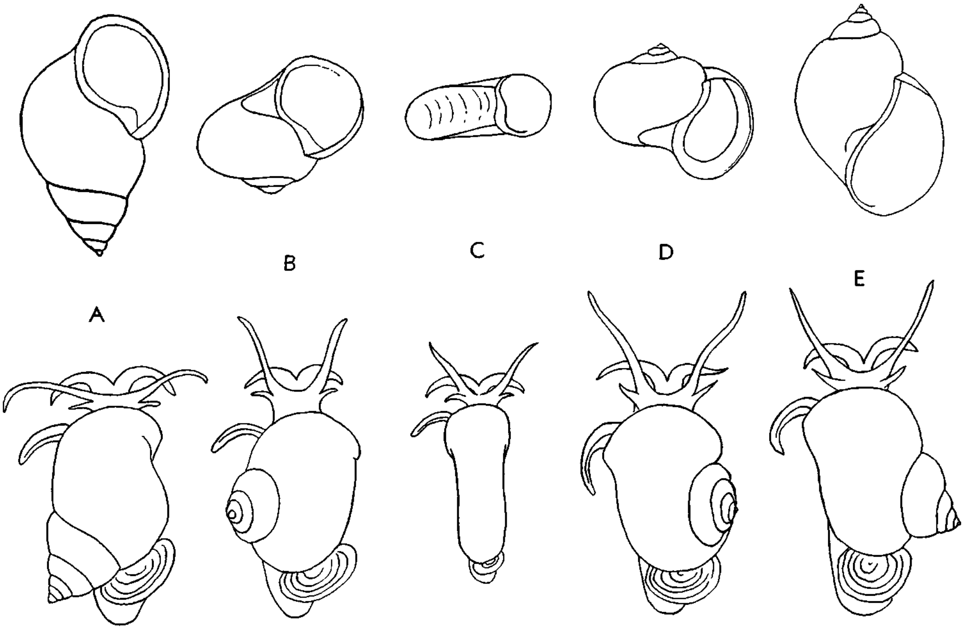

Fig. 67. Hyperstrophic conispiral, discoidal (planispiral), and orthostrophic conispiral species of the family Ampullariidae. In each case the animal is dextrally organized, as shown by the positions of the siphon (always on the left) and operculum. The species represented are *(A) Lanistes (Meladomus) pyramidalis* Bourguignat, W.Afr.; *(B) Lanistes carinatus* (Olivier), Egypt; *(C) Marisa cornuarietis* (Linné), S.Am.; *(D) Ampullarius gevesensis* (Deshayes), S.Am.; *(E) Pila ovata* (Olivier), E.Afr.; all reduced (124, 126).

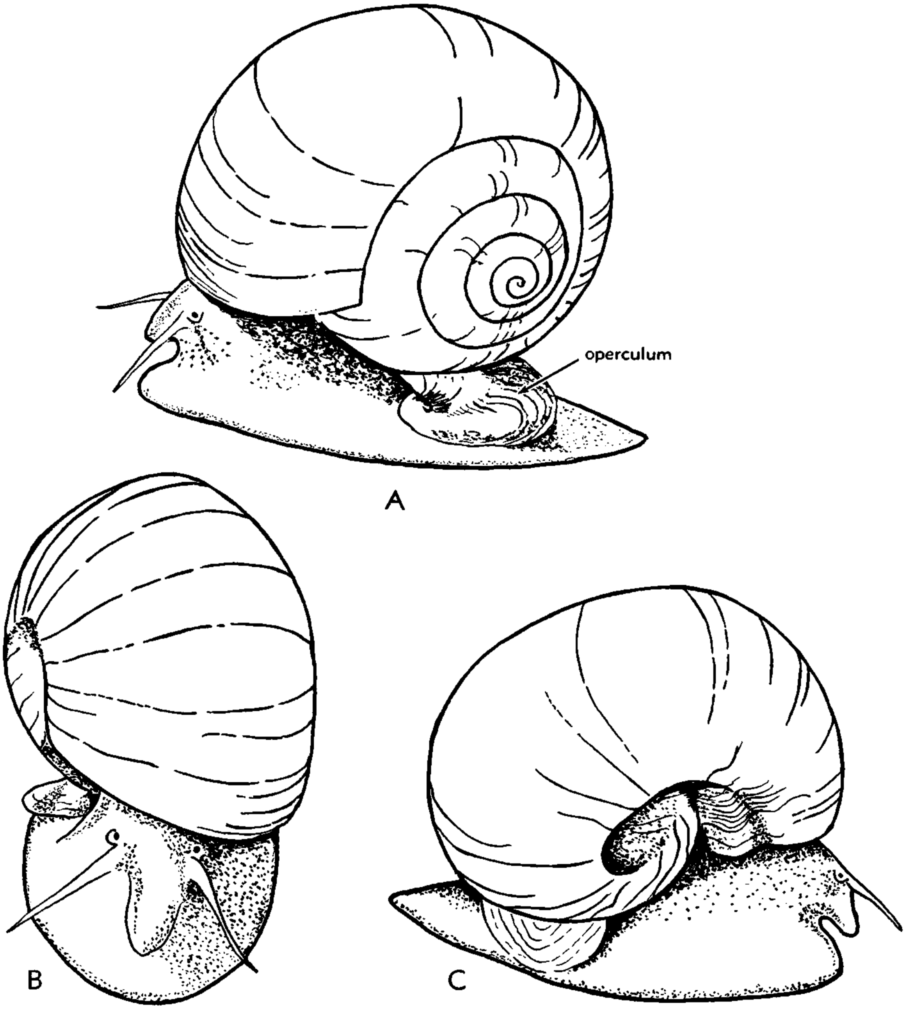

Fig. 68. Restoration of *Palleseria longwelli* (Kirk), Ord., N.Am., an early hyperstrophic marine gastropod (55). *A-C*. Left lateral, oblique front, and right lateral views; note in *A* counter-clockwise coiling of the operculum; ×0.93.

of the later ones, or the early whorls may appear to be coiled in the direction opposite to those succeeding them. The number of such early whorls is usually about two or three, but is as many as eight in some species.

The term **protoconch** is applied to the initial whorls, particularly when these are delimited from the later ones, although it is frequently used when there is no sharp separation; in the latter case the initial whorls so designated are taken to end where the first elements of the ornament of the adult shell appear. The part of the shell formed subsequent to the protoconch may be termed the **teleoconch.**

It is still doubtful if discontinuity between the protoconch and teleoconch always coincides with a definite episode in the life-history of the gastropod. Lemche has noted that in all opisthobranchs studied by him the early, apparently sinistrally coiled, whorls are those of the pelagic larva, the change to a normal mode of coiling taking place when the animal settles and begins to undergo metamorphosis. The significance of the varix or change in shell texture, which may mark the termination of the protoconch, needs further investigation. The discontinuity may occur in forms (e.g., Volutidae) that pass through the veliger stage and undergo metamorphosis while still within the egg, hatching out as creepers. Moreover, the work of Marie Lebour, Thorson, and others suggests that there are many cases where a shell bears no record of the transition from a pelagic to a benthonic mode of life. The first traces of adult ornament may appear while the animal is still a pelagic larva.

The size of the protoconch in proportion to that of the full-grown shell varies greatly. Genera in which it is remarkably large include some members of the Volutidae, such as *Cymbium* and *Scaphella,* in which it forms a smooth, domelike structure, attaining a diameter of 23 mm. in one species. Its size may vary considerably even in the

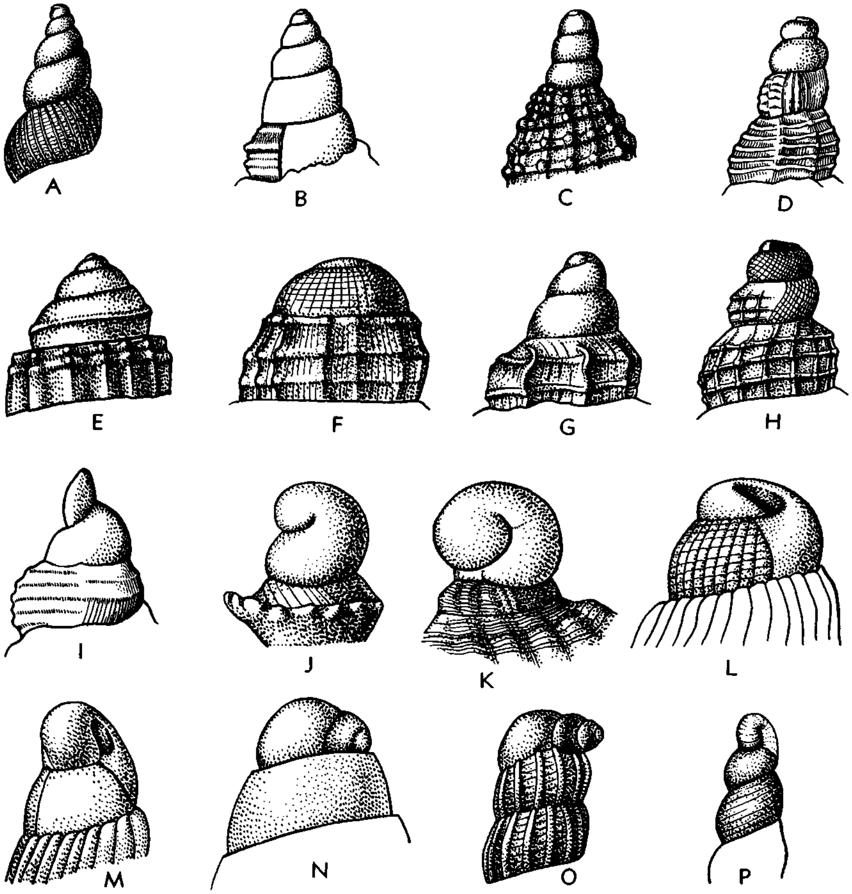

Fig. 69. Various gastropod protoconchs.——*A*. Conical, *Scala dentiscalpium* (Watson), Rec., ×30 (136).——*B*. Conical multispiral, *Cymatium vespaceum* (Lamarck), Rec.; ×8 (123).——*C*. Mammillated, *Cerithiopsis ridicula* Watson, Rec., ×45 (136).——*D*. Mammillated, *Clavilithes rugosus* (Lamarck), Eoc., Fr., ×5.5 (41).——*E*. Obtusely conical, *Nassarius babylonicus* (Watson), Rec., ×13 (136).——*F*. Domelike, paucispiral, with reticulate ornament, *Melatoma tholoides* (Watson), Rec., ×17 (136).——*G*. With papillose ornament, *Murex acanthodes* Watson, Rec., ×18 (136).——*H*. With decussate ornament, *Daphnella compsa* (Watson), Rec., ×18 (136).——*I*. Disjunct, with erect tip, *Charonia (Austrotriton) woodsi* (Tate), Mio., Austral., ×14.5 (123).——*J*. Deviated paucispiral, *Columbarium acanthostephes* (Tate), Mio., Austral., ×11 (120).——*K*. Deviated paucispiral, *Pterospira hannafordi* (McCoy), Mio., Austral., ×2 (120).——*L*. Heterostrophic and submerged, *Partulida spiralis* (Montagu), Rec., ×55 (101).——*M*. Heterostrophic, *Turbonilla lactea* (Linné), Rec., ×52 (101).——*N*. Heterostrophic, *Odostomia albella* (Lovén), Rec., ×48 (101).——*O*. Heterostrophic, *Odostomia dipsycha* Watson, Rec., ×42 (136).——*P*. Heterostrophic, *Eulimella nitidissima* (Montagu), Rec., ×48 (101).

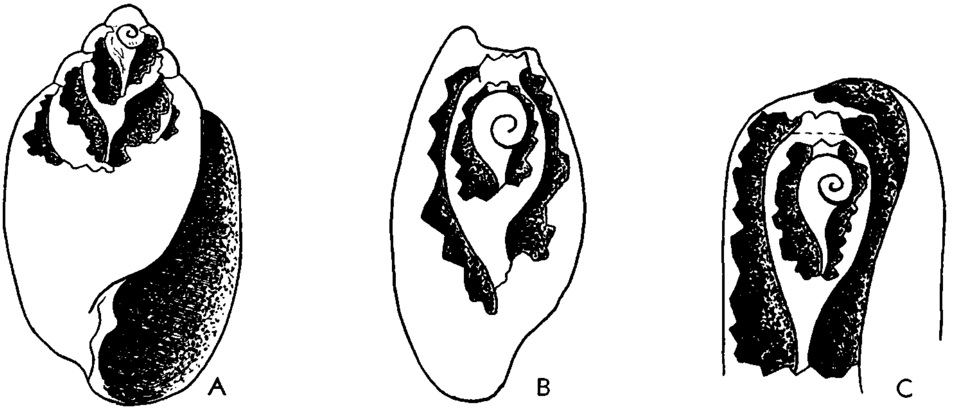

FIG. 70. Submerged heterostrophic protoconchs of Recent European opisthobranch shells, revealed by breaking away shell wall (66). *(A) Acteon tornatilis* (LINNÉ); *(B) Retusa ovata* (JEFFREYS); *(C) Cylichna cylindracea* (PENNANT); all ×18.

offspring of a single individual, the differences being attributed largely to the relative success of embryos in devouring the "nurse eggs," incapable of development, associated with them within the common egg space (102), or in the exercise of cannibal proclivities among individuals newly hatched from an egg cluster. The size of the adult shell does not depend on that of the protoconch.

The remarkable type of protoconch formed of whorls apparently coiled in the direction opposite to those of the teleoconch is described as **heterostrophic** (Fig. 69*L-P*), and is particularly characteristic of, although not confined to, the Opisthobranchia, in which the family Pyramidellidae is now included. In involute opisthobranch genera, such as *Bulla,* the protoconch is commonly hidden, but it may be revealed by breaking away part of the wall of the last whorl (Fig. 70). In the prosobranch family Architectonicidae there is a heterostrophic protoconch, the tip of which points down into the umbilicus of the teleoconch. Where the anatomy of the larval animal has been investigated it has been found that heterostrophic protoconchs are hyperstrophic; thus, although the protoconch of the dextral shell *Odostomia eulimoides* HANLEY appears to be sinistral, the larval animal which secreted it was dextrally organized like the adult animal. This, of course, would be expected. The term **homeostrophic** is used as the converse of heterostrophic, to describe a protoconch obviously coiled in the same manner as the teleoconch. A protoconch is described as **deviated** when its axis forms a well-marked angle with that of the teleoconch; most heterostrophic protoconchs are deviated. According to the number of its whorls, a protoconch (like the whole shell) may be described as **paucispiral** or **multispiral.** Its general form may be described by such self-explanatory adjectives as globular, bulbous, mammillated, subcylindrical, conical, etc. Most protoconchs are smooth, except, perhaps, for the incoming of elements of ornament on their last whorl. In some genera, however, the protoconch whorls have a very distinctive ornament. Thus in *Alvania* they bear spiral lines or rows of puncta, while in some Turridae, such as *Daphnella* (Fig. 69*H*) and *Philbertia* (Fig. 86*A*), they have a very distinctive oblique, reticulate ornament. The ornament of the protoconch of the Paleozoic Pseudozygopleuridae is very constant within the family but that of adult stages is variable and gives a basis for distinguishing the numerous genera and species.

## SPIRE WHORLS AND SUTURES

Each spire whorl (Fig. 64) consists of the part of the surface of the helicocone that is not covered by the succeeding coil, so that its height (i.e., width from suture to suture) depends on the steepness of the coiling, that is, on the slope of the sutures. In many shells this remains almost constant during growth, but in some it becomes more gentle or even reversed in later growth stages, while in others it becomes steeper near the aperture. In many shells with strong ribs or varices the suture undulates where it crosses them, and in some genera of the Cymatiidae the undulations are so marked that the spire has a distorted appearance. In outline a spire whorl may be wholly or partly convex, flat or concave. It may present one or more obtuse angulations, often accentuated to form a **keel** or **carina,** which may be sharp or rounded. A well-marked angulation (**shoulder**) is often present near the adapical suture, from which it is separated by a more or less flat zone known as a **sutural shelf** (if almost perpendicular to the axis) or as a **sutural ramp** (if inclined). The character of the suture obviously depends mainly on two factors, the outline of the outer face of the helicocone and the extent to which each whorl overlaps the preceding one. In many gastropods the suture tends to follow an angulation of the helicocone that forms the boundary of the base of the last whorl. If, as in some species of *Turritella,* the suture drops below this angulation, the whorls are said to **imbricate.** Descriptive terms applied to the suture are mainly self-explanatory. It will be **flush** when the whorl side is flat and the suture follows the angulation just mentioned (Fig. 71*G*); almost flush when the whorl surfaces that meet at it are **adpressed,** that is, very gradually convergent (Fig. 71*A*), as shown by the fact that the aperture (unless there is an infilling of callus) is narrowly angular adapically. A suture is said to be **impressed** when the whorl surfaces are both inturned toward the axis where they meet along it (Fig. 71*F*), or **grooved** (**channeled** of some authors) when only a narrow band of each is inturned (Fig. 71*D*). When (as is more frequently the

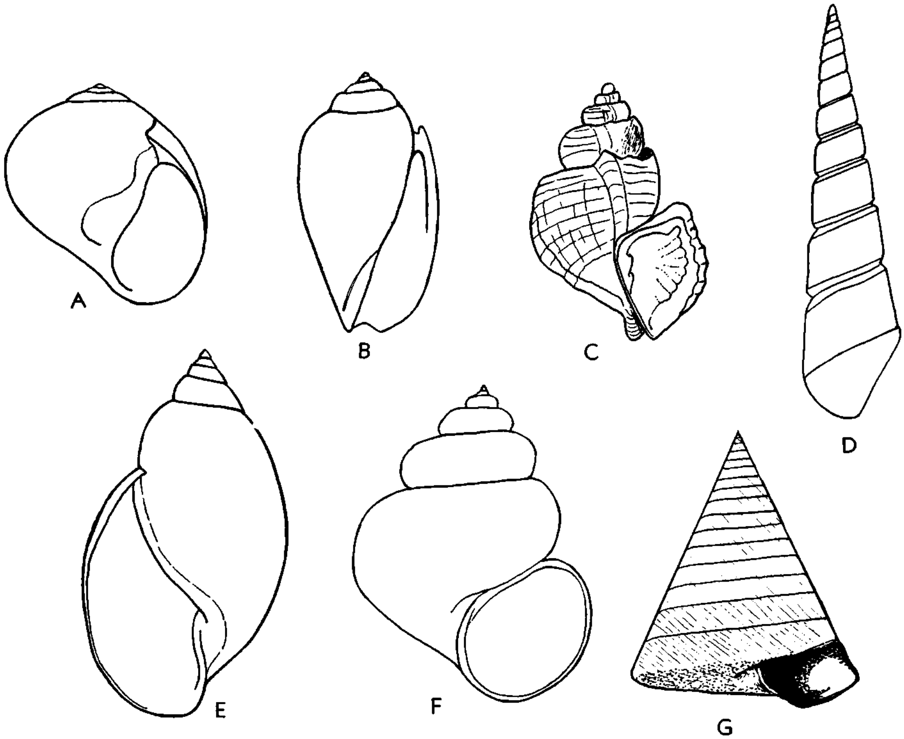

FIG. 71. Types of gastropod shell sutures.——*A.* With whorls adpressed, *Natica floridana* DALL, Mio., Fla., ×4 (116).——*B.* Canaliculate (for mantle appendage), *Olivella lata* DALL, Mio., Fla., ×3.6 (116).——*C.* Canaliculate, *Trigonostoma sericea* (DALL), Plio., Fla., ×2.2 (116).——*D.* Grooved, *Pseudomelania bicarinata* HUDLESTON, M.Jur., Eng., ×1 (121).——*E.* With abutting whorls, *Physa meigsi* DALL, Plio., Fla., ×1.2 (116).——*F.* Impressed, *Viviparus viviparus* (LINNÉ), Rec., Eu., ×1 (105).——*G.* Flush, *Epulotrochus epulus* (D'ORBIGNY), L.Jur.(Lias.), Fr., ×2.5 (128).

case) the surface of the lower whorl only is inturned, it may be said merely to abut against the preceding one when they meet at an angle at the suture (Fig. 71*E*). The suture is **canaliculate** when it lies in a troughlike depression resulting from the fact that the whorl shoulder rises above it (Fig. 71*C*). In *Oliva* and related genera there is a narrow sutural canal (Fig. 71*B*) which is occupied by a cordlike posterior appendage of the mantle when this is not protruded. In some species of the Turridae and other families, the sutures are difficult to see owing to the prominence of spiral ornament. In genera in which the mantle extends widely over the surface of the shell, all or some of the sutures are obscured by the inductura (see below), termed **enamel** when highly polished.

## LAST WHORL AND APERTURE

The last whorl, which begins at the growth line meeting the adapical end of the aperture, is the only whorl of which the entire outer surface remains visible. The outline of its base in most species is convex for some distance from the periphery, but often has a reversal of curvature at the origin of a relatively narrow abapical part of the whorl sometimes known as the **neck.** This usually includes the siphonal canal, referred to below. In *Tibia* the abapical end of the whorl forms a pointed projection or rostrum.

The margin of the aperture is termed the **peristome.** Its abaxial part, extending from the suture to the foot of the columella and forming the termination of the outer side of the helicocone, is termed the **outer lip** or **labrum.** It should be noted that an imaginary extension of the suture in a spiral direction around the last whorl would meet the outer lip at a point X (Fig. 64). The part of the lip on the abapical side of this point may be alluded to as the **basal lip.** The remaining, adaxial, part of the peristome is termed the **inner lip** (less commonly, **labium**) and consists of two parts, the **columellar lip,** formed by the columella, and the **parietal lip,** extending from the columella to the suture. The parietal lip may be formed by the actual surface of the helicocone, in which case the peristome is said to be discontinuous, or else by a coating of smooth shelly matter extending out of the aperture and constituting, in fact, the inner wall of the last coil of the helicocone. This shelly coating, which is secreted by the entire surface of the mantle, has long been known as **callus,** a rather unsatisfactory term which some authors, following Knight, prefer to replace by **inductura.** The inductura may have a distinct margin extending across the inner lip, as in *Viviparus,* so that the whole apertural margin is continuous, and in some shells the terminal part of the helicocone may become slightly detached.

At the abapical end of the aperture the margins of the inner and outer lips may meet in an uninterrupted curve, in which case the shell is described as **holostomatous** (Fig. 72*A*). In many shells, however, the presence of an inhalant siphon gives rise to a discontinuity of the apertural margin at this point, and the shell is termed **siphonostomatous** (Fig. 72*B,C*). The outlet of the canal is marked by a sinus of the margin (**siphonal notch**) often lying in a plane more or less perpendicular to the axis; and this outlet in some groups lies at the extremity of a narrow prolongation of the aperture known as the **siphonal canal.** The latter may be straight, bent, or curved, and is a slender, fragile structure in some species of *Fusinus, Murex,* and other genera. The slender rostrum present in such genera as *Aporrhais* and *Tibia* is not to be mistaken for a siphonal canal. In *Aporrhais* the siphon draws in its current of water through a broad sinus between the rostrum and the outer lip. A small notch of the apertural margin between the columella and outer lip does not necessarily indicate the presence of a siphon. Such a notch is present in some species of the pulmonate genus *Achatina,* in which, of course, there is no siphon.

In some shells the outer and parietal lips meet at the end of the suture in an acute angle to which a distinct groove may lead. A short ridge (**parietal ridge**) situated on the parietal lip a short distance from the suture in some species of the Cerithiidae and other families delimits a small recess in this corner of the aperture. The function of the ridge is unknown. The term "posterior canal" has been applied to this corner of the aperture when narrow and produced, and the mantle fold occupying it, although not a definite siphon, presumably serves (at

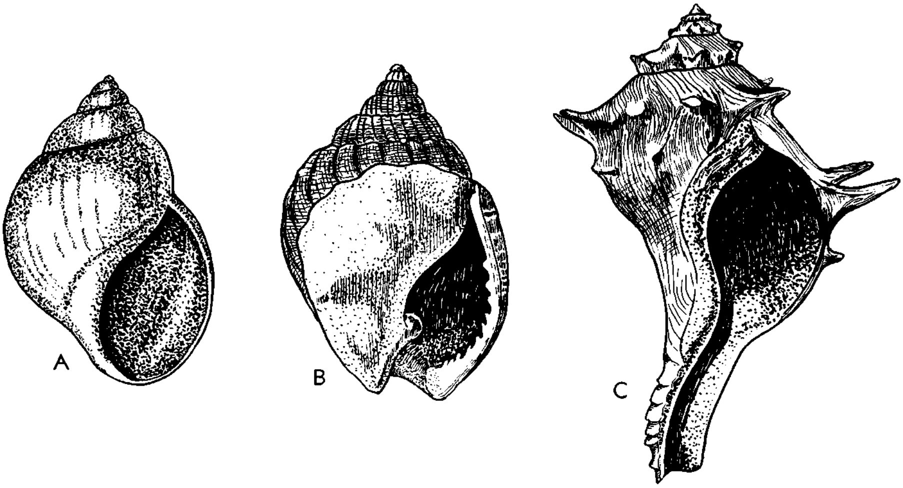

FIG. 72. Holostomatous and siphonostomatous shells.——*A. Ampullella bulimoides* (D'ORBIGNY), L.Cret., Fr., ×0.7 (78).——*B. Nassarius johnsoni* (DALL), Mio., Fla., ×2 (116).——*C. Busycon (Echinofulgur) echinatum* (DALL), Plio., Fla., ×0.8 (116).

least in some species) as an exhalant channel. In some genera of the Strombacea (e.g., *Rimella*) the aperture is continued adapically by a narrow, parallel-sided channel, which may ascend high up the spire and, in some species, ultimately descend again on another side. This channel is not formed until the shell is full-grown. Some authors have assumed that it has an exhalant function, but this has still to be confirmed by observations on the living gastropod. It seems to be equivalent to one of the labral digitations that occur in this superfamily and are mentioned below. In a group of land operculates belonging to the family Cyclophoridae, a narrow tube projects or extends along the suture from where the latter terminates at the margin of the aperture. It is regarded as a device for breathing when the aperture is closed by the operculum.

In some families the outer lip has a parallel-sided slit or a deep sinus. A slit occupies a peripheral position in the Bellerophontacea, and in the Pleurotomariacea it is most commonly either peripheral or on the adapical side of the periphery, but exceptionally (as in the Luciellidae and Portlockiellidae and in *Cataschisma*) it may be on the abapical side of the periphery. In the Nerineidae and Conidae such a slit adjoins the suture. The presence of the slit enables feces and excrement to be discharged where they are not likely to foul the inhalant current. In the Turridae a sinus of varying depth at the shoulder of the whorl or on the ramp between it and the suture fulfills a similar function. In *Haliotis* and a few other genera, a row of orifices (**tremata**), and in the Mesozoic genus *Trochotoma,* a single elongated orifice, also serve or served this purpose.

In some species the thickness of the outer wall of the last whorl remains constant as far as the apertural margin, or this margin may even be somewhat sharpened. Often, however, the outer lip becomes thickened (**varicose**) when spiral growth of the shell is complete, and it may be thickened at intervals before this stage, during growth halts. The thickening may be on the inner or outer sides, or partly on both. In some forms the shell wall is turned outward and backward (**reflected** or **everted**) at the apertural margin, or else inward (**inflected**), as in the Cypraeidae. In *Cassis* it is both thickened on the inner side and has a thin marginal reflection. The outer lip in many forms bears crenulations, ridges, denticles or spines at its edge, while just within the aperture the outer wall may bear threads or thicker ridges, often termed **lirae.** These correspond to depressions on the exterior of the shell. In some genera of the Strombacea the outer lip is greatly expanded at full growth, sometimes forming a **wing,** one side

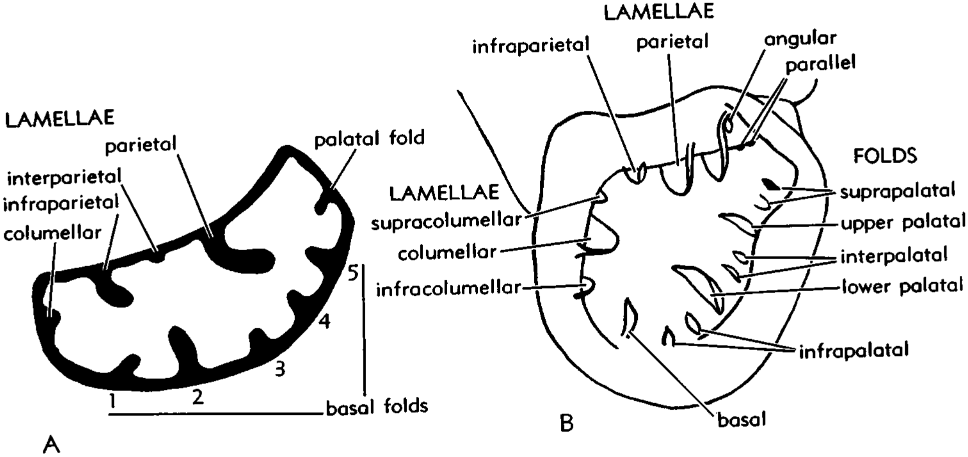

FIG. 73. Apertural lamellae and folds; terminology in *(A)* Strobilopsidae and *(B)* Pupillidae (131).

of which may adhere to the spire. Fingerlike processes (**digitations**) project from the wing. The habits of the living species *Aporrhais pespelicani* (LINNÉ) do not change when the wing develops and its function, if any, is unknown.

The inductura may extend over the columella, as well as over the parietal region, and its margin may become very distinct abapically and detached in many genera, forming a thin wall. This is conspicuously developed in *Cassidaria,* for example. When there is a well-defined siphonal notch in the apertural margin, lamellae marking its successive growth stages frequently form a rounded or angular ridge (**siphonal fasciole**) (Fig. 64), which disappears beneath the margin of the inductura. The siphonal fasciole may sweep around in so broad a curve that it surrounds a well-marked cavity (**false umbilicus**).

In some groups the whole inner lip is modified considerably by additional shelly matter. In *Nassarius* and *Phalium* the inductura becomes detached even adapically, forming a broad, flattened expansion of the lip. In the Cypraeidae a thick coating extends over the whole surface of the apertural side of the last whorl, which it more or less flattens. An adapical extension of this coating forms the margin of a canal-like outlet at that end of the aperture, while further shelly matter greatly broadens the abapical part of the inner lip, leaving in many forms a median depression or **fossula.**

In the Neritidae a wide, flattened plate of shelly matter, sometimes termed a septum, projects from the last whorl so that its oblique, often denticulate edge forms the inner lip, the columella and most of the internal walls of the shell having disappeared by resorption. It is proposed to employ the term **labial area** for the surface of this plate or any similar more or less flattened surface, the margin of which is formed by the inner lip. In some species of the Phymatopleuridae the parietal surface is commonly resorbed and smoothed. The labial area frequently bears folds, ridges, denticles, and other protuberances not connected with the whorl ornament. Strong transverse ridges occur on it in the Cypraeidae, Cassididae, and other families, and in some Neritidae it bears groups of pustules or weak oblique ridges. Strong folds of the inner lip which pass spirally up the interior of the shell are discussed in the section on internal shell features.

Teeth, folds, and lamellae protruding from various parts of the peristome and constricting the aperture are found in many genera of land pulmonates. Lamellae are particularly numerous in the Clausiliidae. Figure 73 indicates the terms applied to them in the families Pupillidae and Strobilopsidae. The adjective **palatal,** applied to structures located on the outer lip, is to be noted.

## UMBILICUS

The old terms "perforate" and "imperforate," applied to a shell in order to denote the presence or absence of an umbilicus, are inappropriate and best abandoned. The alternative adjectives **umbilicate** or **omphalous** may be used in the first connection, and **nonumbilicate** or **anomphalous** in the second. If the umbilicus is completely open at its entrance, the shell is described as **phaneromphalous,** if partly plugged there by shelly matter, as **hemiomphalous,** and if a plug completely obscures its presence, as **cryptomphalous.** The European Eocene species, *Cepatia cepacea* (LAMARCK), in which the umbilicus is hidden by a convex wad marking the termination of the inductura, is a good example of a shell of the last type.

Being enclosed by the adaxial part of the helicocone wall, the umbilicus in most shells is a spiral cavity with the wall of each coil bulging inwards towards the axis. In some shells the boundary of the umbilicus at its opening in the base of the shell is marked by a well-defined angulation, or perhaps a beaded cord, but its margin is often indefinite, particularly when the shell is smooth. In *Globularia* and some related genera an angulation, termed a "rim" by WRIGLEY and a *"limbe"* by French authors, continues or branches off from the sharp margin of the outer lip, encircling the umbilical opening and ascending spirally into the umbilicus. Between it and the margin of the inner lip is a smooth, rather flattened band termed a "sheath" by WRIGLEY. A rather similar ridge, originating somewhat higher on the inner lip, is present in some species of *Angaria* and *Turbo,* and marks the limit to which the shell ornament extends. In many Naticidae a thick cord of shelly matter, semicircular in cross-section, ascends spirally into the umbilicus from near the middle of the inner lip and is termed the **funicle.** In some umbilicate Nerineacea, folds of the adaxial wall of the whorls project into the umbilicus, as well as into the shell interior. In families such as the Architectonicidae, in which there is a broad umbilicus, this surface of the whorls frequently has its own system of ornament, differing from that on the spire.

## GROWTH LINES AND ORNAMENT

Successive stages of growth at the aperture remain marked on the surface of the shell by growth lines, which may or may not stand out in relief. Long growth halts are sometimes indicated by more conspicuous markings (**growth rugae**) or, in some genera, by prominent ribs (**varices**). From a study of the growth lines it is possible to reconstruct the shape of the outer lip even when the aperture of the shell is damaged. A growth line, or part of one, leaning in the direction of growth of the helicocone (i.e., to the left in a dextral shell as usually viewed) is described as **prosocline;** if leaning away from this direction, as **opisthocline;** and if crossing the whorl in a direction perpendicular to the suture, as **orthocline** (Fig. 74). Growth lines frequently have a simple or sigmoidal curve. If arched forward they may be termed **prosocyrt,** if backward, **opisthocyrt** (Fig. 74). In shells in which a sinus or slit is present in the outer lip, its track, as clearly indicated by the growth lines, forms a band, termed an **anal fasciole,** on the surface of the shell. Its position and characters may serve as a basis of classification, as in the family Turridae. If, as in most Pleurotomariacea, the outer lip has a parallel-sided slit or a narrow notch, this generates on the surface of the whorls a narrow, well-defined band on which the growth lines form a series of crescents or **lunulae,** because the end of the slit or notch is usually more or less semicircular. This type of anal fasciole is termed a **selenizone** (slit band in older literature).

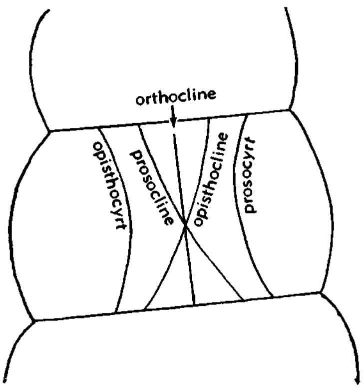

FIG. 74. Directional terminology for growth lines in dextral shell (115n).

The relief pattern present on many gastropod shells is variously termed **ornament,** ornamentation, or sculpture; the first term is here preferred. Gastropod ornament has two components. **Collabral ornament** results from rhythmic or periodic fluctuations in the shell-secreting activity of the whole

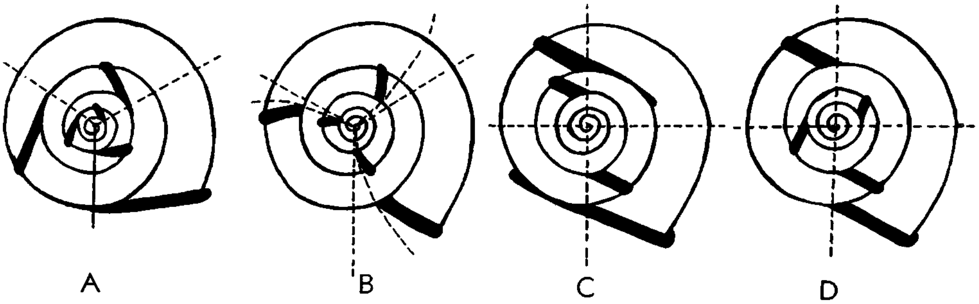

FIG. 75. Arrangement of varices in Cassididae (108); *(A) Cassis flammea* (LINNÉ); *(B) Phalium strigatum* (GMELIN); *(C) Phalium plicaria* (LAMARCK); *(D) Phalium glaucum* (LINNÉ). The shells are viewed in plan from above the apex; all reduced.

mantle edge, producing elevations and depressions parallel with the outer lip (labrum) and growth lines. **Spiral ornament,** passing continuously round the whorls parallel with the suture, is the result of differential secretory activity of various parts of the mantle edge. Elements of ornament that are markedly oblique both to the direction of growth and to the growth lines occur much more rarely in the gastropods than in the pelecypods. Among forms in which such ornament is present are the Paleozoic Luciellidae and *Planozonides*. The protoconch of the living genus *Philbertia* (Fig. 86*A,C*) has oblique reticulate ornament. The term **axial** has been much used for elements of ornament which are more or less parallel with the axis, but is clearly inappropriate for depressed shells. The term **transverse** is applicable to any element crossing a whorl in a direction which would intersect both sutures. In certain Turridae ribs passing transversely across the whorls are not exactly collabral.

There is such great variety in the elements of gastropod ornament that it is difficult to devise a precise descriptive terminology for them. Collabral elements are described as threads, riblets, costae (or ribs) and varices according to their width and prominence; while spiral elements include striae and grooves, if depressions, and threads, cords, ribbons, bands, carinae, astragals, etc., if elevations.

The elements of spiral ornament may override the collabral elevations or be confined to their intervals. Various patterns are formed by a combination of the two types of ornament. When narrow elements of both types intersect, the resulting pattern is described as **cancellate.** Rounded protuberances termed **tubercles** if large, **pustules** if somewhat smaller, or **granules** if small, or pointed ones termed **spines,** often occur where spiral and collabral elements intersect, or they may be present on the costae even in the absence of spiral ornament. In the Muricidae vaulted scales protrude from the varices and costae where these are crossed by the spiral elements. Spiral grooves or striae present on some shells may have a series of minute depressions (**puncta**) and are then said to be **punctate.** When both transverse and spiral elements are broad and low, the spiral depressions may consist of rows of rounded pits.

Costae may extend right across a whorl from suture to suture or only across part of the whorl. In some shells they are in exact alignment across successive whorls, in others they are in partial alignment, and in still others they have no tendency to alignment. When varices are interspersed with costae of normal prominence, their distribution is often related to the coiling of the whorls. In some Muricidae varices, three to every whorl, are aligned down the sides of the shell. In the Cymatiidae and Bursidae they are also in alignment, but are present only on alternate whorls. WRIGLEY (108) has shown that when some Cassididae (Fig. 75) are viewed in plan from above the apex, the angular intervals between successive varices (reckoning backwards from the aperture) are 225°, 225°, 270°, 225°, 225°, 270°, etc. Each cycle of three varices thus occupies a total angle of coiling of 720°, that is, two complete whorls. Nevertheless, there are shells in which the distribution of varices follows no regular plan.

## INTERNAL CHARACTERS OF SHELL

As fossil gastropods frequently occur in the form of internal molds (termed "steinkerns" by some workers), the internal characters of the shell are of interest to paleontologists. Internal molds of thick-shelled species often differ considerably in appearance from the original shell, as in some Cypraeidae, where the mold shows spiral coiling which is obscured by enamel on the exterior of the shell. In thin-shelled forms, such as some Tonnidae, the main features of the external ornament are impressed on the interior of the shell, but in thick-shelled forms there are traces only of the more prominent carinae and tubercles. When, as in many Muricidae, Cymatiidae, Bursidae, and Cassididae, a thickened outer lip with internal denticles and lirae is formed periodically during growth halts, denticulate ribs often remain on the interior of the shell, producing pitted grooves on the internal molds. There is an elaborate pattern of circular pits on internal molds of some species of *Campanile.*

Folds present on the columellar lip in genera of certain families, such as the Volutidae, Mitridae, Cancellariidae, and Vasidae, remain coiled spirally around the columella almost to the apex; they are termed **columellar folds** (Fig. 64). When the aperture has a siphonal notch or canal, this may be represented by a distinct fold (**siphonal fold**) on the abapical part of the columella of each whorl. Most genera of Nerineidae and Itieriidae have internal folds of varying prominence and complexity, and these are alluded to as **columellar, parietal, palatal,** and **basal folds** according to their respective situation on the columella, the adapical wall of the whorl, the outer wall, or the basal or abapical wall (part overlapped by a succeeding whorl and backing on to its adapical wall). In certain genera of these families the internal folds are so elaborate that the space left for the soft parts to occupy was very restricted and tortuous (Fig. 76). The same condition existed in some of the Soleniscinae.

In some shells the tip of the visceral spiral becomes withdrawn from the earlier whorls during growth, and these are completely filled with shelly matter (as in *Terebra*) or else sealed off at intervals by irregularly spaced septa. In some genera the internal walls of the shell are removed by resorption. The process is only partial in the Cypraeidae and Conidae, in which the walls are reduced to considerable tenuity. Their complete removal takes place in the Neritidae and Ellobiidae and in the genus *Olivella,* among other groups.

In coiled shells the head-foot mass is attached to the columella by a broad, partly coiled columellar muscle (Fig. 53). The attachment area, which is situated within

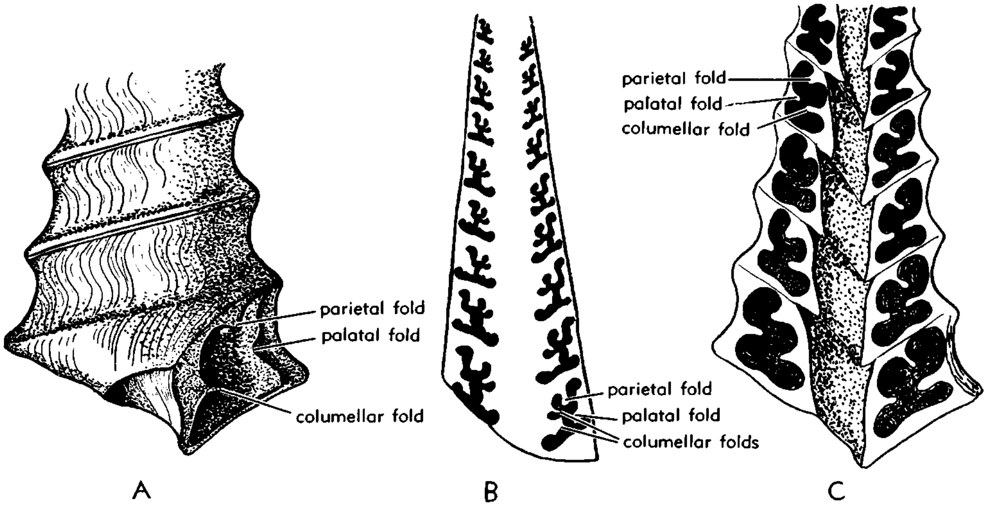

FIG. 76. Internal characters of the shell in Nerineidae; *(A,C) Cossmannea dilatata* (D'ORBIGNY), U.Jur., Fr., internal folds as seen in axial section and at aperture, ×1 (128); *(B) Bactroptyxis brevivoluta* (HUDLESTON), M.Jur., Eng., axial section, ×2 (121).

the last whorl some distance back from the aperture, advances progressively as the shell grows, but rarely leaves an easily visible scar. In *Bellerophon* and *Sinuites* there are two symmetrically arranged muscle scars on the adaxial wall of the last whorl half a coil back from the aperture. Patelliform shells often retain distinct muscle attachment scars. Usually the scar has the form of a horseshoe and is open on the anterior side.

In some genera of the Capulidae and Calyptraeidae, which have a depressed, cap-like shell, there is a thin internal process projecting from part of the wall of the shell. It ranges from a cap-shaped structure projecting from near the middle of the shell (as in *Crucibulum*) to a thin, flat plate attached around part of the margin (as in *Crepidula*). Its function appears to be to help the animal to remain secure to its shell.

## STRUCTURE OF SHELL

In living gastropods the calcareous shell, at least at some period during growth, has a coating of horny material (**conchiolin**) known as the **periostracum** or **epidermis.** This protects the shell against the chemical or solvent action of the moist medium in which the mollusk lives. It varies greatly in thickness and its surface, although plain in many species, in others is covered with hairs or bristles. It soon disappears when the animal dies and it is not preserved. The same is true of other conchiolin parts such as most operculae.

The solid shell is an aggregate of crystals of calcium carbonate, with traces of other chemical substances, penetrated by a fine membranaceous network of organic material. Analyses of gastropod shells belonging to 20 different living marine species, published by CLARKE & WHEELER (15), show that organic matter and combined water together account for from 1.14 to 9.06 per cent of the total weight, the most common amount being about 2 per cent. Calcium carbonate forms at least 96.6 per cent and usually about 98 per cent of the total amount of inorganic constituents. Small quantities of silica, alumina and oxide of iron occur in most shells, and in some there is a small amount of magnesium carbonate. The shells of land gastropods often contain calcium phosphate. A later work of reference in this connection is that of VINOGRADOV (104).

The calcium carbonate of gastropod shells occurs mainly as aragonite, but calcite is present in some species.. BØGGILD (6) refers to a *Bellerophon* shell which proved to consist entirely of calcite, but secondary change is to be suspected, although he considered it to be "without doubt the original structure." X-ray analysis of some Pennsylvanian bellerophontids preserved in a bituminous matrix, according to KNIGHT, shows two shell layers, the outer one calcitic and the inner one aragonitic but lacking the lamellar structure that characterizes the nacreous layers of pleurotomariids, trochids or turbinids (KNIGHT, *in litt.*). The same author recognizes several distinct types of shell structure, as determined by the mode of crystal aggregation, and two or more of them are present as distinct layers in most shells.

**Nacreous structure** (always originally of aragonite) is formed by thin leaves of equal thickness (less than 0.001 mm.), which are parallel with the shell surface or almost so, and are separated by equally thin leaves of an organic substance, so that they flake away very easily. Nacre has a characteristic pearly luster, and forms the inner layer of the shell in a great many Archaeogastropoda, although not in all. Unpublished X-ray investigations indicate that the nacreous layer of molluscan shells may be altered in fossilization to calcite without losing its characteristic luster and probably laminar structure. Conditions rather than time seem to have been the controlling factor. Thus in some Ordovician gastropods and Upper Cretaceous ammonites with excellent luster, X-ray diffraction methods have shown that the nacre consists of calcite, whereas in certain Upper Carboniferous ammonites and nautiloids it remains as aragonite (information from J. B. KNIGHT).

**Crossed-lamellar structure** (aragonite except in a few rare instances) is the most frequent structure of the layers of gastropod shells. It consists of more or less rectangular, parallel lamellae which are perpendicular to the surface of the shell, with their long side parallel to it (Fig. 77). Their thickness is of the order 0.02 to 0.04 mm., and each (when the structure is most regular) is as wide as the thickness of the shell layer to

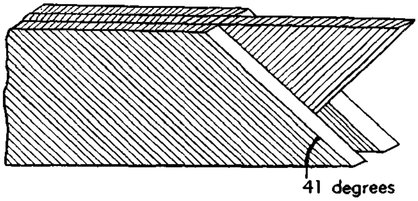

FIG. 77. Crossed-lamellar structure (6). Parts of three lamellae of the first order are seen, each composed of thin lamellae of the second order inclined in alternate directions; the top (narrow) face of the primary lamellae is usually parallel with the surface of the shell; much enlarged.

which it belongs and up to several mm. in length, thinning out as a wedge between other lamellae at each end. These primary lamellae are built up of parallel lamellae of a second order, which are less than 0.001 mm. thick and lie transverse to the primary lamellae; they are inclined to the longer side of the latter at an angle of 41 degrees, the direction in which they slope alternating in adjacent primary lamellae.

The prismatic structure is confined to calcite layers in the great majority of gastropod shells, but *Buccinum undatum* has an outer layer of prismatic aragonite. The regularity of the structure varies considerably in different species. The prismatic layer is most commonly the outer one, and the prisms are usually perpendicular to the surface, but in some shells (e.g., Neritidae) they are oblique or parallel to the surface. Among species examined by BØGGILD, an outer calcitic prismatic layer was found to be present in all Scalidae, Janthinidae, and Neritidae, and in some Patellidae, Fissurellidae, Littorinidae, Muricidae, Thaididae, and Fusinidae, among other families. In some *Haliotis* shells a layer of prismatic calcite was found to lie between aragonitic layers.

Structure of the type termed homogeneous by BØGGILD is found in the heteropods and pteropods, the mineral being aragonite in these groups. The calcium carbonate appears structureless in ordinary transmitted light, but under crossed nicols whole areas extinguish in one direction. The **foliated structure** described by the same worker is confined to calcite, and consists, like the aragonite nacreous structure, of parallel flakes of the mineral. He mentions its presence in species of *Bellerophon* and *Patella*. KNIGHT is doubtful of the described structure in *Bellerophon*.

**Grained structure**, confined to calcite, consists of a mass of grains irregular in shape and in optical orientation. There are transitions between it and prismatic structure, and it is stated to occur in *Janthina* and in some species of *Scala*.

The **complex structure** studied by BØGGILD, confined to aragonite, is a highly irregular modification of crossed-lamellar structure. It forms the inner shell layer of some species of *Nerita*.

It will thus be seen that the structure of gastropod shells is highly varied. The great majority of such shells, including all opisthobranchs and pulmonates, are formed of three, four, or in some of more than four distinct layers, all with crossed-lamellar structure, the direction of the primary lamellae differing in the various layers. In the majority of higher prosobranchs the number of layers is three, the primary lamellae of the middle layer being perpendicular to those of the innermost and outermost layers.

In the course of fossilization aragonitic shells are usually the first to disappear by solution. Hence, in many formations gastropod shells are represented only by molds, with the exception of those belonging to such genera as *Scala*, in which the shell is partly calcitic. Replacement of original aragonite by calcite is also very common.

## COLOR PATTERN

Many living gastropods have a color pattern, simple or elaborate, which is a great aid in specific recognition. Like the relief ornament or sculpture, this may be resolved into two components, a spiral one marking a tendency of particular parts of the mantle edge to secrete pigment continuously, and a transverse component, marking a rhythm in secretory activity. The transverse component, however, shows more tendency to be oblique to the growth lines than in the case of the relief ornament, and in some species it consists of zigzagging lines or of loops. The lighter and darker spiral color bands respectively coincide with or else represent raised sculptural bands and depressions (109).

The biochemistry of shell pigments has been the subject of recent work. It is thought that the secretion of pigment is primarily a means of disposal of waste products of metabolism, although color patterns may play their part in natural selection. Thus the color of some marine gastropods harmonizes well with that of the seaweed on which they live and some species of *Ovula* are either yellow or red, depending on the color of the *Gorgonia* with which they are associated. The color pattern of some land snails may serve to render them less conspicuous in their surroundings.

That color patterns are not necessarily protective is shown by the fact that many marine shells in which they are particularly elaborate are, in actual life, coated with a thick periostracum. A distinction can be drawn between pigments (indigoids, pyrroles) which can be extracted from a crushed shell by solution in acid, and a group (melanins) which is intimately associated with the conchiolin of the shell and insoluble in acid. Pigments of the first group occur mainly in the Archaeogastropoda and

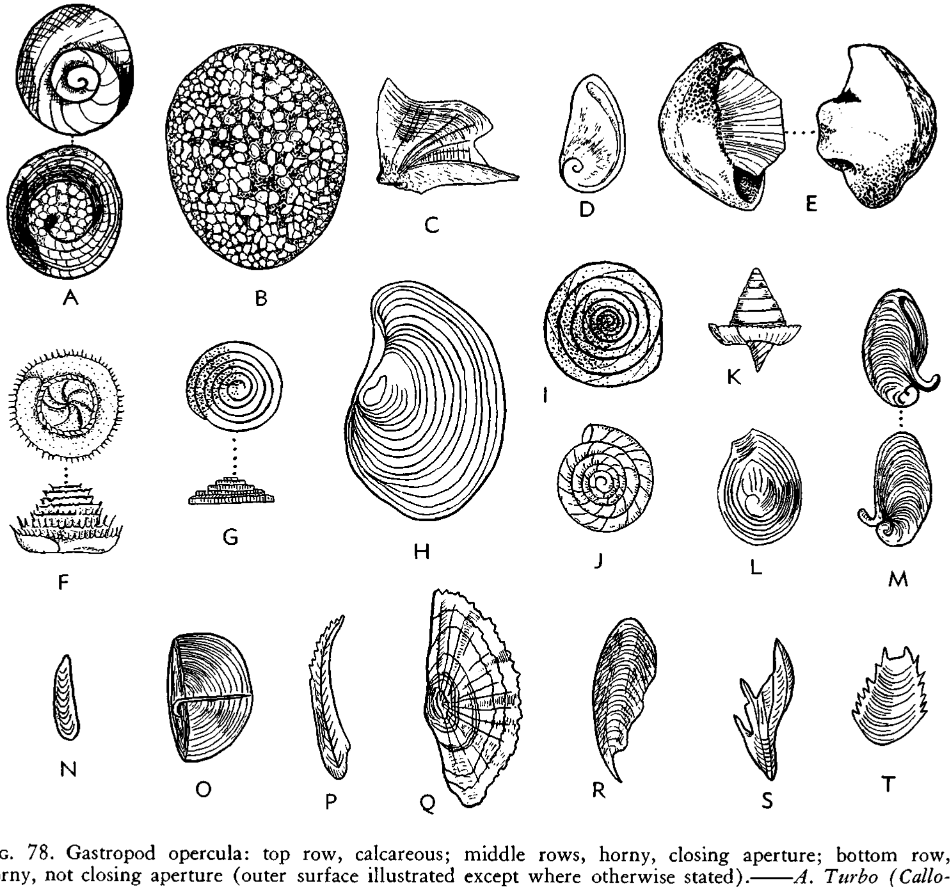

FIG. 78. Gastropod opercula: top row, calcareous; middle rows, horny, closing aperture; bottom row, horny, not closing aperture (outer surface illustrated except where otherwise stated).——*A. Turbo (Callopoma) saxosus* WOOD, Rec., W.C.Am., inner surface above, ×1 (20).——*B. Turbo sarmaticus* LINNÉ, Rec., S.Afr., ×1 (115n).——*C. Septaria janelli* (LEGUILLOU), Rec., E.Indies, ×1 (115n).——*D. Natica multipunctata* WOOD, Plio., Eng., ×1 (137).——*E. Neritopsis radula* (LINNÉ), Rec., IndoPac., inner surface on left, ×2 (115n).——*F. Tenagodus bernardi* MÖRCH, Rec., Austral., side view below, ×3 (35).——*G. Palaeocyclotus exaratus* (SANDBERGER), U.Eoc., Italy, side view below, ×6 (133).——*H. Pila reflexa* (SWAINSON), Rec., W.Indies, ×1 (20).——*I. Cittarium pica* (LINNÉ), Rec., W.Indies, ×0.7 (115n).——*J. Aulopoma grande* (PFEIFFER), Rec., Ceylon, ×1.3 (115n).——*K. Torinia variegata* (GMELIN), Rec., IndoPac., ×2 (35).——*L. Gabbia australis* TRYON, Rec., Austral., (89). ×6——*M. Rissoina inca* D'ORBIGNY, Rec., Peru, inner surface above, much enlarged (35).——*N. Conus* sp., Rec., ×2 (20).——*O. Rissoella globularis* (FORBES & HANLEY), Rec., Eng., much enlarged (35).——*P. Strombus pugilis* LINNÉ, Rec., W. Indies, ×1 (20).——*Q. Cassis tuberosa* (LINNÉ), Rec., Brazil, ×1 (35).——*R. Struthiolaria scutulata* (MARTYN), Rec., N.Z., ×2 (115n).——*S. Terebellum terebellum* (LINNÉ), Rec., IndoPac., ×4 (115n).——*T. Alectrion (Xeuxis) dispar* (ADAMS), Rec., IndoPac., ×2 (35).

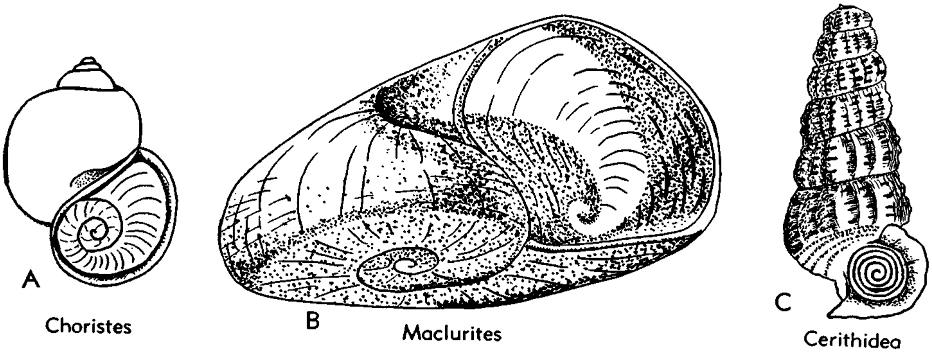

FIG. 79. Spiral opercula of dextral gastropods (the middle one hyperstrophic), showing counter-clockwise coiling of outer side.——*A. Choristes elegans* CARPENTER, Rec., N.Am., ×5 (32).——*B. Maclurites logani* SALTER, Ord., N.Am., ×0.75 (115n).——*C. Cerithidea obtusa* (LAMARCK), Rec., IndoPac., ×1.1 (114).

the tectibranch opisthobranchs, while the second group is found in the higher prosobranchs and in the pulmonates (16-18).

Gastropods retaining traces of color pattern are known from Ordovician beds onward. It is particularly persistent in the Neritacea, being preserved in some specimens of *Naticopsis* from the Devonian and Carboniferous, and commonly in *Neritoma* from the Jurassic and in *Theodoxus* and related genera from later formations. Its preservation is moderately common in *Pseudomelania* from the Jurassic but much less so in other genera, such as *Mourlonia* of the Carboniferous. It is noteworthy that the color pattern may persist in silicified shells (for example, in many specimens from the Upper Carboniferous and Permian of North America) even when they have been etched out with hydrochloric acid.

## SOLID STRUCTURES ASSOCIATED WITH SHELL

The **operculum** is usually the only solid accessory to the shell (Fig. 78). It is present in the majority of prosobranch genera, although absent in many Cancellariidae, Conidae, Harpidae, Marginellidae, Volutidae, Mitridae, Cypraeidae, and Tonnidae. It is absent in all adult opisthobranchs, except the Acteonidae and Pyramidellidae, and in all pulmonates, except *Amphibola.* The primary function of the operculum, which is secreted and borne by the rear part of the dorsal side of the foot, is to close the aperture when the head-foot mass has retreated into the shell, but in many forms in which it is present, it is much reduced and does not serve this purpose. It may sometimes have a secondary use. Thus, some species of *Lambis* and *Strombus,* in which the operculum is long and sharp, make use of it for progression, digging it into the sand and then extending the foot by a sudden movement. The Xenophoridae also make use of the operculum in locomotion.

Most opercula are light structures of horny material, but some, including the massive bodies found in certain Turbinidae, are calcareous. Most calcareous opercula (but not that of *Septaria*) conform with the shape of the aperture of the shell. Some 20 main types of opercula have been distinguished (95), and these have been divided into three main classes according to whether their structure is spiral, concentric, or lamellar. Most opercula are flat and platelike, but conical and cylindrically spiral types occur. The circular, spiral form with numerous volutions seems to be most primitive. In dextral gastropods the operculum, if spiral, always grows in a direction that is counter-clockwise when its outer surface is viewed (Fig. 79), while in sinistral forms the direction is opposite. This provides a means of distinguishing between a truly sinistral and a hyperstrophic dextral shell when a spiral operculum is preserved with it. In this way we know that the Ordovician gastropod *Maclurites* was hyperstrophic. WRIGLEY (110) has described the complicated internal structure of the calcareous operculum of *Natica.*

Only calcareous gastropod opercula have been described in the fossil record, and they are rare except in certain formations. In the family Oriostomatidae (Silurian-Devonian) the operculum is multispiral and domed, with the thickness exceeding the diameter in some species. Fossil *Neritopsis* opercula have been mistaken for cephalopod jaws and allotted the generic names *Peltarion* Eudes-Deslongchamps (Liassic, France), *Cyclidia* Rolle (Tertiary, Rumania), *Scaphanidia* Rolle (Liassic, England, and Cretaceous, Germany) and *Rhynchidia* Laube (Triassic, Tyrol). A Cretaceous fresh-water gastropod, *"Ampullaria?" powelli* Walcott, originally thought to be Carboniferous in age, has a flat, oval, calcareous operculum of the "concentric" type. Opercula very similar to that of this species and resembling those of *Viviparus,* except for their calcareous composition, abound in a thin layer of nonmarine origin in the Pliocene Etchegoin Formation in the San Joaquin Valley of California, and were described by Hanna & Gaylord as *Scalez petrolia.*

Mention must also be made of the **epiphragm** secreted by some pulmonate gastropods to function as a temporary operculum, sealing the aperture during winter hibernation or dry-weather estivation. Merely a thin membrane in some genera, in certain species of Helicidae it is a strong disc of calcium carbonate formed by the hardening of a white sticky fluid secreted by the mantle. When the animal again becomes active the epiphragm is pushed aside and discarded. There is no reason why these bodies should not be found in deposits containing fossil land shells.

A further type of accessory to a gastropod shell is the calcareous support constructed and cemented to the substratum by certain Hipponicidae, in which the animal is sessile. This support, secreted by the foot, is held by a strong muscle, and when the shell rests upon it, its opening is tightly sealed. In *Rothpletzia* the support is a conical or cylindrical structure which is much deeper than the actual shell.

A unique type of calcareous structure within the shell is the **clausilium** found in the land pulmonate genus *Clausilia.* It is a narrow, thin, curved plate with a stalklike process at one end which curves around the columella; it lies within the last whorl well back from the aperture. It functions as an operculum by sliding into position to close the shell when the head-foot mass is well withdrawn into it.

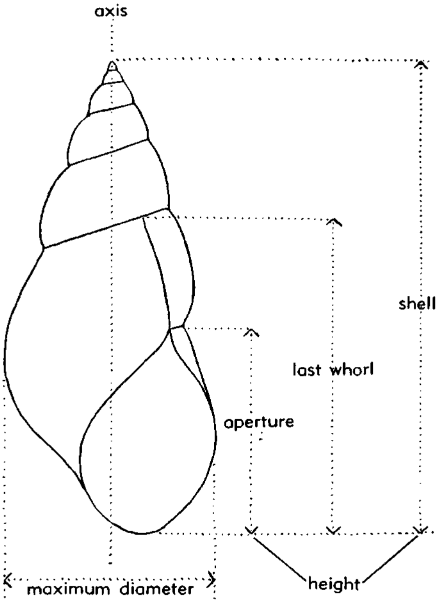

Fig. 80. Standard measurements of a conispiral gastropod shell (115n).

## MEASUREMENT OF GASTROPOD SHELLS

Certain standard measurements are usually given when gastropod shells are described. Other measurements, chosen according to the type of shell under consideration, have been used in various statistical studies and cannot here be discussed. The standard measurements are made in directions either parallel with or perpendicular to the axis of the shell.

The **height** of a shell or of its spire, last whorl, or aperture, is for most genera defined as the perpendicular distance between two planes perpendicular to the axis and touching both extremities of the shell or of the part measured (Fig. 80). It should be noted that the heights of the spire and of the aperture are together equal to that of the whole shell, and that the measurement usually given as the height of the last whorl is the sum of the height of the aperture (i.e., of the ultimate height of the helicocone) and of the distance (parallel with the axis) advanced by the adapical side of the helicocone when describing the last coil. The measurement usually cited as the height of any preceding whorl, however, is the projection on to the axis of the distance between the two sutures of the whorl at some selected position; it is the distance there advanced by the adapical side of the helicocone when describing a complete coil. With depressed shells it is preferable to record the breadth of any whorl, that is, the actual distance from suture to suture.

The maximum (or major) and minimum (or minor) **diameters** of the shell are, respectively, the maximum and minimum distances between two planes parallel with the axis and touching the shell on exactly opposite sides. In most shells the maximum diameter lies between the outer lip and the opposite side, and the minimum diameter is perpendicular to this.

The main difficulty likely to arise when these measurements are made is that of determining the exact direction of the axis. Slight differences in the tilt of the shell do not greatly affect the measurements of height, but often appreciably affect those of diameter. For this reason, BOYCOTT (10) preferred to define the diameter of the shell as "the greatest dimension that can be found starting with the edge of the lip to a point on the opposite side of the shell on the last whorl." The direction of this measurement may be very oblique to the axis.

It must be added that in certain groups, such as the Bellerophontacea and Cypraeacea, the custom has arisen of taking as the "height" of the shell a measurement not determined in the way stated above. The height of a patelliform shell is that of a perpendicular from the apex to the plane of the aperture, the length is the anteroposterior diameter of the aperture, and the breadth is the diameter of the aperture from left to right.

The angular measurements of a shell most frequently recorded relate to the spire and to the slope of the sutures (Fig. 81). If the whorls increase in diameter at a regular rate, straight lines can be drawn from the apex or from just above it (since the apex is not a mathematical point) so as to touch all the whorls. The **spire angle** (or spiral angle) is the angle between two such lines passing down opposite sides of the shell. The angle between straight lines touching any two adjacent whorls on opposite sides of the shell may be termed the **incremental angle** of that part of the shell. When the whorls in question are near the apex, the incremental angle is known as the **apical angle.** In a coeloconoid shell the incremental angle increases steadily during growth, and in a cyrtoconoid shell it decreases steadily. It is sometimes useful with shells of these types to cite the **mean spire angle,** measured by the angle between straight lines joining the apex to the periphery of the last whorl on opposite sides of the shell.

The steepness of coiling of any particular part of a shell is best measured by the angle between the suture, viewed normally to the axis so as to appear as a straight line, and

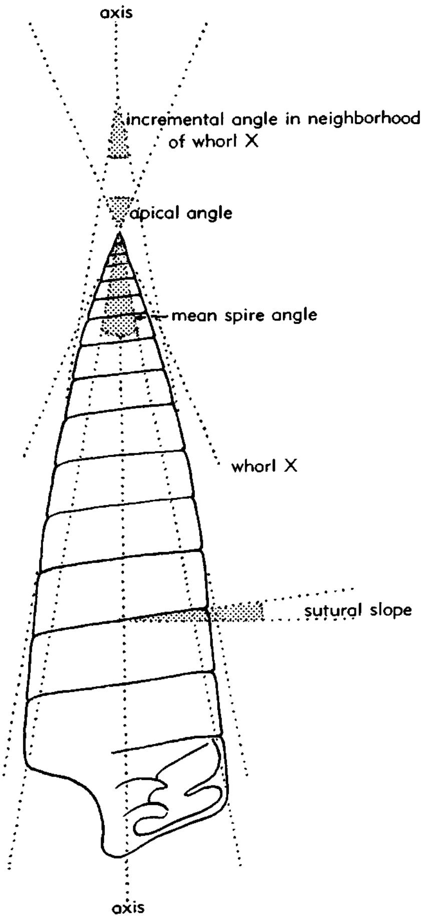

FIG. 81. Angular measurements of a conispiral gastropod shell. When the whorl diameter increases at a constant rate the apical angle, incremental angle, and mean spire angle are identical, and may be termed the spire angle (115n).

a plane perpendicular to the axis. This may be termed the **sutural slope.** This measurement is termed the "sutural angle" by many writers, but, as originally defined by D'ORBIGNY (the pioneer of conchological measurement or conchometry), the sutural angle is the angle between the suture, viewed as stated, and a line down the side of the shell touching the whorls (78).

## SHELL GROWTH IN RELATION TO LIFE HISTORY

So far as is known, the coiling of a gastropod shell has no periodicity. Regularity in the distribution of varices on the whorls of a shell in some forms shows that growth halts and coiling may be interrelated, but it is unknown if they are influenced by external factors. In some species growth of the spiral shell continues throughout life. This is the case with *Trochus niloticus* LINNÉ, specimens of which attain an age of ten years in the Andaman Islands, their growth slowing down towards the end but never ceasing. In the Zonitidae, a terrestrial group, many species are stated to add to their whorls almost indefinitely, the rate of growth varying with the season and food supply. In many species, however, growth of the shell ceases long before the death of the animal, and at full growth definite structures of the aperture, such as the winglike outer lip of *Aporrhais,* are in some forms developed for the first time. In full-grown specimens of *Campanile* from the English Eocene, the heavy shell is much worn down on the same side as the aperture, suggesting that it lived long enough after growth had ceased for such abrasion to occur by continual dragging of the shell along the sea floor. In some gastropods the last whorl of the full-grown shell is more irregular in shape or more loosely coiled than the preceding ones.

In many shells secretion of calcium carbonate continues when growth has finished. It usually takes place from the entire surface of the mantle, thickening the shell walls from the interior, especially near the apex.

## SEXUAL DIMORPHISM IN PROSOBRANCH SHELLS

The sexes are separate in most prosobranchs (*Valvata* being the most important exception), while the pulmonates and opisthobranchs are hermaphrodite. Sexual dimorphism, if present in the first group, affects both size and proportions of the shell, the females, when full-grown, tending to have larger and broader shells than the males (Fig. 82). Extreme cases are those of *Lacuna pellucida* DA COSTA and *Crepidula plana* SAY, female shells of which at certain stations were found respectively to average 10 and 15 times the weight of the males. In many species, however, differences between the shells of the two sexes are inappreciable.

## CALCAREOUS EGGS

In the higher prosobranchs the eggs are usually enclosed in parchment-like capsules of various shapes, which are frequently washed up on sea beaches. The volutid genus *Alcithoe* produces calcareous egg capsules, which are attached isolated to stones or shells. The writer knows of no record of a fossil egg capsule. At the time of deposition of the famous Solnhofen beds (Jurassic) of Germany, in which such remains could conceivably have been preserved, it is possible that few capsule-producing gastropods had evolved.

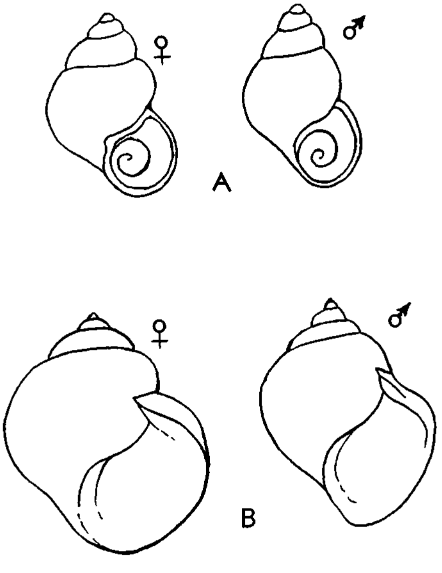

FIG. 82. Sexual dimorphism in gastropods.——*A. Pomatias elegans* (MÜLLER), female with the more tumid whorls, ×1.25 (136).——*B. Littorina rudis* (MATON), female, ×4, with larger shell, more tumid whorls, and less angular aperture than male, ×5 (130).

Land pulmonates produce comparatively few eggs, which may be laid in hollows on the ground and perhaps slightly covered by earth. Some forms, such as large tropical shells of the family Achatinidae, produce eggs of considerable size with a calcareous shell, a recorded length, possibly a maximum, being 45 mm. Large oval bodies up to 30 mm. in length, believed to be fossil eggs of *Filholia elliptica* (J.SOWERBY), are found in the Oligocene of England, and similar bodies, probably eggs of *Limicolaria,* occur in the Miocene deposits of Koru, Uganda.

## MORPHOLOGICAL TERMS APPLIED TO GASTROPOD SHELLS

Terms considered most important are in capitals (as **APERTURE**); less important terms are printed in uncapitalized letters (as **advolute**); use is not recommended of those in italics (as *altitude*).

**ABAPERTURAL.** Away from shell aperture.

**ABAPICAL.** Away from shell apex toward base along axis or slightly oblique to it.

**ABAXIAL.** Away from shell axis outward.

**aciculate.** Slender, tapering to sharp point.

**ADAPERTURAL.** Toward shell aperture.

**ADAPICAL.** Toward shell apex along axis or slightly oblique to it.

**ADAXIAL.** Toward shell axis inward.

**adpressed.** Condition of whorls that overlap in such manner that their outer surfaces converge very gradually.

**advolute.** Condition of whorls that barely touch one another, not distinctly overlapping.

**alate.** Expanded like a wing; refers commonly to outer lip.

*altitude. See* height.

**anal fasciole.** Band on whorls generated by indentation of outer lip (either a sinus, notch, or slit) situated close to the adapical suture and anal opening (*see* selenizone, slit band).

**anastrophic.** Heterostrophic, with protoconch coiled about same axis as teleoconch and nucleus directed toward base of shell, as in *Architectonica.*

**ancyloid.** Shaped like the genus *Ancylus* (i.e., patelliform), with apex strongly directed anteriorly.

**ANGULATION.** Edge along which two surfaces meet at an angle.

**ANOMPHALOUS.** Lacking umbilicus.

*antecurrent. See* prosocline.

**ANTERIOR.** Direction in which head tends to point when animal is active; in a crawling gastropod, the head is closest to part of the apertural margin lying farthest from the shell apex and in high-spired conispiral gastropod shells and some other types "anterior" is equivalent to "abapical."

*anterior canal. See* siphonal canal.

**APERTURAL.** Pertaining to aperture or on same side as aperture.

**APERTURE.** Opening at last-formed margin of shell, providing outlet for the head-foot mass.

**APEX.** First-formed end of shell, generally pointed.

**apical angle.** In plane through axis, angle subtended between two straight lines that touch adjacent whorls on opposite sides near apex; identical with spire angle if whorls increase at regular rate.

*appressed. See* adpressed.

**astragal.** Steep-sided, round-topped elevation of major strength extended spirally around whorls.

**auriform.** Ear-shaped.

**AXIAL.** Parallel or subparallel with shell axis.

**AXIS.** (1) Imaginary line through shell apex about which whorls of conispiral and discoid shells are coiled; (2) in isostrophic shells (such as bellerophonts), imaginary line through initial point of helicocone directed normal to plane of symmetry.

*basal fasciole. See* siphonal fasciole.

**basal lip.** Margin of aperture extending from foot of columella to position of imaginary continuation of suture; usually regarded as part of outer lip, but usefully distinguished at times.

**BASE.** (1) In conispiral shells, part of surface lying on abapical side of periphery of last whorl or (when so defined, in certain genera) of a carina or angulation that forms an obvious lower boundary on side of whorl; (2) in patelliform shells, the abapically located apertural side. [This term is not applicable to isostrophic shells like *Bellerophon,* and its use for the flattened apertural side of cypraeid shells is inconsistent with normal usage.]

**beak.** Short spout constituting a rudimentary siphonal canal, formed by protrusion of apertural margin near foot of columella.

**biconical.** Having form resembling that of two cones placed base to base.

*body whorl. See* last whorl.

**boss.** Rounded elevation somewhat larger than shell prominence termed "tubercle."

**bucciniform.** Having approximate shape of a *Buccinum* shell.

**callosity.** Local thickened part of inductura.

**CALLOUS.** Coated with thickened inductura.

**CALLUS.** Thickened inductura on parietal region or extending from inner lip over base or into umbilicus; shelly substance composing thickened inductura.

**CANAL.** Narrow, semitubular extension of aperture (*see* siphonal canal).

**cancellate.** Having ornament of intersecting spiral and transverse threads or cords.

**capuliform.** Having shape of a simple depressed cone with eccentric apex and near-apical part of shell slightly coiled, as in *Capulus.*

**CARINA.** Prominent spiral ridge or keel.

**CARINATE.** Bearing a keel (carina).

**cingulate.** Spirally ornamented.

**clathrate.** Having ornament of spiral and transverse components that intersect to form a broad lattice.

**clausilium.** Small plate that functions as an operculum in Clausiliidae, being received into a groove in columella.

*clausium. See* clausilium.

**clavate.** Club-shaped.

**COELOCONOID.** Approaching conical but with concave sides.

**coinductura.** Rather thick, obliquely layered shelly coating, extending in some bellerophont gastropods over inner lip from within aperture, covering part of inductura proper.

**COLLABRAL.** Conforming to shape of outer lip, as shown by growth lines.

**COLUMELLA.** Solid or hollow pillar surrounding axis of a coiled shell, formed by adaxial walls of whorls.

**COLUMELLAR FOLD.** Spirally wound ridge on columella that projects into shell interior.

**COLUMELLAR LIP.** Adaxial part of inner lip comprising visible terminal part of columella.

*concrescent. See* collabral.

**conical.** Cone-shaped, with tip of cone formed by shell apex; best restricted to conispiral shells.

**CONISPIRAL.** With spire projecting as cone or conoid.

**conoidal.** Approaching a cone in shape; restriction of this term to shells with convex sides, according to usage of some authors, is unjustified (*see* cyrtoconoid, coeloconoid).

**CONVOLUTE.** With last whorl completely embracing and concealing earlier ones; like involute but lacking umbilici; (definition in this way is accepted generally, although common earlier usage does not discriminate convolute from involute). [LINNÉ termed *Conus* a concolute shell.]

**CORD.** Round-topped moderately coarse spiral or transverse linear elevation on shell surface.

**coronate.** Bearing tubercles or nodes at shoulder of whorls.

**COSTA.** Round-topped elevation of moderate width and prominence (greater than cord) disposed collabrally on shell surface.

**costate.** Having costae.

**costella.** Like costa but smaller.

**costellate.** Having costellae.

**crenate.** With outer lip notched serially or scalloped or bearing minute rounded teeth.

**crispate.** With crinkled margin.

**cryptomphalous.** With opening of umbilicus completely plugged.

**CYRTOCONOID.** Approaching a cone in shape but with convex sides.

**decollation.** Discarding of apical whorls.

**decussate.** Having ornament consisting of two sets of obliquely disposed linear ridges that cross to form a series of X's; this term, often misapplied to mean cancellate, correctly refers to the ornament of protoconchs of some Turridae.

**depressed.** Low in proportion to diameter.

**deviated.** Condition of protoconch in which its axis forms distinct angle with axis of teleoconch.

**DEXTRAL.** Right-handed; term originally applied to any shell with aperture on observer's right when shell apex is directed upward, or with apparent clockwise coiling when viewed from above apex, but in fact definition depends on features of soft anatomy. A dextral gastropod has genitalia on the right side of the head-foot mass or pallial cavity and the shell of such an animal commonly has the aperture on right when viewed with the apex uppermost; in hyperstrophic dextral species, however, the apex is directed downward when aperture is on right.

**DIAMETER.** Distance, conventionally only in conispiral shells, between two planes parallel with each other and with shell axis which touch opposite sides of shell; diameter generally designated as maximum or minimum.

**digitation.** Finger-like outward projection from outer lip.

**DISCOIDAL.** Approaching a disc in form; convolute or involute and more or less flattened.

**disjunct.** Condition of whorls when out of contact.

**effuse.** Condition of aperture when margin is interrupted by short spout for siphonal outlet.

**elevated.** High in proportion to diameter.

**emarginate.** With margin of outer lip notched or variously excavated.

**embryonic shell.** Part of shell formed before hatching.

**enamel.** Glossy inductura.

**endogastric.** Coiled so as to extend backward from aperture over extruded head-foot mass, as is normal in most adult gastropods (*see* exogastric).

**entire.** Condition of aperture when margin is uninterrupted by siphonal canal or other emargination.

**everted.** With edge of outer lip turned outward.

**evolute.** Coiled with whorls out of contact; this term is used commonly to signify "with broad umbilicus" when applied to ammonites but not so referring to gastropods.

**excurvate.** Bent outward.

**exhalant channel** (or **canal**). Channel at junction of outer and parietal lips, or canal between extensions of these lips, occupied by mantle fold by which exhalant current leaves mantle cavity (*gouttière postérieure* of French authors). [The channeled posterior digitation of such genera as *Rimella* should not be mistaken for an exhalant channel.]

**exogastric.** Coiled so as to extend forward from the aperture over front of extruded head-foot mass, as in earliest gastropod ontogeny before torsion.

**explanate.** With outer lip spreading outward and becoming flattened.

*extraconic.* Nearly conical but with concave sides (*see* coeloconoid).

**false umbilicus.** Depression at base of shell affecting only last whorl, usually bordered by siphonal fasciole, sometimes termed pseudumbilicus.

**fasciculate.** Arranged in clusters.

**fasciole.** Band generated by narrow sinus or notch in, or lamellose projection of, successive growth lines.

**fimbriated.** Regularly puckered at the margin.

**flaring.** Widening outward toward opening.

**fold.** Spirally wound ridge on interior of shell wall (*see* columellar fold, parietal fold).

**fossula.** Shallow linear depression of inner lip in some cypraeids.

**funicle.** Spirally wound narrow ridge extending upward from inner lip into umbilicus, as in Naticidae.

**fusiform.** Slender spindle-shaped, tapering almost equally toward both ends, as in genus formerly called *Fusus.*

**gibbose, gibbous.** Very convex or tumid.

**globose.** More or less spherical.

**gradate.** Rising in steps owing to presence of whorl shoulders.

**granulated.** Covered with grains or small tubercles.

**GROWTH LINES.** Collabrally disposed surface markings of shell, generally not prominent as to relief, that denote former positions of outer lip.

**GROWTH RUGAE.** Irregular ridges or undulations of shell surface determined by former positions of outer lip.

**HEIGHT.** Distance between two planes perpendicular to shell axis and touching adapical and abapical extremities of shell or part being measured; this definition does not apply to Bellerophontacea or Cypraeacea, in which established practice differs (*see* remarks concerning whorl).

**heliciform.** Shaped more or less like shell of *Helix.*

**HELICOCONE.** Distally expanding coiled tube that forms most gastropod shells.

*helicoid. See* heliciform; use of this term in a geometrical sense is unsuitable for gastropod shells.

**hemiomphalous.** With umbilicus partly plugged at its opening.

**HETEROSTROPHIC.** Condition of protoconch when whorls appear to be coiled in opposite direction to those of teleoconch.

**HOLOSTOMATOUS.** With apertural margin uninterrupted by siphonal canal, notch, or by other extension.

**homeostrophic.** Having whorls of protoconch clearly coiled in same direction as those of teleoconch.

**HYPERSTROPHIC.** Dextral anatomically, with genitalia on right, but shell falsely sinistral, being actually ultradextral; or *vice versa.*

**immersed.** Condition of initial whorls when sunk within later ones and concealed by them.

*imperforate. See* anomphalous and remarks concerning "perforate."

**impressed.** Condition of suture having both adjoined whorl surfaces turned inward adaxially.

**incremental angle.** In plane through entire axis, angle between two straight lines that touch contiguous whorls on opposite sides at part of shell in question.

**INDUCTURA.** Smooth shelly layer secreted by general surface of mantle, commonly extending from inner side of aperture over parietal region, columellar lip, and (in some genera) part or all of shell exterior.

**inflated.** Swollen.

**inflected.** With edge of outer lip turned inward.

**INNER LIP.** Adaxial margin of aperture extending from foot of columella to suture and consisting of columellar and parietal lips.

**INVOLUTE.** With last whorl enveloping earlier ones so that height (or "width" in shells like bellerophonts) of aperture corresponds to that of shell; early whorls more or less visible in umbilici (*see* convolute).

**ISOSTROPHIC.** With two faces of shell symmetrical with respect to a median plane perpendicular to axis.

**keel.** Prominent spiral ridge (*see* carina).

**labial area.** Flattened or callus-coated surface extending from inner lip.

*labium. See* inner lip.

**labral.** Pertaining to outer lip.

**labrum.** Outer lip.

**lamella.** Thin plate.

**lanceolate.** Shaped like a lance-head (i.e., sharply pointed at one end), broader at other.

**larval shell.** Hard parts of pelagic larva before it settles down and undergoes metamorphosis.

**LAST WHORL.** In coiled shells, last-formed complete volution of helicocone.

**left.** Side of shell closest to left side of head-foot mass when this is extruded and active; side on left when shell is oriented with aperture facing observer and apex upward, except in depressed and discoidal shells.

**lenticular.** Having form of a biconvex lens.

**lira.** Fine linear elevation on shell surface or within outer lip.

**lirate.** Bearing lirae.

*longitudinal.* Diversely used by different authors; best avoided in describing gastropod shells.

**lower.** According to conventional orientation (except generally in France, Italy, Sweden), lower refers to abapical part of shell.

**lunula.** Crescentic linear ridge on selenizone, concave toward aperture.

**mammillated.** (1) With dome-shaped protuberance forming protoconch; (2) with dome-shaped protuberances forming shell ornament.

**marginate.** Condition of outer lip with strengthened margin.

**mean spire angle.** In plane through shell axis, angle between two straight lines that touch a whorl near apex and last whorl on opposite sides.

**multispiral.** With numerous whorls.

**muricate.** Spiny.

**naticiform.** With globose last whorl and small spire, like shell of *Natica.*

**neck.** Distal part of base of siphonostomatous shell, beginning where outline of left side changes from convex to concave.

**nodose.** With small knotlike protuberances.

**nucleus.** Earliest-formed part of shell or operculum; this term preferably should not be used for juvenile shell designated as "protoconch."

**obconical.** Approximately cone-shaped but with cone inverted.

**obovate.** Egg-shaped with narrower end downward.

*oligogyral. See* paucispiral.

**omphalous.** With an umbilicus.

**operculate.** With an operculum.

**OPERCULUM.** Corneous or calcareous structure borne by foot and serving for closure of aperture, wholly or partly.

**OPISTHOCLINE.** Leaning (i.e., inclined adapically) backward with respect to growth direction of helicocone, referring commonly to growth lines.

**opisthocyrt.** Arched backward with respect to growth direction of helicocone, referring to growth lines.

**ORNAMENT.** Relief pattern on surface of many shells (*see* sculpture).

*ornamentation. See* ornament.

**ORTHOCLINE.** At right angles to growth direction of helicocone, referring commonly to growth lines.

**ORTHOSTROPHIC.** Coiled in normal manner, not hyperstrophic.

**outer face** (of whorl). Surface between shoulder and abapical suture or margin of base; same as side of whorl.

**OUTER LIP.** Abaxial margin of aperture extending from suture to foot of columella.

**ovate.** Egg-shaped.

**palatal.** Belonging to outer lip, referring commonly to folds and lamellae.

**parasigmoidal.** Curved like reversed "S."

**PARIETAL FOLD.** Spirally wound ridge on parietal region that projects into shell interior.

**parietal lip.** Part of inner lip situated on parietal region.

**PARIETAL REGION.** Basal surface of helicocone just within and just without aperture; the redundant expression "parietal wall" should not be used, for "parietal" signifies pertaining to wall.

**parietal ridge.** Protuberance from parietal lip near adapical corner of aperture.

**patelliform.** Forming a simple depressed cone; limpet-shaped.

**patulous.** Condition of aperture marked by somewhat strong expansion.

**paucispiral.** With relatively few whorls.

**penultimate.** Next to last-formed, commonly referring to whorl preceding last.

*perforate.* With umbilicus; although much used in literature in sense indicated, it is highly inappropriate, for an umbilicus is not a perforation.

**perinductura.** Continuous outer shell layer in some gastropods formed by edge of mantle reflected back over outer lip.

**PERIOSTRACUM.** Coat of horny material (conchiolin) covering calcareous shell at least during some part of growth.

**PERIPHERY.** Part of shell or any particular whorl farthest from axis.

**peristome.** Margin of aperture.

*peritreme. See* peristome.

**PHANEROMPHALOUS.** With completely open umbilicus; may be wide, narrow, or very minute.

*pillar. See* columella.

**planispiral.** Coiled in a single plane, ideally with symmetrical sides, as in *Bellerophon* (*see* isostrophic); loosely used for discoidal shells with asymmetrical sides.

**pleural angle.** In plane through entire shell axis, angle between two straight lines lying tangential to last two whorls on opposite sides.

**plication.** Spirally wound ridge on interior of shell wall (*see* fold).

*polygyral. See* multispiral.

**POSTERIOR.** Direction opposite to that in which head tends to point when animal is active; this term is used often to mean adapical, but such practice is undesirable except in high-spired shells.

**primary.** Describing element of spiral ornament appearing early in ontogeny.

**PROSOCLINE.** Leaning (i.e., inclined adapically) forward with respect to growth direction of helicocone, referring commonly to growth lines.

**prosocyrt.** Arched forward with respect to growth direction of helicocone.

**PROTOCONCH.** Apical whorls of shell, especially where clearly demarcated from later ones.

*protractive. See* prosocline.

**pseudoselenizone.** Band on shell surface resembling a selenizone but not identifiable as trace of an apertural sinus or slit.

**pseudumbilicus.** Depression or cavity in shell base affecting only last whorl, and therefore not a true umbilicus; sometimes termed false umbilicus.

**punctate.** Minutely pitted.

**punctum.** Minute pit on shell surface but not a tubule penetrating shell substance as in some brachiopods. [Plural, "puncta," not "punctae."]

**pupiform.** Cylindrical, with rounded ends, like an insect pupa or shell of the genus formerly called *Pupa.*

**pustule.** Small rounded surface elevation, according to convention more diminutive than "tubercle."

**pyramidal.** Having form of a pyramid (i.e., with lateral surface divided into several similar and more or less flattened parts).

**pyriform.** Pear-shaped.

**RAMP.** Abapically inclined flattened band on shell surface, which in some shells forms the adapical part of whorls, limited abaxially by a ridge or angulation.

**recurved.** With distal end (e.g., of siphonal canal) bent away from observer when shell is viewed from apertural side.

**reflected.** Turned outward and backward at margin, referring to outer and columellar lips.

**resorption.** Removal of once-formed shell by action of the living gastropod.

**reticulate.** Forming a network of obliquely intersecting linear ridges.

*retractive. See* opisthocline.

*retrocurrent. See* opisthocline.

**revolving.** Passing spirally around whorls.

*rib. See* costa.

**ribbon.** Flat spiral surface elevation.

*riblet. See* costella.

**ridge.** Extended, somewhat angular linear elevation on shell surface.

**right.** Compare remarks under "left."

**rimate.** Consisting of a very narrow cavity, referring commonly to umbilicus.

**rostrum.** Attenuated extremity of last whorl other than siphonal canal, as in *Tibia*.

**rotelliform.** Almost lenticular but with low obtuse spire, like shell of genus formerly called *Rotella* (*see* umboniform).

**scalariform.** With whorls disjunct or tending to become so, referring commonly to a pathological condition.

**SCULPTURE.** Relief pattern on shell surface; virtually identical to "ornament" and about equally used.

**secondary.** Describing element of spiral ornament appearing later than the earliest ones in ontogeny.

**SELENIZONE.** Spiral band of crescentic growth lines or threads (lunulae) generated by a narrow notch or slit and characteristic of dibranchiate gastropods; corresponds to "anal fasciole" of some other groups.

**septum.** Transverse plate secreted within early-formed whorls of some shells (as Euomphalidae) for closing them off.

**SHOULDER.** Angulation of whorl forming abaxial edge of sutural ramp or shelf.

*shoulder angle.* Shoulder, as defined above.

**side** (of whorl). Surface between shoulder, if present, and abapical suture or margin of base.

**sigmoidal.** S-shaped.

**SINISTRAL.** With genitalia on left side of head-foot mass or pallial cavity, soft parts and shell arranged as in mirror image of dextral (*see* dextral).

**SINUS.** Curved re-entrant of apertural margin or of growth lines.

**SIPHONAL CANAL.** Tubular or troughlike extension of anterior (abapical) part of apertural margin for inclosure of inhalant siphon.

**SIPHONAL FASCIOLE.** Distinctive band of abruptly curved growth lines near foot of columella marking successive positions of siphonal notch.

**siphonal fold.** Ridge corresponding to siphonal notch wound spirally around columella.

**SIPHONAL NOTCH.** Narrow sinus of apertural margin near foot of columella serving for protrusion of inhalant siphon.

**SIPHONOSTOMATOUS.** With apertural margin interrupted by canal, spout, or notch for protrusion of siphon.

**SLIT.** Parallel-sided re-entrant of outer lip ranging from shallow incision to deep fissure as much as half a whorl in extent.

**slit band.** Trace of slit around whorls (*see* selenizone).

**spine.** Thornlike protuberance.

**SPIRAL** (adj.). As applied to elements of ornament, passing continuously around whorls, almost parallel with suture.

**spiral** (noun). Curved line or surface starting from point of origin and extending outward with continuously increasing radius of curvature.

**SPIRE.** Adapical visible part of all whorls except last.

**spire angle.** In plane through entire shell axis, angle between two straight lines which touch all whorls on opposite sides; such lines can be drawn only if rate of whorl increase is constant.

**spout.** Rudimentary siphonal canal.

**squamose.** With scales.

**squat.** Broad in proportion to height (in a family or genus in which most species are slender).

**stria.** Very narrowly incised shallow groove.

**strombiform.** Roughly biconical but with expanded outer lip, as in shell of *Strombus*.

**styliform.** Parallel-sided except at sharp-pointed apex.

**subulate.** Slender and tapering to point, sides convex, awl-shaped.

**sutural shelf.** Horizontal flattened band, which in some shells adjoins adapical suture of whorls.

**sutural slope.** Angle between suture and plane perpendicular to axis; equivalent to "sutural angle" of many authors but not as first defined by D'ORBIGNY (1842).

**SUTURE.** Continuous line on shell surface where whorls adjoin.

**TELEOCONCH.** Entire shell exclusive of protoconch.

**THREAD.** Fine linear surface elevation.

*transcurrent.* Passing continuously around whorls across growth lines (*see* spiral).

**TRANSVERSE.** Crossing direction of helicocone growth (*see* collabral).

**TREMA.** Orifice in outer wall of some shells for excretory function; occurs singly or in series (plural, tremata).

**trochiform.** With flat-sided conical, not highly acute spire and rather flat base, like shell of *Trochus*.

**tubercle.** Moderately prominent small rounded elevation on shell surface.

**turbinate.** *See* turbiniform.

**turbiniform.** With broadly conical spire and convex base, as in shell of *Turbo*.

*turreted.* Used with different meanings, by most authors in the same sense as turriculate (q.v.).

**turriculate.** With acutely conical spire composed of numerous rather flat whorls; term derived from Latin *turricula* (little tower), much used by French authors *(turriculé).*

*turrited. See* turriculate.

**ultradextral.** With shell seemingly sinistral but soft parts organized dextrally (*see* hyperstrophic).

**ultrasinistral.** With shell seemingly dextral but soft parts organized sinistrally (*see* hyperstrophic).

**umbilical suture.** Continuous line separating successive whorls as seen in umbilicus of phaneromphalous shells.

**umbilicate.** With an umbilicus.

**UMBILICUS.** Cavity or depression formed around shell axis between faces of adaxial walls of whorls where these do not coalesce to form a solid columella; in conispiral shells (except hyperstrophic ones) its opening is at base of shell but involute shells may have two umbilici (upper or adapical and lower or abapical in asymmetrical forms, left and right in isostrophic forms).

**umboniiform.** Almost lenticular, but with low obtuse spire, like shell of genus *Umbonium* (formerly *Rotella*).

**varicose.** Bearing a varix or varices.

**VARIX.** Transverse elevation more prominent than costa and generally spaced more widely; it is evidence of growth halt during which a thickened outer lip developed (plural, varices).

**volution.** Any complete coil of helicocone (*see* whorl).

**wall.** Any part of framework of shell.

**WHORL.** (1) Any complete coil of helicocone; (2) exposed surface of any complete coil of helicocone. Distinctions here indicated are important, for in defining height of last whorl the complete coil is considered, whereas height of spire whorls takes account only of the exposed surface of a coil between successive sutures.

**wing.** More or less flattened expansion of outer lip.

## CLASSIFIED MORPHOLOGICAL TERMS

A grouping of morphological terms that relate to characters of gastropod shells for the purpose of classification in various categories is considered to be useful. In the lists that follow, terms rated as most important are printed in boldface type (as **spire**) and others in lightface type (as pupiform); italicized terms given in the foregoing glossary are here omitted because use of them is not recommended.

*Terms relating to main parts of shell.* **Aperture, apex, axis, base, helicocone, last whorl,** neck, operculate, **operculum, protoconch, spire, suture, teleoconch, umbilicus, wall, whorl.**

*Directional and dimensional terms.* **Abapertural, abapical, abaxial, adapertural, adapical, adaxial, anterior, axial, diameter, height, left, lower, opisthocline,** opisthocyrt, **orthocline, posterior, prosocline,** prosocyrt, right, spiral, **transverse.**

*Form terms.* Aciculate, alate, ancyloid, auriform, biconical, bucciniform, capuliform, **carinate,** clavate, **coeloconoid,** conical, **conispiral,** conoidal, **convolute, cyrtoconoid,** depressed, deviated, **dextral, discoidal,** disjunct, elevated, evolute, excurvate, fusiform, gibbose, gibbous, globose, heliciform, **heterostrophic, hyperstrophic,** immersed, inflated, **involute, isostrophic,** lanceolate, lenticular, marginate, multispiral, naticiform, obconical, obovate, ovate, patelliform, paucispiral, planispiral, pupiform, pyramidal, pyriform, recurved, rotelliform, scalariform, **sinistral,** squat, strombiform, styliform, subulate, trochiform, turbinate, turbiniform, turriculate, ultradextral, ultrasinistral, umboniiform.

*Terms relating to sutures and coiling.* Adpressed, advolute, anastrophic, **convolute, dextral,** disjunct, endogastric, exogastric, **heterostrophic,** homeostrophic, **hyperstrophic,** impressed, **involute, isostrophic, last whorl,** multispiral, **orthostrophic,** paucispiral, penultinate whorl, planispiral, **sinistral, suture,** umbilical suture, volution, **whorl.**

*Terms relating to umbilicus.* **Anomphalous,** cryptomphalous, false umbilicus, funicle, hemiomphalous, omphalous, **phaneromphalous,** pseudumbilicus, rimate, umbilical suture, umbilicate, **umbilicus.**

*Terms relating to axis.* **Abaxial, adaxial, axial, axis, columella, columellar fold, columellar lip,** fold, plication, siphonal fold.

*Terms relating to spire and protoconch.* **Abapical, adapical,** anastrophic, **apex,** apical angle, channeled suture, decollation, deviated, gradate, **heterostrophic,** homeostrophic, **hyperstrophic,** immersed, incremental angle, mammillated, mean spire angle, multispiral, nucleus, **orthostrophic,** outer face (of whorl), paucispiral, penultimate whorl, **periphery,** pleural angle, **protoconch, ramp,** rostrum, **shoulder,** side (whorl), **spire,** spire angle, sutural shelf, sutural slope, **suture, whorl.**

*Terms relating to aperture.* **Abapertural, adapertural,** alate, **apertural, aperture,** basal lip, beak, **callus, canal, columellar lip,** crenate, crispate, digitation, effuse, emarginate, entire, everted, excurvate, exhalant channel, explanate, flaring, fossula, funicle, **holostomatous,** inflected, inhalant channel, **inner lip,** labial area, labral, labrum, marginate, **outer lip,** palatal, **parietal fold,** parietal lip, **parietal region,** parietal ridge, patulous, peristome, profile, recurved, reflected, **sinus, siphonal canal, siphonal notch, siphonostomatous, slit,** spout, **varix,** wing.

*Terms relating to surface features.* Anal fasciole, **angulation,** astregal, boss, callosity, **callous, callus,** cancellate, **carina, carinate,** cingulate, clathrate, coinductura, **collabral, cord,** coronate, **costa,** costate, costella, costellate, decussate, enamel, fasciculate, fasciole, fimbriated, granulated, **growth lines, growth rugae, inductura,** keel, lira, lirate, lunula, mammillated, muricate, nodose, **opisthocline,** opisthocyrt, **ornament, orthocline,** parasigmoidal, perinductura, **periostracum,** primary, **prosocline,** prosocyrt, pseudoselenizone, punctate, punctum, pustule, reticulate, revolving, ribbon, ridge, **sculpture,** secondary, **selenizone,** sigmoidal, **sinus, siphonal fasciole,** slit band, spine, **spiral,** squamose, stria, **thread, trema,** tubercle, varicose, **varix.**

## FOSSIL TRACES OF GASTROPODA

Some geological formations may yield indirect evidence of the presence of gastropods on the sea floor where they accumulated as sediment. Tracks and burrows will be considered first.

Gastropoda crawl by means of a series of waves of contraction of the muscles of the sole of the foot. According to movement of these waves, they may be divided into two groups, in the first of which the waves pass from rear to front, and, in the second, in the opposite direction. Both groups include **monotaxic forms,** in which the whole sole is affected by a single series of waves, and **ditaxic forms,** in which a median band divides the sole longitudinally into two halves, each with its own series of waves. The first group also includes some **tetrataxic forms,** in which each half of the foot is itself divided longitudinally into two areas affected by distinct series of waves, so that there are four systems of waves in all. It will thus be seen that a gastropod crawling, for example, over a sand flat exposed at low tide, will leave a track the nature of which will depend partly upon the system of muscle waves of the foot. The nature of the track will also be affected when, for example, the foot has a propodium that ploughs aside the sediment as the animal crawls; and when progression is irregular, owing to mechanical difficulties in carrying the shell. In the case of some species with a tall spire, the shell is lifted and trailed alternately and leaves an interrupted groove, usually within the main track. The amount of detail preserved in the track will, of course, depend upon the nature and moisture content of the sediment in which it is formed.

Among tracks formed by living gastropods of the ditaxic groups are those of *Nucella lapillus* (LINNÉ) (Fig. 83), long ago figured by NICHOLSON & ETHERIDGE (77), *Littorina littorea* (LINNÉ), and *Monodonta lineata* (DACOSTA). Such tracks are divided by a median groove into two parts, each with transverse ridges, often slightly arched. In *Monodonta lineata* these ridges are relatively wide-spaced and oblique. ABEL (1, p. 207-219) has made detailed observations on the fast-crawling South African species, *Bullia rhodostoma* GRAY, the track of which appears tripartite owing to the presence of two longitudinal grooves formed by posterior projections of the foot.

Among the fossil tracks preserved in certain shallow-water formations are some which have been attributed to gastropods, in some cases very tentatively, by workers who described and assigned generic names to them. Thus *Archaeonassa* FENTON & FENTON was founded upon parallel-sided furrows, bounded by lateral ridges and crossed by arched transverse ridges, found in the Lower Cambrian of British Columbia; *Palaeobullia* GÖTZINGER & BECKER upon tracks with a median furrow and obliquely ridged lateral bands, from the Eocene Greifenstein sandstone of Austria; and *Subphyllochorda* of the last two authors on tracks of a different type from the same formation. The introduction of generic names suggesting affinity with certain Recent genera seems injudicious. ABEL (1, p. 241) gave a list of generic names assigned to "problematica" which, in his view, are gastropod tracks.

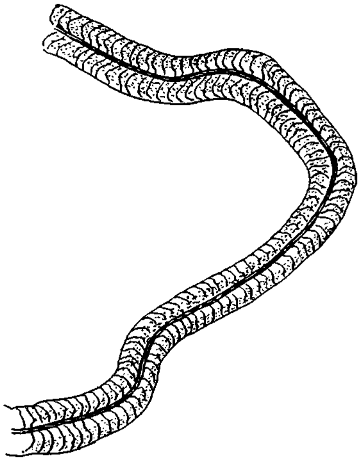

FIG. 83. Track of *Nucella lapillus* (LINNÉ) on firm sand, ×0.4 (77).

They are *Nereites, Nemertites, Myrianites, Nereograpsus, Nemapodia, Gyrochorda, Phyllochorda,* and *Phyllodocites.* The same worker thought that the Upper Cambrian track *Climactichnites* Logan was formed by a shell-less opisthobranch. Structures from the Pennsylvanian of Texas described under the generic names *Aulichnites* and *Olivellites* by Fenton & Fenton were regarded as possibly burrows rather than surface tracks of gastropoda. Although it is probable that some of these tracks and burrows were formed by gastropods, it is doubtful if there are any reliable criteria by which those due to animals of this group can be distinguished from those of some other invertebrates.

Some carnivorous gastropods, notably *Natica,* bore into the shells of other mollusks by means of their proboscis and radula (probably assisted chemically in the case of *Natica*) and extract the soft parts for food, leaving a circular perforation in the shell of their prey as evidence of its fate. Fossil shells bored in this manner occur commonly in many Tertiary formations, but only rarely in older deposits. The oldest known examples are brachiopods from the Ordovician of North America. Several such specimens have also been described from the Devonian of that continent and from the Permian of Russia.

It is now known that fecal pellets of invertebrates, including gastropods, are an important constituent of many marine and estuarine muds, and also that each species excretes its own characteristic type of pellet. While the pellets in ancient sediments will in most cases have become obliterated in the course of diagenesis, it is possible that they are preserved in some formations, and the subject deserves investigation.

## ONTOGENY

### EMBRYONIC AND LARVAL LIFE

In most archaeogastropods the ova are shed into the sea and there fertilized; in the higher groups of gastropods fertilization takes place internally, and in most case the eggs are laid or shed before the young animal hatches out, but some forms are viviparous, and emergence from the ovum takes place within the parent, most commonly in the terminal part of the oviduct. In many marine gastropods the young animal hatches out as a larva, which is very different in appearance from the adult animal and leads a free-swimming existence in the plankton for a period. In fresh-water and land gastropods and in some marine forms there is no free larval stage and the animal emerges from the egg in its final creeping (plantigrade) stage, with the main morphological features of the adult animal already developed. It is not unusual to find that, of two congeneric species sharing the same habitate, one has a pelagic larva, while in the other the young hatch out in the crawling stage. Respective examples in the British fauna are the intertidal forms *Littorina littorea* (Linné) and *L. littoralis* (Linné). A third member of the genus, *L. neritoides* (Linné), lives well above high-water mark, but yet has a pelagic larva. In some marine forms temperature conditions may control whether the animal hatches out in time to pass through a free larval stage or whether (in a colder sea) it undergoes the corresponding changes within the egg. Embryonic life is shortest in some Archaeogastropoda, as in such forms the larva emerges from the egg at an earlier stage of development than in any other gastropod group.[1] Under experimental conditions it was found that in *Haliotis tuberculata* Linné larvae had emerged within 8 to 13 hours after fertilization, and in *Patella vulgata* Linné within 24 hours. The period between fertilization and hatching out is naturally much longer when development to the plantigrade stage is completed within the egg and a free larval stage omitted. In the marine prosobranch *Littorina littoralis* (Linné) it was found to be three weeks, and in the land prosobranch *Pomatias elegans* (Müller) as long as three months.

The size and, to some extent, the form of the protoconch are known to depend within any given genus upon the duration of embryonic life in the particular species. In species in which the gastropod emerges from the egg in the crawling stage the

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[1] By no means all Archaeogastropoda hatch out as a trochophore larva. Of 17 British species listed by M. Lebour (65), nine do so and eight, including *Diodora apertura* (Montagu) and *Calliostoma zizyphinum* (Linné), hatch out in the creeping stage.

protoconch tends to be much larger and more domelike than in congeneric species that pass through a pelagic larval stage. Moreover, the percentage of gastropod species in which this stage is passed through increases from nil in Arctic and Antarctic seas to 85 per cent or more in tropical seas. This fact suggests that when widespread genera, such as *Natica,* are well represented in a given fossil fauna, the dominant type of protoconch may throw some light on contemporary temperature conditions (102).

## EARLY ONTOGENY OF PROSOBRANCHIA

The early stages of development following fertilization of the ovum, those of cleavage and gastrulation, have been studied in a number of gastropod species, and follow much the same course as in other invertebrate groups, as described in standard works on embryology. The earliest stage of development to which reference need now be made is that of the **trochophore** or **trochosphere,** the form in which the larva emerges early from the egg in certain Archaeogastropoda. The appearance of the trochophore larva of *Patella* is familiar from reproductions of the illustrations of PATTEN & F. G. W. SMITH (Fig. 84). Its diameter is about 0.18 mm. and its shape may be described as that of a cup with a domelike lid. It swims in the plankton by means of cilia that surround the periphery and cover its anterior end. Near its posterior end, on one side, there remains at first the primitive opening of the gastrula stage, the blastopore. This then closes temporarily and opens again to form the stomodaeum, an invagination located where the mouth later opens. A shallow dorsal depression marks the beginning of the shell gland.

The trochophore develops within a few hours into the **veliger larva** (Fig. 85), the stage at which a great number of marine gastropods hatch out from the egg. Its chief feature is the swimming organ known as the velum. In its simplest form (found in *Patella* and *Haliotis,* for example) this consists of an anterior girdle of large ciliated cells which have developed from the cells encircling the periphery of the trochophore. In some genera, however, the velum consists of two, four or six large, radiating, paddle-shaped lobes (Fig. 86). Movements of the powerful cilia borne by the velum cells or lobes cause the larva to spin around in a counterclockwise direction and to move upward in the water. When their motion ceases, it sinks again. At about the same time as the velum forms, the shell gland begins to secrete a shell, at first horny and then calcareous. This is at first bowl-shaped, but soon deepens, beginning to assume a coiled nautiloid form as the visceral hump within it grows. At the same time the mantle flap has begun to develop on the ventral side of the animal, its margin adjoining that of the shell aperture. Within the mantle flap is a rudimentary mantle cavity, and between the edge of the mantle flap and the velum a bulge represents the foot.

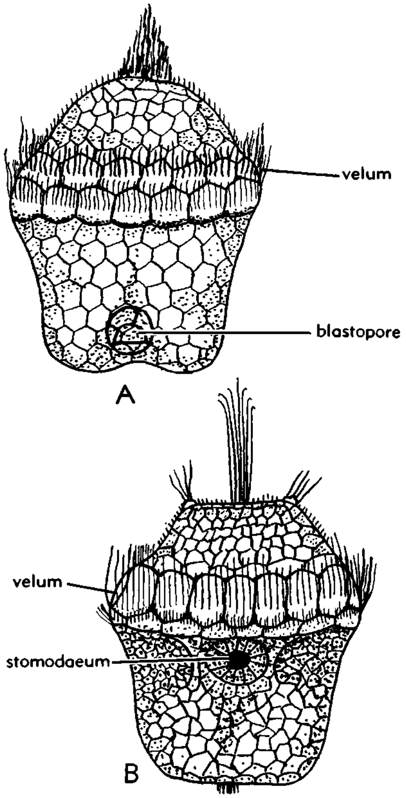

FIG. 84. Two stages in development of trochophore larva of *Patella vulgata* LINNÉ, *(A) ca.* 30 hours, *(B) ca.* 44 hours after fertilization, ×270 (92).

While still a veliger, the young prosobranch gastropod undergoes a fundamental change in the orientation of its organs, which may be regarded as a combination of

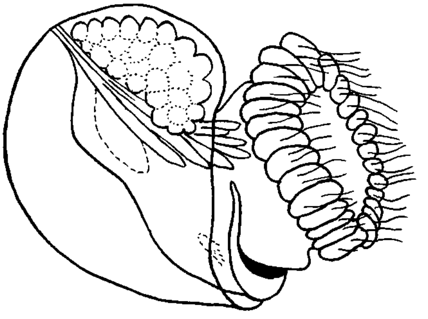

FIG. 85. Pretorsional veliger larva of *Haliotis tuberculata* LINNÉ, 27 hours after fertilization, ×190 (25)

two movements.[1] As the result of the first, known as the "anopedal flexure," the alimentary canal, instead of being aligned from front to rear, becomes bent so that the rectum points to the front and the anus discharges into the mantle cavity. The second change, described as the process of **torsion,** involves a rotation of the mantle and juvenile shell, with its enclosed viscera, through an angle of 180 degress in relation to the velum (from which the head later develops) and the foot.[2] As a result the mantle cavity comes to occupy an anterodorsal position, while the coiling of the shell assumes the endogastric direction typical of the adult gastropod. Effects of this torsion on the cells from which various organs of the adult animal later arise are far-reaching. Thus, when they develop, the nerve cords connecting the cerebral and pleural to the visceral ganglia are found to be crossed (most obviously in the Archaeogastropoda and less advanced Caenogastropoda) rather like a figure 8, instead of being parallel. The gut has been twisted into a loop. It is, moreover, obvious that the positions of the left and right ctenidia, osphradia, hypobranchial glands, heart auricles, and kidneys of the ancestral untorqued form become transposed as the result of torsion, so that when, as in most prosobranchs, only one of each of these organs remains, this, although now on the left-hand side, represents the original right-hand organ.

Torsion appears to be a steady process in some gastropods, as, for example, in *Pomatias elegans* (MÜLLER), in which it occurs within the egg, not beginning until 3.5 weeks after the first cleavage, and continuing for 10 days. In other gastropods, however, it takes place in two stages, each involving a rotation of 90 degrees or thereabouts. In *Calliostoma zizyphinum* (LINNÉ), *Patella vulgata* LINNÉ, and *Haliotis tuberculata* LINNÉ, torsion starts respectively about 60, 60, and 30 hours after fertilization, its first stage occupies 4, 10 to 15, and 3 to 6 hours, and the second stage 32, 30, and 200 hours. Recent work by CROFTS (26) has shown that torsion originates through the action of a single asymmetrically placed larval retractor muscle attached to the shell interior on the right side of the apex.

The period of larval life (clearly an important factor in dispersal) and the stage in development when the larva settles on the sea floor vary greatly. In most Archaeogastropoda pelagic life is of relatively short duration. In *Haliotis tuberculata* it lasts only 40 hours, and the slow second phase of torsion takes place largely when the animal is benthonic and in process of losing the velum with its cilia. Feeding starts as soon as swimming ceases. Complete metamorphosis is a gradual process, about two months elapsing before the organs of the adult animal are fully developed. Many Caenogastropoda, on the other hand, have a long life as a veliger larva even after torsion, and during this period a spiral shell of several whorls (8 being the largest number recorded) may grow, on which elements of the adult ornament may already have begun to appear (Fig. 86). Ultimately the larva sinks to the bottom where, if the sea floor is suitable, it begins to crawl and undergoes metamorphosis to the adult condition. Large numbers of larvae must fail to find suitable conditions on sinking and they perish.

Certain generic names were assigned to gastropod larvae before their identity was realized. Among such names were *Sinusigera* D'ORBIGNY and *Macgillivraya* FORBES. KROHN gave the generic name *Echinospira* to a type of larva in which the true shell is surrounded by a secondary thin, transparent, membranaceous noncalcareous shell, which acts as a float. This type of larva occurs most commonly in the cypraeid families Eratoi-

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[1] As evidence of the distinctness of the processes of flexure and torsion, PELSENEER (83, p. 120), refers to some abnormal embryos which exhibit the effects of the former but not of the latter, and which have a shell not coiled in a spiral.

[2] Figure 9 illustrates the process of torsion in the veliger larva of *Patella vulgata.*

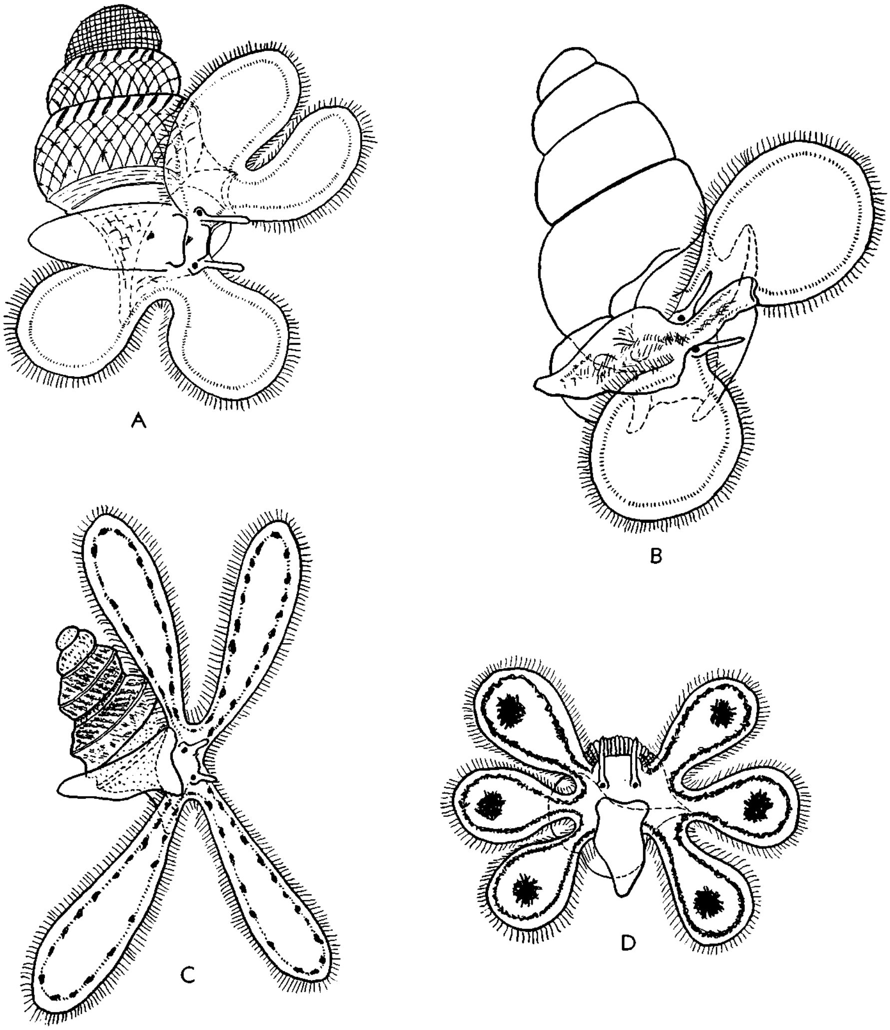

FIG. 86. Late veliger larvae, showing larval shells (mostly hidden in *(D)* by the foot and lobes of velum). ——*A. Philbertia linearis* (MONTAGU), ×70 (127).——*B. Cerithiopsis tubercularis* (MONTAGU), ×80 (65).——*C. Philbertia gracilis* (MONTAGU), ×16 (65).——*D. Aporrhais pespelicani* (LINNÉ), ×32 (65).

dae and Lamellariidae but is also found in the species *Capulus ungaricus* (LINNÉ).

## EARLY ONTOGENY IN OPISTHOBRANCHIA AND PULMONATA

Owing partly to practical difficulties in rearing larvae of opisthobranch gastropods in the laboratory—less easily overcome than in the case of the Archaeogastropoda, in which the ova are fertilized externally—less is known of the embryology and early postembryonic ontogeny of the opisthobranchs. *Aplysia punctata* CUVIER, *Philene aperta* (LINNÉ) and *Adalaria proxima* (ALDER & HANCOCK) are among the opisthobranchs of which the development has been studied. The early ontogeny is much accelerated in comparison with that of an archaeogastropod. Torsion and anopedal flexure take place at an early stage, well before hatching. THOMPSON (100) has described how, in *Adalaria proxima,* torsion is brought about during the later stages of cleavage and is not recognizable as a mechanical process. The shell, which is endograstric from the beginning, and the velum are formed before hatching. The animal emerges from the egg as a veliger larva, and this begins to undergo metamorphosis before settling.

The larval shells of most opisthobranchs are hyperstrophic, that is, they appear to be coiled sinistrally although the animal is dextral. When the larva settles on the sea floor the coiling begins to become orthostrophic, so that in the adult gastropod the protoconch, which was the larval shell, is heterostrophic. It has, however, been shown that when (as may happen in a few opisthobranch species) the pelagic larval stage is omitted and the animal hatches out in the plantigrade stage, the initial whorls of the shell are not heterostrophic. In many adult opisthobranch shells the protoconch is completely hidden by the later whorls, but it can be revealed by carefully cutting part of these away (Fig. 70). In some cases the larval shell varies considerably in specimens of the same species. Thus at some localities that of *Diaphana minuta* (BROWN) alternates between two types, one with half a whorl only, and the other with one and a half whorls.

In its postveliger ontogeny the opisthobranch undergoes a series of changes, commonly referred to as "detorsion," by which the effects of an original torsion through an angle of 180 degrees are to a varying extent reversed. Thus, the opening of the pallial cavity, which is anterior and dorsal in the veliger, is displaced to the right or even somewhat to the rear. The anus, anterior in the veliger, is similarly displaced to the rear to a varying extent, as are also the ctenidium and osphradium. The auricle, which lies to the right of the ventricle in the early postveliger, moves to a position behind it. The process in the species *Onchidella celtica* (FORBES & HANLEY) has been described step by step by FRETTER (37, p. 709) and in *Adalaria proxima* (ALDER & HANCOCK) by THOMPSON (100); the first species, previously regarded by some authorities as a pulmonate, has no free larval stage and hatches out as a crawler. The effects of opisthobranch "detorsion" are also seen in the euthyneurous condition of most genera, but it should be made clear that uncrossing of the visceral loop is not a process that can be followed step by step in ontogeny. The more elevated position of the supra-intestinal ganglion in relation to that of the infra-intestinal ganglion in the adult opisthobranch is the chief evidence of ancestral streptoneury displayed by the nervous system.

The development of the embryo has been studied in a number of species of the Pulmonata, in which group, of course, there is no free larval stage. Early ontogeny is condensed, and stages corresponding to the trochophore and veliger larvae are not recognizable. Torsion does not constitute so distinct an episode as in the case of the lower prosobranchs, but the adult animal reveals its effects and those of anopedal flexure in the usual way—by the endogastric shell, the dorsal, anteriorly directed pulmonary chamber, and the more or less anteriorly directed anus, and its situation on the right. While some authorities have considered that the effects of "detorsion" are observable in the adult pulmonate, just as in the opisthobranch, others are not of this opinion, pointing out that the heart occupies the same position as in the prosobranchs. Other theories have been advanced, therefore, to account for the euthyneurous condition of the pulmonates. According to the "zygosis theory" of KRULL (57), the nervous system of pulmonates has arisen from that of the prosobranchs by a series of events involving the loss of the left-hand half of the visceral loop and the acquisition of new ganglia and a connective on the right side (53). This, however, is pure speculation, not confirmed by any sequence of events in ontogeny.

## ONTOGENY OF SHELL

Reference has already been made to the gastropod protoconch and the frequent discontinuity between it and the later whorls, a discontinuity that is not, apparently, necessarily associated with the transition from a planktonic to plantigrade condition, except in the case of the opisthobranchs. In ornamented shells the first elements of ornament may or may not appear on the protoconch; in rather rare instances (e.g., *Daphnella*, Fig. 69*H*), the protoconch has well-marked ornament differing from that of the succeeding whorls. During the period when paleontological research was much influenced by the work of HYATT and others, who sought to demonstrate that the MÜLLER-HAECKEL Law of Recapitulation was applicable to the hard parts of the developing invertebrate, detailed studies were carried out on the changes in ornament and whorl outline that take place during the growth of the gastropod shell. Thus among the Eocene Fusinidae of Europe, studied by GRABAU (41), there are species in which an even convexity of the whorl outline and ornament of collabral costae crossed by spiral threads continue throughout growth, whereas in other forms these characters are confined to the earlier whorls, the later ones losing their ornament, becoming flattened laterally, and developing a distinct shoulder. These facts were held to prove that shells of the latter type were descended from shells of the former. Shells in which elements of the adult ornament had already begun to appear on the protoconch were regarded as instances of "accelerated" development, while shells in which ornament was lost on the later whorls were described as "phylogerontic." The inferences drawn from such studies are now largely discredited. In some gastropod shells (e.g., certain Cerithiidae and Strombidae) there are very pronounced changes in whorl ornament during growth, but their significance is unknown, and it seems improbable that they throw any light on phylogeny. Allusion may, finally, be made to certain features of the shell which do not appear in some gastropod genera until sexual maturity is reached. Such features are the winged outer lip found in many Strombacea; the toothed inner and outer lips, and the projections of both enclosing anterior and posterior canals in many Cypraeacea; and the expanded inner lip of some Cassididae.

## EVOLUTION OF GASTROPODA

An extensive literature contains discussions of the origin and significance of torsion, gastropod asymmetry, and the evolution of the various groups of gastropods now living. It is very generally accepted that the class arose originally from mollusks that did not undergo torsion and had complete bilateral symmetry. WENZ and KNIGHT considered that this ancestral form may well have been a representative of the Monoplacophora, a group of mollusks with simple univalve shells, represented in the earliest Cambrian rocks, but they wrote before the recent discoveries of living species assigned to this group, and if the Paleozoic forms were all organized like the Recent ones, it is evident that they could not have included the immediate ancestor of the gastropods. In the present work YONGE discusses the various theories accounting for torsion, and favors GARSTANG's hypothesis that it originated as a sudden mutation in the larva, which proved to have great survival value. The new developments of anopedal flexure and torsion, with the resulting anterior anus and endogastrically curved shell, may have afforded the possibility for the latter to develop into a spiral structure into which the head-foot mass could retreat for protection, and which it could carry when actively crawling; it was, perhaps, owing to this protection that the gastropod was able to explore life in other marine environments. Asymmetry of the adult shell was not a necessary consequence of torsion, for, as KNIGHT has shown, there is good evidence that the bellerophontids were torqued. Embryological work has shown that in modern gastropods asymmetry precedes torsion, but this cannot be accepted as evidence that such was the case in phylogeny. Asymmetry may have been determined by mechanical causes arising from a changed poise of the coiled shell, itself due to some change in habits. The originally isostrophic shell would thus have been modified into an anisostrophic and ultimately conispiral structure, and the organs on the right side of the animal, occupying in orthostrophic dextral forms the inner side of the coil, would have undergone progressive reduction because of the more restricted space available for them, eventually to become atrophied in many lines of descent. This does not explain why dextrality of organization and coiling became the rule except in relatively rare instances, but this may have been determined by the original direction of torsion.

The earliest forms considered to be true gastropods belong to the family Coreospiridae and appear in the Lower Cambrian. They are bilaterally symmetrical, completely or partially coiled forms referred to the Bellerophontacea, but differ from other members of that superfamily in the absence of an anal emargination. It is unknown if these or, indeed, any of the Bellerophontacea, had an operculum, although the protective efficiency of the shell, endogastric as a consequence of torsion, would have been imperfect unless the aperture was sealed by this structure, borne by the foot as the last organ to retreat into it. The Upper Cambrian marked the incoming of the first asymmetrical gastropod shells, belonging to the Pleurotomariacea and the Macluritacea. The former superfamily is of great interest as its representatives have survived to the present day, so that their anatomy can be studied. Their primitive character is shown by the fact that the organs of the pallial complex are paired, and those on the right-hand side are only slightly smaller than those on the left in the Pleurotomariidae themselves. The operculum is corneous in those modern representatives of the family in which it is known. Presumably it was of similar composition in extinct forms, as there is no record of the preservation of fossil opercula attributable to any pleurotomariacean. The Macluritacea are a highly interesting group which did not survive the Devonian Period. The shell (Fig. 79*B*) is apparently sinistral, but was provided (at least in *Maclurites*) with a heavy calcareous operculum, from the direction of coiling of which we know that it was, in fact, hyperstrophic. Thus, the hyperstrophic condition, met with rarely in the adult stage of later gastropods, was early and apparently unsuccessfully explored in one whole superfamily. The Ordovician saw the incoming of several other gastropod superfamilies referred to the Archaeogastropoda but now extinct. Of the chief superfamilies of this order which are still living, the Patellacea (if represented by the Metoptomatidae) first appeared in the Middle Silurian, the Neritacea in the Middle Devonian, and the Trochacea in the Triassic.

Study of the respiratory processes in some modern representatives of the Pleurotomariina *(Haliotis, Emarginula, Diodora)* indicates the relationship of the labral emargination in the first two genera, and of the apertural orifice in the last, to the inhalant currents and the positions of the ctenidia. In modern Pleurotomariina we know that the two ctenidia lie on either side of the line of the labral emargination, row of tremata, or apical orifice, as the case may be, and that in *Emarginula, Haliotis,* and *Diodora* (and presumably in genera of the Pleurotomariidae, although they have not yet been studied living) the inhalant currents enter the mantle cavity from the front symmetrically about this line, the exhalant current leaving by way of the emargination, tremata, or apical orifice. The presence of a labral emargination well removed from the suture in extinct forms is thus evidence of the existence of two ctenidia, one possibly reduced. The complete loss of the right ctenidium, a condition found in the Trochacea and probably already acquired in early Paleozoic times by such groups as the Microdomatacea, meant the introduction of a new mode of circulation of the respiratory currents, by which the inhalant current enters the mantle cavity to the left of the head, and the exhalant current is discharged over the right "shoulder." This system of circulation has persisted in higher prosobranchs, the marginal part of the mantle at the entry of the inhalant current being eventually extended to form a siphon in many forms.

The primitive Archaeogastropoda — in fact, all superfamilies of this order, except the Neritacea—also differ from more advanced gastropods in their method of reproduction. The ova and spermatozoa are shed by way of the right kidney and exhalant current into the sea, where fertilization occurs. Not until the mechanism for internal fertilization was acquired, by development of the pallial genital ducts and their associated organs, was there a possibility of migration to fluviatile and terrestrial habitats.

The remaining gastropods differ from the Archaeogastropoda (except the Patellacea and Helicinidae) in having only one auricle, a condition originally associated with the loss of the right-hand ctenidium. They comprise, first, the higher prosobranchs (Caenogastropoda), the obvious direct descendants of the archaeogastropods, which mostly retain the mantle cavity and left ctenidium, with the auricle lying in front of the ventricle, the sexes being distinct in most species, and the visceral nerve cords crossing, least obviously in the more advanced forms owing to anterior concentration of the nerve ganglia. They also include the opisthobranchs and pulmonates, in which the animal is hermaphrodite, the visceral commissures do not cross, the nerve ganglia are much concentrated anteriorly, and an operculum is mostly lacking. Subordinate living groups are the pelagic heteropods and pteropods, now considered to belong respectively to the prosobranch order Caenogastropoda and to the Opisthobranchia.

The assignation of extinct families and genera to higher taxa must necessarily be based on the somewhat uncertain evidence of shell characters. In WENZ's work (105) marine Caenogastropoda are considered to have appeared first in the Triassic with genera assigned to the superfamilies Littorinacea, Cerithiacea, and Naticacea. Certain Paleozoic nonmarine genera, however, are tentatively assigned to superfamilies of this order, *Dendropupa* to the Cyclophoracea and *Bernicia* to the Rissoacea, from which the reader might be tempted to conclude that nonmarine caenogastropods were probably the earliest to appear. Contributors to the present *Treatise* consider, however, that certain extinct groups which WENZ included in the Archaeogastropoda were more advanced evolutionally. The first of these groups is the Subulitacea, which appeared in the Ordovician. Among its members are shells which are bucciniform, fusiform and mitriform in shape, and have apertures that are notched or even slightly produced and contracted abapically. The inference is that the Subulitacea had an inhalant canal, and since in living gastropods this feature is confined to certain Caenogastropoda and since also (in contrast to the Murchisoniacea, referred to below) the Paleozoic group had no counterbalancing archaeogastropod shell features, the presence of the canal is thought to be an adequate reason for including the group in the more advanced order. The resemblance of the Subulitacea to modern Buccinidae and Mitridae may, however, be due to convergence, for among Mesozoic gastropods are no genera linking them with these families, nor is there any convincing evidence for associating them with the Strombidae, near which FISCHER and STOLICZKA placed them.

The Loxonematacea, which appeared first in the Middle Ordovician, were also thought by WENZ to be Archaeogastropoda. They are, however, turriculate, many-whorled forms much resembling certain families, particularly the Turritellidae, included in the caenogastropod superfamily Cerithiacea, to which a number of workers, including contributors to the present *Treatise,* have thought them ancestral. The presence of a deep mid-labral sinus in earlier members of the Loxonematacea certainly suggests that they were dibranchiate. In later members, however, the sinus became shallower and located nearer the suture, from which it is probably to be inferred that in any case such forms had lost the right ctenidium. A broad labral sinus is present in many living Cerithiacea (some Turritellidae, *Potamides,* and others), although these are monobranchiate, and its functional significance is unknown, for it now has no connection with the exhalant current; it may be a vestigial feature. The view is taken by contributors to the present *Treatise* that, whether or not the earliest Loxonematacea were dibranchiate, caenogastropod characters were predominant in at least the great majority of members of the superfamily; the group has, therefore, been removed from the Archaeogastropoda. As first suggested by KNIGHT in 1944 (56) certain genera, such as *Acanthonema* of the Lower Devonian, placed by WENZ in the Loxonematacea, are here included in the Turritellidae.

Evidence as to the evolutionary advancement of another early group, the Murchisoniacea, is ambiguous. In this group, which makes its appearance in the Upper Cambrian or Lower Ordovician, there is an emargination near the middle of the labrum, usually generating a selenizone, and it is to be inferred from its presence that the ctenidia were paired and the respiratory currents directed as in the Pleurotomariacea. Some Murchisoniacea, however, have a distinct incipient canal at the abapical end of the aperture, strongly suggesting that the animal had a short inhalant siphon. We are, therefore, faced with the problem of reconciling the presence of this structure (now found only in gastropods belonging to the Caenogastropoda) with that of paired ctenidia, and we must accept the possibility that in the Murchisoniacea the typical zygobranch respiratory system had been modified by at least partial localization of the inhalant currents. Moreover, this was the earliest gastropod superfamily to include relatively high-spired forms, the general morphology of the shell being very similar to that of the much later Cerithiidae. In the present state of our knowledge it is impossible to decide if archaeogastropod or caenogastropod characters predominated in the Murchisoniacea, and the group has been retained in the more primitive order, but with its position queried.

Apart from the groups just considered, the earliest known caenogastropods are the nonmarine forms already mentioned. They comprise certain pupoidal genera of Carboniferous age, once thought to be pulmonates but all included in the Cyclophoracea in the *Treatise,* together with the small naticiform shell *Bernicia,* originally assigned to the Hydrobiidae, but transferred to the Viviparidae by KNIGHT, BATTEN & YOCHELSON herein. The Permian Karroo beds of Rhodesia have yielded small fresh-water gastropods indistinguishable from *Hydrobia.* Of important modern caenogastropod superfamilies other than those already mentioned, the Scalacea and Strombacea first appeared in the Jurassic, and the Calyptraeacea, Cypraeacea, and Tonnacea in the Cretaceous. It was not until the Tertiary that the most advanced prosobranch groups, particularly those with long siphonal canals, reached the acme of their development.

There is little evidence as to the precise ancestry of most of these caenogastropod groups. The most convincing line of descent, evidence for which has been accepted both by COSSMANN and by contributors to the present *Treatise,* is one leading from the Pleurotomariacea by way of the Murchisoniacea to the Loxonematacea and ultimately to the Cerithiacea. There is little doubt that other caenogastropods sprang from archaeogastropods belonging to groups entirely distinct from the Murchisoniacea, although there are objections to some alleged lineages reconstructed by COSSMANN and others. There is every reason to believe that the Caenogastropoda arose polyphyletically.

The remaining two subclasses now recognized in the Gastropoda are the Opisthobranchia and the Pulmonata. Although at an earlier period some zoologists considered the opisthobranchs to be more primitive than the prosobranchs, there is now general agreement that the prosobranchs were the source from which both of the subclasses in question were derived. It might be thought highly probable that different groups classed as opisthobranchs or as pulmonates would prove to be derived independently from different prosobranch groups, in the case of the pulmonates by adaptation along parallel lines to a terrestrial life. In all discussions of their origin by competent authorities, however, the view has been taken that both groups were monophyletic, and most authors have considered them to be closely related phylogenetically. Their hermaphrodite organization and euthyneurous condition led to their association by various authorities from SPENGEL onward in a major taxon, the Euthyneura. GRAHAM (74), from his work on the molluscan stomach, has concluded that both pulmonates and opisthobranchs were evolved from one of the higher groups of monotocardian prosobranchs (i.e., caenogastropods). MORTON (14) has considered that the two groups "did not come off remotely from each other, but arose quite close together, possibly at a single point," and has thought this point of origin to be some advanced archaeogastropod which (like modern Trochacea) had lost the right-hand pallial organs, and which in addition had acquired pallial genital organs. His reason for not accepting a more advanced prosobranch as the ancestral form lies mainly in the relatively primitive radula in both groups. One remarkable feature of opisthobranchs that have retained a spiral shell is the heterostrophic protoconch, resulting from hyperstrophic coiling of the larval shell, and this feature is also present in some primitive pulmonates, although it has been lost in most members of this order, possibly because there is no free larval stage. No satisfactory theory has been advanced attributing any functional significance to the heterostrophic protoconch, nor does it seem likely that it is an instance of recapitulated ancestry. It may, like torsion, have originated as a mutation affecting the larval stage.

Two families now classified as opisthobranchs, the Pyramidellidae and Acteonidae, are less removed from prosobranchs than other families of their order, and so appear to have undergone less evolutionary change since its original divergence. Both groups are operculate and have shells into which the entire head-foot mass can retreat, and in both the auricle is anterior to the ventricle; the Acteonidae, furthermore, are conspicuously streptoneurous and have the penis uninvaginable—both prosobranch characters. Opisthobranch characters possessed by both groups are a heterostrophic protoconch, a hermaphrodite organization, and certain features of the alimentary canal; the Pyramidellidae, it should be noted, are euthyneurous, with a marked concentration of ganglia, and they lack a ctenidium.

The Pyramidellacea were probably the first opisthobranch superfamily to make its appearance. The earliest forms included in this taxon by contributors to the *Treatise* belong to the family Streptacididae, of which the genus *Donaldina* is found possibly in the Devonian and certainly in the Lower Carboniferous. The protoconch is heterostrophic in some genera *(Streptacis* and *Donaldina)* of the family, although in *Platyconcha* it is discoidal and undeviated. According to the views of KNIGHT, the Pyramidellacea arose from the Loxonematacea, and since the latter group, as already seen, may well have been transitional from archaeogastropod to caenogastropod in evolutionary advancement, such an origin would be in keeping with MORTON's views. The Acteonidae appeared first in the Lower Carboniferous with the genus *Acteonina,* in which the protoconch, apparently consisting of a single whorl, is reported to be deviated and partly immersed. If the hypothesis of a monophyletic origin of the opisthobranchs is correct, derivation of the Acteonidae from the Pyramidellacea should presumably be assumed, but must have been accompanied by a considerable modification in shell characters. The tectibranch, or, at least, tectibranch-like opisthobranchs became moderately abundant in the Mesozoic, *Acteonina* and *Cylindrobullina* occurring in the Triassic, to be joined by *Bulla*-like forms *(Palaeohydatina)* in the Jurassic. The most notable genus of fossil opisthobranchs, *Acteonella,* consisting of mostly large, ovate, thick-shelled forms with prominent columellar folds, is particularly characteristic of the Cretaceous.

The affinities and origin of the Nerineacea, an important group of Jurassic and Cretaceous shells, mostly with complicated internal folds (in this respect resembling *Acteonella)* are problematic. In some genera belonging to this group, particularly those constituting the families Ceritellidae and Itieriidae, the shell has a distinctly opisthobranch facies, and the protoconch is known to be heterostrophic in at least two genera, *Pseudonerinea,* belonging to the former family, and, according to COSSMANN (21, v. 12, p. 209), *Itruvia,* belonging to the latter. COSSMANN, therefore, erected a new opisthobranch suborder, Entomotaeniata, for the superfamily. The group, however, has certain features not found in typical opisthobranchs—a short siphonal canal and a narrow anal emargination of the outer lip, situated, as in the Conidae, next to the suture and giving rise to an anal fasciole. YOCHELSON has suggested derivation of the nerineids from the Permian genus *Labridens,* which has comparable internal folds and is referred by him to the Subulitidae. On the other hand, if columellar folds could have been developed in one group they could also have appeared in another, and the nerineids could have had their origin in the Pyramidellacea. Their systematic position and the part they played in gastropod evolution must for the present remain undecided.

Malacologists, relying on the evidence of soft anatomy, have differed to some extent in their views as to the precise source of origin and interrelationships of the pulmonates. PELSENEER (80) thought it probable that they were derived from a primitive opisthobranch, such as *Acteon,* and further regarded the Ellobiidae as their most primitive family, ancestral both to the remaining Basommatophora and to the Stylommatophora. BOETTGER (5) has accepted the view that the pulmonates sprang from the Acteonidae, but has considered their most primitive family to be the Siphonariidae rather than the Ellobiidae, which he places near the middle of the tree of descent of the Basommatophora and from which he considers the Stylommotophora to have been derived. HUBENDICK (53), basing his argument on the more primitive type of radula found in the pulmonates and on the nervous system, has disagreed with the theory of their opisthobranch origin, and has thought that they arose directly from Archaeogastropoda. Reference has already been made to the views of GRAHAM (44) and MORTON (74). The latter worker, from a study of living Ellobiidae, has no doubt that this family was the basal stock of the pulmonates, constituting "one of the most ideally primitive living groups."

Turning, now, to the fossil record, we find that the earliest gastropods which have been regarded as pulmonates occur in the Lower Carboniferous and belong to the genus *Maturipupa,* in which the shell aperture has a prominent parietal tooth. This genus continues into the Upper Carboniferous where we also find *Anthracopupa,* with both columellar and parietal teeth, and *Dendropupa,* the apertural details of which are uncertain. The authors who originally described these genera noted their resemblance to modern land gastropods of the family Pupillidae, to which they accordingly referred them. WENZ (105), however, referred *Anthracopupa* and *Maturipupa* to the pulmonate family Ellobiidae and *Dendropupa* to the prosobranch family Cyclophoridae. In this *Treatise* KNIGHT, BATTEN and YOCHELSON propose to include all these genera in the Cyclophoridae. Among modern representatives of this family are several genera quite similar in external appearance to those Paleozoic forms and with toothed apertures. On the other hand, there can be no doubt as to the close resemblance of the fossil forms to some Ellobiidae. Modern Cyclophoridae are land shells; most modern Ellobiidae are aquatic, some living in the sea between tide marks and some in fresh water, but a few have a terrestrial habitat. The Paleozoic forms occur in nonmarine formations, but it is not possible to say definitely if they lived on land or in fresh water. The reasons for considering them to be Cyclophoridae rather than pulmonates are not very strong. Discoidal shells found in Permian nonmarine formations have been referred by some authors to the pulmonate genus *Planorbis* and a genus *Palaeorbis* is available for them. They are almost certainly worms.

Records of pulmonates from early Mesozoic formations, for example, of supposed species of *Helix, Planorbis,* and *Vertigo* from the English Lower Lias published in 1867 by MOORE (71), were with little doubt based on misidentifications. Unquestionable Basommatophora, represented by such genera as *Lymnaea, Physa, Planorbis,* and *Ellobium,* make their appearance in abundance in late Jurassic fresh-water formations. These also contain the earliest gastropods (apart from those from the Upper Paleozoic already mentioned) which have been regarded as land prosobranchs. The first reliable records of land pulmonates (Stylommatophora) are from the Upper Cretaceous. Deposits of this age in southern France have yielded some particularly interesting species of this group.

An interesting theory of the origin of the pteropods (or at least of the family Spiratellidae) is that of LEMCHE (66), that they originated as opisthobranch larvae which failed to sink to the bottom and undergo metamorphosis, but continued to lead a pelagic life until maturity was reached. Pteropods are first known definitely from the lowest beds of the Eocene, a few records from the Cretaceous being unreliable. The opinion of earlier workers that certain Lower Paleozoic organisms, such as *Conularia* and *Hyolithes,* were pteropods has now been abandoned. Were the forms in question to be accepted as such, the views expressed above as to the origin of the opisthobranchs could scarcely be maintained. The heteropods, pelagic prosobranchs, first appeared in the Albian stage of the Middle Cretaceous, if the genus *Bellerophina* D'ORBIGNY is correctly referred to this group. Little is ever likely to be known of the geological history of the shell-less gastropod groups, some of which are opisthobranchs and others pulmonates, and for discussions as to their relationships reference must be made to the neontological literature.

## GASTROPOD CLASSIFICATION

### HISTORY

In a brief review of the history of classification of the Gastropoda it is unnecessary to go back beyond CUVIER, who first recognized the group as a distinct taxon of the mollusks, and whose earliest classification, of 1797 and 1800 (27, 28), was based on obvious external characters. Major groups were defined by the presence or absence of a visible shell, and groups of the second rank by the nature of the shell (multivalve, as in *Chiton,* and "conivalve" or "spirivalve"); spirivalve shells were classified according to the characters of the aperture, whether entire, notched, or canaliculate. CUVIER did not name his taxa or define their status.

A classification proposed in 1801 by LAMARCK was based on much the same external criteria, but he included both gastropods and cephalopods (as now understood) in his order *mollusques céphalés,* shell-bearing cephalopods being separated from other univalves only in his secondary "taxis" (arrangement of members of any given taxon in taxa of next subordinate rank). Even in 1812 (60) and 1819 LAMARCK failed to recognize the essential unity of the gastropods, as now understood. His *mollusques céphalés* were divided into five taxa (given the rank of orders in 1819), four of which are now included in the gastropods. He restricted the term *gastéropodes* to one of these, consisting of forms without an external shell, while forms with simple external spiral shells constituted the second, for which the name *trachélipodes* was proposed. The other two were CUVIER's (1804) *ptéropodes* and a newly recognized group, *hétéropodes.* The distinctions between LAMARCK's five orders were based on external morphology, particularly the nature of the foot and of the shell. The *trachélipodes* were subdivided according to the presence or absence of an inhalant siphon. RAFINESQUE (87) followed LAMARCK, but renamed the *trachélipodes* as Spironotia. No subsequent worker accepted LAMARCK's restricted definition of a gastropod.

Meanwhile, other workers had begun to pay attention to the respiratory system as a possible basis of classification. DUMÉRIL in 1806 (32) adopted CUVIER's conception of the Gastropoda, dividing this group into three taxa: Dermobranchiata, with external gills; Tubispirantia, with internal gills and an inhalant siphon; and Adelobranchiata, with internal gills but no siphon. This classification was based on imperfect knowledge, and only the second of these taxa consisted of forms placed in one subclass at the present day. DUMÉRIL followed CUVIER in regarding the Pteropoda as a distinct molluscan order. In DEBLAINVILLE's earliest scheme, first outlined in 1814 with knowledge of unpublished work by CUVIER, the name gastropods was not assigned to any taxon, the *mollusques céphalés* being divided into no fewer than ten newly named orders based primarily on the respiratory organs. In seven of these, which included the *cryptodibranches* (*céphalopodes* of CUVIER) and the *ptérobranches* (*ptéropodes* of CUVIER) these organs and the shell (if present) are symmetrical, and in three, which included the *pulmobranches* (air-breathing forms) and the *pectinibranches,* asymmetrical. CUVIER's considered classification of the gastropods, regarded as a molluscan class, appeared in 1817 (30), and was based mainly upon their respiratory organs and sexual organization, although reference was also made to the presence or absence of an operculum. Seven orders were recognized: *nudibranches,* no shell, gills on back; *inférobranches,* no shell, gills below mantle edge; *tectibranches,* shell present but covered by mantle, gills on back or side, hermaphrodite; *pulmonés,* air-breathing with pulmonary cavity, hermaphrodite; *pectinibranches,* with spiral shell, sexes separate, gills pectinate, in mantle cavity; *scutibranches,* gills as in *pectinibranches,* but animal supposed to be self-fertilizing; and *cyclobranches,* shell not spiral, numerous gills arranged in a circlet. *Chiton* was associated with *Patella* in the last group.

The classification proposed by GOLDFUSS in 1820 (40) was largely based on that of CUVIER, but the chitons were separated as a distinct order, Crepidopoda, and the Pectinibranchia were reduced by the separation of siphonate forms as a taxon of correlative rank, Siphonobranchia. In his treatment of the chitons he was not followed by other authors until long after. In the same year SCHWEIGGER (88) adopted CUVIER's classification, assigning new names to some of his orders, among them Aspidobranchiata for the *scutibranches.*

In 1821 GRAY (46) announced his "natural arrangement of Mollusca according to their internal structure." The heteropods and pteropods (under new names) figured as classes ranking equally with the Gasteropodophora, as he termed the remaining gastropods. This last class was divided into two subclasses, the first consisting of air-breathing forms and the second of forms breathing by means of branchia under the mantle. This second subclass was divided into no fewer than 11 orders, the diagnoses of which refer to the nature of the branchia, reproductive processes, presence or absence of an operculum, shell characters, and (in some cases) the retractor muscle.

DEBLAINVILLE, in a classification published in 1824 (4), adopted a new basis for his primary taxis of the Paracephalophora (as he renamed the Gastropoda), dividing the class into three subclasses, the first dioecious, the second monoecious, and the third supposedly self-fertilizing. The respiratory system was in each the basis of the secondary taxis. The pteropods were reduced in rank so as to constitute merely a family of the order Nucleobranchiata of the monoecious subclass. We may note DEBLAINVILLE's transference of *Dentalium* from the phylum Vermes, in which it had been included by CUVIER and LAMARCK, to the self-fertilizing subclass of his Paracephalophora, of which it constituted an order named Cirrhobranchiata. It continued to form a low-ranking gastropod taxon until 1862, when BRONN (11) recognized and named the Scaphopoda as a distinct class.

LATREILLE (1825) (64), like DEBLAINVILLE, made the genital system his primary "taxobasis" (character upon which a taxonomic subdivision or taxis is based), dividing a restricted class Gastropoda into two so-called "sections" (i.e., subclasses), Hermaphrodita and Dioecia, and removing the Scutibranchia and Cyclobranchia to an entirely different branch of the Mollusca characterized by the absence of a penis.

In 1840 GRAY (47) departed considerably from his earlier system, and recognized two main subdivisions of the Gastropoda, Ctenobranchiata and Heterobranchiata, which corresponded, respectively, to the Streptoneura and Euthyneura of later systems, although the respiratory organs formed his taxobasis. We may note the division of the Ctenobranchiata into two taxa, Zoophaga and Phytophaga, according to the supposed method of feeding. This classification was extended by GRAY in 1850 (48), the Ctenobranchiata being then divided into orders Pectinibranchiata (a restriction of the original use of this term) and Scutibranchiata, the latter including the foreign elements Dentaliidae and Chitonidae. In 1853, however, GRAY (49) redistributed the majority of ctenobranch families among two suborders, Proboscidifera and Rostrifera, according to the presence or absence of a retractile proboscis.

MILNE EDWARDS (70) introduced in 1848 a new idea and terminology into the classification of the gastropods. He divided the class into two subclasses, *gastéropodes ordinaires* and *gastéropodes nageurs (hétéropodes),* appending the chitons as a "group satellite." The *gastéropodes ordinaires* were divided into two "sections," *gastéropodes pulmonés* and *gastéropodes branchifères,* and this last group into the two orders *opisthobranches* and *prosobranches,* according to relative positions of the heart and branchia. The Opisthobranchiata and Prosobranchiata were soon widely accepted as gastropod taxa of major rank, although they were ignored by GRAY.

S. P. WOODWARD (1851), in his well-known *Manual* (107), recognized as orders the three main gastropod subdivisions (termed by him Prosobranchiata, Pulmonifera, and Opisthobranchiata) of the present day, with the heteropods, for which he adopted DEBLAINVILLE's name Nucleobranchiata, forming a fourth order. He divided the prosobranchs into the Siphonostomata and Holostomata according to apertural characters. His last arrangement, being based on shell characters, was long favored by paleontologists, but corresponds to no grouping based on soft anatomy. Among WOODWARD's Holostomata were included such foreign elements as the Dentaliidae and Chitonidae.

In the classification of ADAMS & ADAMS (2) the Prosobranchiata, Opisthobranchiata, and Pulmonifera are recognized as subclasses of the Gastropoda, although the Heteropoda are accepted as a fourth subclass and the Pteropoda regarded as a distinct class. The arrangement adopted by these two workers was largely based on that of GRAY, but under the prosobranch order Pectinibranchiata we find a new suborder, Toxifera, added to the Proboscidifera and Rostrifera.

LOVÉN, in 1848 (67), was responsible for fundamental studies of the gastropod radula and the suggestion that this organ might be a useful taxobasis. GRAY (49) adopted the idea and divided each of his ctenobranch suborders, Prosocidifera and Rostrifera, into taxa based on the radula and bearing such names as Toxoglossa, Taenioglossa, Gymnoglossa, and Rachiglossa, although it should be noted that the first three names were assigned to groups in both suborders. This scheme was adopted in GRAY's elaborate but uncompleted classification of the gastropods published in 1857 (50). One innovation introduced by GRAY was the reduction of the Heteropoda from the rank of subclass to that of a mere section of the order Pectinibranchiata.

It remained for TROSCHEL & THIELE (103) to study the radula throughout the Gastropoda and to emend GRAY's classification. The groups into which TROSCHEL divided the "Gastropoda dioecia" (i.e., Prosobranchia) on the basis of the radula are the Taenioglossa, Toxoglossa, Rhachiglossa, Pteroglossa, Rhipidoglossa, and Docoglossa.

In the voluminous treatise of BRONN and KEFERSTEIN (11) we find the Pteropoda at last reunited with the Gastropoda, forming one of five orders, of which the four others are the Opisthobranchia, Heteropoda, Prosobranchia, and Pulmonata, all designated by their modern names. The Chitonidae appear as the first of five suborders of the Prosobranchia, the others being the Cyclobranchia, Aspidobranchia, Ctenobranchia, and Neurobranchia (the last comprising the Cyclostomatidae, Helicinidae, and Aciculidae). The primary subdivisions of the Ctenobranchia are the Siphonostomata and Holostomata. KEFERSTEIN was the first to designate both major subdivisions of the Pulmonata by the names (Stylommatophora, Basommatophora) that they still retain, although A. SCHMIDT had proposed the former some years previously. LACAZE-DUTHIERS had already shown that the Dentaliidae could not be included among the gastropods, but had considered them to form an order of the Acephala [Pelecypoda]. BRONN first raised them to a distinct class of the Mollusca, which he termed the Scaphopoda or Prosopocephala.

Yet another primary taxobasis for the gastropods was proposed by MÖRCH in 1865 (72). His Monotocardia included forms in which the heart has a single auricle and reproduction is by copulation, and the Diotocardia comprised forms in which there are two auricles and in which the genital products are discharged for external fertilization. The Monotocardia were then subdivided into a hermaphrodite group (consisting of the Pulmonata and Opisthobranchia) and a dioecious group, termed the Exophallia. The taxon Prosobranchia was thus abandoned, its constituents being divided between the Diotocardia (Aspidobranchia of older classifications) and the Monotocardia Exophallia.

VON IHERING (54) based far-reaching conclusions on his researches on the molluscan nervous system. He claimed to have found evidence for a diphyletic origin of forms previously classed as Gastropoda. The Prosobranchia, which he renamed Arthrocochlides and considered to rank as a phylum, were derived from segmented worms, whereas the pulmonates and opisthobranchs, grouped together as a class called Ichnopoda and included with the pteropods and cephalopods in a further phylum, Platycochlides, were derived from flatworms. The chitons, renamed Placophora, together with his Aplacophora (chaetoderms and *Neomenia*), belonged to yet another phylum, which he named the Amphineura. VON IHERING then subdivided his Arthrocochlides into the classes Chiastoneura and Orthoneusa, according to whether there was obvious crossing of the visceral nerve cords or not.

SPENGEL in 1881 (94) strongly criticized these conclusions, particularly the idea that the gastropods were diphyletic. He also showed that the distinction between orthoneurous and chiastoneurous prosobranchs was unimportant, the nerve cords actually crossing in both groups. SPENGEL was the first to demonstrate that structure of the nervous system and distribution of respiratory and other organs in the prosobranchs are to be regarded as the result of torsion, of which he found no evidence in the opisthobranchs and pulmonates. Accepting VON IHERING's conclusion that the Amphineura comprise a distinct taxon, he divided the gastropods into an order Streptoneura, coinciding with the prosobranchs (with suborders Zygobranchia and Azygobranchia defined by the presence of two ctenidia or one) and an order Euthyneura, composed of the "tribes" Ichnopoda (restricted to Opisthobranchia), Pulmonata, and Pteropoda.

A paper by MACDONALD (68) is of interest as proposing a formal scheme of gastropod classification in which the reproductive system, radula, and respiratory organs are adopted as taxobases at successive declining levels, with suggestion that the otocysts (previously studied by LACAZE-DUTHIERS) are of taxonomic use.

FISCHER (35), in his well-known *Manuel,* reverted to older ideas. The Pteropoda were regarded as a molluscan class distinct from a broadly conceived class Gastropoda, and the latter was considered to include six orders: Pulmonata, Opisthobranchiata, Nucleobranchiata (heteropods), Prosobranchiata, Polyplacophora, and Aplacophora.

LANKESTER in 1883 (63) introduced the concept of the archimollusk and developed the ideas of SPENGEL on torsion and asymmetry. His conception of the Gastropoda was the same as that of FISCHER, the group being divided into a subclass Isopleura (identical with VON IHERING's Amphineura) and a subclass Anisopleura (virtually identical with the Gastropoda as now restricted) with two branches, Streptoneura and Euthyneura. The heteropods, which many authors had interpreted as a distinct order or subclass, had already been included by GRAY (50) in his suborder Rostrifera of the Pectinibranchiata; LANKESTER also regarded them as a group of subordinate rank, forming a taxon (Natantia) of the azygobranch Streptoneura. He included the pteropods, however, among the Cephalopoda.

BOUVIER (9) produced in 1887 a revised classification of the Prosobranchia in the light of work on the nervous system and was responsible for uniting the most advanced monotocardian prosobranchs (Rachiglossa and Toxoglossa) as a single group, the *sténoglosses.* This group, destined to become the order Neogastropoda, consisted of the Zoophaga of GRAY with exception of certain families, notably the Strombidae and Cypraeidae.

In a scheme of classification published in 1888 (59) LACAZE-DUTHIERS adopted the nervous system as his taxobasis, and introduced a series of new names for the taxa of the highest two gastropod categories. In their contents, however, these taxa coincided with or differed very little from those already recognized, and his nomenclature has been ignored by later writers.

PERRIER (86) proposed in 1889 to subdivide the Diotocardia and the stenoglossate Monotocardia according to the characters of the nephridium.

The main contribution of PELSENEER (79) to gastropod taxonomy was the complete merging of the Pteropoda with the tectibranch Opisthobranchia. In his 1906 *Treatise* (82) we find the Thecosomata included in one tribe of this order and the Gymnosomata in another. PELSENEER regarded the Amphineura as a distinct class of the Mollusca.

The latest neontological classification of the Gastropoda is that of THIELE, first published in 1925 (97) and extended in the first volume of his *Handbuch der systematischen Weichtierkunde* (98). The class Gastropoda, from which the chitons, designated by SCHUMACHER's name Loricata, are excluded, is divided into three subclasses, the Prosobranchia, Opisthobranchia, and Pulmonata. The Prosobranchia are divided into three orders, two of which are renamed. The order Archaeogastropoda is co-extensive with the Diotocardia of MÖRCH and BOUVIER. The five "Sippen" or "stirpes" (groups that would rank as subclasses or superfamilies in the present standard hierarchy) into which it is divided include the Zeugobranchia and Docoglossa. The order Mesogastropoda consists mainly of the Taenioglossa and includes the Heteropoda as one of 15 "stirpes." The name Stenoglossa, for the most advanced prosobranch order, which includes four "stirpes," is adopted from BOUVIER and PELSENEER; WENZ (105) has since replaced it by the name Neogastropoda. The Opisthobranchia are divided into four orders, Pleurocoela (Tectibranchia of earlier authors), Pteropoda, Sacoglossa, and Acoela (composed of the suborders Notaspidea and Nudibranchia). The Pulmonata are divided, as by many previous authors, into the orders Basommatophora and Stylommatophora.

It is noteworthy that, although so many different features of soft anatomy have been used as bases of classification, a considerable measure of agreement obtains as to the main groups into which living gastropods fall. There have naturally been differences in assessment of the relative taxonomic ranks of different groups, resulting, for example, in disagreement as to whether two subclasses, Prosobranchia (=Streptoneura) and Euthyneura, or three, namely, Prosobranchia, Opisthobranchia, and Pulmonata, should be recognized. Moreover, problems have been encountered in deciding where to place certain (but remarkably few) borderline families, such as the Acteonidae, Pyramidellidae, and Siphonariidae, while the taxonomic rank and position of highly aberrant groups, notably the pteropods and heteropods, has been a source of uncertainty. There have been no widely discrepant systems of neontological classification, however.

Paleontologists, although able to view the whole succession of gastropod faunas from Cambrian times to the present day, have made few contributions to gastropod taxonomy except at family and lower levels, but have accepted the taxa based on living forms, attempting to fit extinct groups of gastropods into them. Unlike students of the pelecypods, they have mostly hesitated to propose schemes of classification based solely on shell features. An exception is the suggestion of GENEVIÈVE TERMIER (31) that all marine gastropods, fossil and living, may be separated by their growth lines into three groups, each corresponding to a main line of descent. In Group I the growth lines are prosocline or prosocyrt, in Group II they are opisthocyrt, and in Group III opisthocline. Groups I and II do not coincide with any groups defined by soft anatomy. All the shell-bearing opisthobranchs, together with the Stenoglossa and the Nerineacea, fall, however, into Group III.

There has been no other serious attempt to reconstruct a tree of gastropod descent from the succession of fossil forms and to found a scheme of classification in which subclasses and orders correspond to its main branches. Authors such as LANKESTER (63) have, indeed, presented a scheme of classification based on the comparative morphology of living forms as an alleged tree of descent, and NAEF (76) published a hypothetical phylogenetic tree with the six gastropod orders recognized by him coming off as branches at various levels. It is clear that only intensive study of fossil shells and the discovery of many new faunas will enable us to unravel gastropod phylogeny. At the present time we are not in a position to abandon the neontological classification, although it may well cut across true lines of descent.

As can readily be understood, authorities have differed in their views regarding the positions to assign to some extinct gastropod groups in neontological classification. The bellerophontids have usually been regarded as aspidobranch prosobranchs, but some workers have considered them to be heteropods, and SIMROTH (90) thought that they were a distinct class of Mollusca intermediate between the Cephalopoda and the Gastropoda. WENZ (106) accepted them as gastropods, but thought that they should constitute a subclass ranking equally with the prosobranchs, while they formed one of NAEF's (76) six gastropod orders. Reference has already been made to differences in opinion as to the systematic position of the Nerineacea, and of the Murchisoniacea and Loxonematacea. There are several early Mesozoic families, such as the Pseudomelaniidae, regarded by WENZ (105) as archaeogastropods on evidence not accepted by contributors to the present *Treatise*.

In the numerous classifications of the Gastropoda that have been proposed, a great number of names have been assigned to groups of higher rank than families. Some of these names soon dropped into oblivion, but some have been in frequent use, although the groups that they designate have constantly changed their taxonomic rank. For convenience of reference, a list of the most important of such names follows.

## MOST IMPORTANT NAMES APPLIED TO HIGHER TAXONOMIC CATEGORIES OF GASTROPODA

**Acoela** THIELE, 1926 (97, p. 110). Order of the subclass Opisthobranchia; consists of the Nudibranchia, together with the Notaspidea.

**Archaeogastropoda** THIELE, 1925 (97, p. 74). Order of the subclass Prosobranchia; consists of the group formerly known as Scutibranchia or Aspidobranchia, together with the Docoglossa.

**Aspidobranchia** SCHWEIGGER, 1820, as "Aspidobranchiata" (88, p. 616, 720). Proposed for the group termed "scutibranches" by CUVIER and extended by later authors (KEFERSTEIN, BERNARD) so as to remain equivalent to the Scutibranchia, as also subsequently extended, in which sense the group includes all Archaeogastropoda except the Docoglossa and is identical with the Rhipidoglossa (PELSENEER included the Docoglossa also).

**Azygobranchia** SPENGEL, 1881 (94, p. 373). Proposed for a suborder of the order (later subclass) Streptoneura (=Prosobranchia), in which only one ctenidium is present, and used by LANKESTER as an ordinal name in this sense; restricted by BOUVIER and others, however, to Diotocardia (now

Archaeogastropoda) with only one ctenidium, and thus restricted, its chief families are the Trochidae, Turbinidae, Neritidae, and Helicinidae.

**Basommatophora** Keferstein, 1864 (Bronn's *Klassen und Ordnungen des Thier-Reichs,* v. 3, p. 1246); often attributed to A. Schmidt. Order of the subclass Pulmonata consisting essentially of the aquatic forms.

**Caenogastropoda** Cox, 1959 (23). Proposed for the order of Prosobranchia formerly known by the name Pectinibranchia, as restricted by Gray in 1850. It combines the Mesogastropoda and the Stenoglossa or Neogastropoda.

**Cephalaspidea** Fischer, 1883 (35, p. 550). Division of the Opisthobranchia characterized by a cephalic disc and including the benthonic forms with spiral shells; regarded by Thiele as a suborder of the opisthobranch order Pleurocoela and by Boettger as an order of a subclass Euthyneura.

**Ctenobranchia** Schweigger, 1820, as "Ctenobranchiata" (88, p. 616, 723). Proposed for the group termed "pectinibranches" by Cuvier; adopted by Gray (1840, 1853) for a major subdivision of the Gastropoda almost identical with the present subclass Prosobranchia.

**Cyclobranchia** Cuvier, 1817, as "cyclobranches" (30, p. 451), latinized as "Cyclobranchiata" by Schweigger, 1820 (88). Group originally consisting of the Patellidae and the chitons, in which a circlet of gill lamellae is present; restricted by later authors by elimination of chitons and in this sense it corresponds to the Docoglossa.

**Diotocardia** Mörch, 1865 (72, p. 399). Gastropoda in which (typically) the heart has two auricles, although the Docoglossa were included; identical with the order Archaeogastropoda of the Prosobranchia.

**Docoglossa** Troschel, 1866 (103, p. 10). Subdivision of the Gastropoda defined by radular characters and identical with the superfamily Patellacea of the Archaeogastropoda (synonym, Cyclobranchia of authors).

**Entomotaeniata** Cossmann, 1896 (21, p. 5). Proposed as a suborder of the Opisthobranchia to include the Nerineidae and related families.

**Euthyneura** Spengel, 1881 (94, p. 373). Gastropoda in which the visceral nerve cords do not cross; a major subdivision consisting of the subclasses Opisthobranchia and Pulmonata.

**Gymnoglossa** Gray, 1853 (49, p. 129). Group of Gastropoda lacking a radula and consisting mainly of the Eulimidae and Pyramidellidae, usually referred to the Prosobranchia; Thiele terms this group the Aglossa, but Fischer introduced that name for several taxonomically distinct groups with no radula.

**Gymnosomata** deBlainville, 1824 (4, p. 273). One of two subdivisions (now suborders) of the Pteropoda, including forms in which the mantle and shell are absent in the adult.

**Heteropoda** Lamarck, 1812, as "hétéropodes," (60, p. 124), latinized as "Heteropoda" by Children (1823). Group of pelagic gastropods considered by some early authors to form a distinct order, but considered by Thiele to form a "stirps" (suborder) of the order Mesogastropoda; the chief genera are *Atlanta, Carinaria,* and *Pterotrachea.*

**Holostomata** Fleming, 1828 (*History of British Animals,* p. 297). Proposed as subdivision of the Pectinibranchia of undefined status and adopted by S. P. Woodward, Zittel, and other authors, mainly paleontologists.

**Mesogastropoda** Thiele, 1925 (97, p. 74). Order of the subclass Prosobranchia consisting of the Pectinibranchia (Ctenobranchia of earlier authors), except for families now included in the Stenoglossa or Neogastropoda; almost co-extensive with the Taenioglossa.

**Monotocardia** Mörch, 1865 (72, p. 398). Name originally assigned to all Gastropoda having a heart with single auricle; some authors who have adopted the name (e.g., Cooke, 1895) have restricted it to Prosobranchia in which there is only one auricle, and in this sense it is an alternative name to Pectinibranchia as restricted by Gray.

**Neogastropoda** Wenz, 1938 (105, p. 71). Proposed as new name for the Stenoglossa, the most advanced of the three orders of the subclass Prosobranchia.

**Neurobranchia** Keferstein, 1864 (in Bronn's *Klassen und Ordnungen des Thier-Reichs,* v. 3, p. 1023, 1061). Proposed as a suborder of the Prosobranchia for the three land operculate families Cyclostomatidae, Helicinidae, and Aciculidae; not now considered to form a taxonomic unit.

**Nucleobranchia** deBlainville, 1824, as "Nucleobranchiata" (4, p. 282). Originally proposed as an order for all pelagic gastropods, i.e., the Heteropoda (=Nectopoda of deBlainville) and the Pteropoda, but restricted by Fischer to the latter, regarded as an order.

**Nudibranchia** deBlainville, 1814, as "nudibranches" (*Bull. Soc. philomat. Paris,* p. 188, *ex* Cuvier, MS), latinized as "Nudibranchiata" by H.R.Schinz (1822). Order or suborder of the Opisthobranchia in which a shell is absent in the adult and a normal ctenidium is absent or replaced by secondary gills.

**Opisthobranchia** Milne Edwards, 1848, as "opisthobranches" (70, p. 107), latinized as "Opisthobranchiata" by S. P. Woodward (1851) and Morris & Lycett (1951). Subclass (originally order) of the Gastropoda, in most genera with auricle is posterior to the ventricle.

**Pectinibranchia** deBlainville, 1814, as "pectinibranches" (*Bull. Soc. philomat. Paris,* p. 178, *ex* Cuvier, MS.), latinized as "Pectinibranchia" by Goldfuss (1820). Instituted by Cuvier as an order for gastropods with comblike ctenidia, the group originally being almost equivalent to the Prosobranchia; restricted by GRAY (1850) by omission of the Scutibranchia, and used in this sense by later authors.

**Platypoda** GRAY, 1857 (50, p. 64). Group of Prosobranchia included by GRAY in his suborder "Rostrifera" and now included in the Taenioglossa; characterized by a more or less flattened foot adapted for creeping.

**Pleurocoela** THIELE, 1926 (97, p. 105). Order of the subclass Opisthobranchia consisting of Tectibranchia of earlier authors except Notaspidea.

**Prosobranchia** MILNE EDWARDS, 1848, as "prosobranches" (70, p. 107), latinized as "Prosobranchiata" by S.P.WOODWARD (1851) and MORRIS & LYCETT (1851). Subclass (originally order) of the Gastropoda in which the auricle is anterior to the ventricle and the visceral loop forms a figure 8.

**Ptenoglossa** GRAY, 1853 (49, p. 129). Suborder of the Prosobranchia in which the radula has a large number of hooked teeth; as now restricted, the Ptenoglossa contain only two families (Scalidae, Janthinidae).

**Pteropoda** CUVIER, 1804, as "ptéropodes" (29, p. 232), latinized as Pteropoda by DUMÉRIL (1806). Group of pelagic Mollusca long considered to constitute a class ranking equally with the Gastropoda but now regarded as an order of the Opisthobranchia.

**Pulmonata** CUVIER, 1817, as "pulmonés" (30, p. 401), latinized as "Pulmonifera" by FLEMING (1822) and as "Pulmonata" by WIEGMANN & RUTHE (1832). Subclass of the class Gastropoda characterized by modification of the mantle cavity for air-breathing.

**Rachiglossa** GRAY, 1853 (49, p. 127). Group of prosobranch Gastropoda defined by characters of the radula; originally confined to the Volutidae, but as extended by TROSCHEL, consists of the superfamilies Muricacea, Buccinacea, and Volutacea.

**Rhipidoglossa** MÖRCH, 1865, as "Rhipidoglossata" (72, p. 399), published in the form Rhipidoglossa by TROSCHEL (1866). Group of Gastropoda characterized by features of the radula, and identical with the Aspidobranchia or Scutibranchia; the Rhipidoglossa, together with the Docoglossa, constitute the order Archaeogastropoda.

**Sacoglossa** VONIHERING, 1876 (54, p. 146). Order of the Opisthobranchia in which the radula has a single series of strong teeth, preserved in a special sac when worn out; the shell is much reduced or absent.

**Scutibranchia** CUVIER, 1817, as "scutibranches" (30, p. 445), latinized as Scutibranchia by GOLDFUSS (1820). Name originally applied to *Haliotis, Fissurella,* and *Emarginula* (i.e., the Zygobranchia), together with some extraneous elements, but has been extended by some authorities to include all Archaeogastropoda except the Docoglossa, being thus equivalent to the Rhipidoglossa.

**Siphonostomata** DEBLAINVILLE, 1824 (4, p. 195). Proposed as a "family" of DEBLAINVILLE's order Siphonobranchiata; the name was applied by S.P. WOODWARD to a "section" of the order Prosobranchia and has been adopted by ZITTEL and other paleontologists for one of two groups of the Taenioglossa.

**Stenoglossa** BOUVIER, 1887, as "sténoglosses" (9, p. 471), latinized as Stenoglossa by PELSENEER (1906). Order of the subclass Prosobranchia combining the Toxoglossa and Rachiglossa; renamed Neogastropoda by WENZ (1938).

**Streptoneura** SPENGEL, 1881 (94, p. 373). One of two major subdivisions of the Gastropoda consisting of forms in which the visceral nerve cords cross, the visceral loop forming a figure 8; virtually equivalent to the subclass Prosobranchia.

**Stylommatophora** A.SCHMIDT, 1856 (*Abhandl. naturwiss. Ver. Sachsen u. Thüringen,* v. 1, p. 8). One of two major subdivisions of the Pulmonata, now considered to rank as an order, comprising the terrestrial forms.

**Taenioglossa** F.H.TROSCHEL, 1848, as "Taenioglossata" (in WIEGMANN's *Handb. der Zoologie,* ed. 3). Group of gastropods characterized by features of the radula and including most families now classified in the prosobranch order Mesogastropoda.

**Tectibranchia** CUVIER, 1817, as "tectibranches" (30, p. 395), latinized as Tectibranchia by GOLDFUSS (1820). Group now considered as an order of the subclass Opisthobranchia; a ctenidium is present on the right side, and there is usually an external or internal shell.

**Thalassophila** GRAY, 1850 (48, p. 119). Originally proposed for the pulmonate families Amphibolidae and Siphonariidae and accepted by FISCHER as a suborder; these families are now included in the order Basommatophora.

**Thecosomata** DEBLAINVILLE, 1824 (4, p. 271). One of two subdivisions (now suborders) of the Pteropoda, including forms in which a shell is present.

**Toxoglossa** TROSCHEL, 1848, as "Toxoglossata" (in WIEGMANN's *Handb. der Zoologie,* ed. 3). Group of gastropods characterized typically by features of the radula (although obsolete in some forms) and comprising part of the prosobranch order Neogastropoda (families Conidae, Turridae, and Terebridae); name refers to the poison gland associated with the radula of *Conus.*

**Zeugobranchia** VONIHERING, 1876 (54, p. 139). Group of the Archaeogastropoda in which two ctenidia are present; contains families Pleurotomariidae, Haliotidae, and Fissurellidae.

**Zygobranchia** SPENGEL, 1881 (94, p. 372). Same as Zeugobranchia.

## CLASSIFICATION ADOPTED IN THIS TREATISE

In accordance with the most general practice, the gastropods are here divided into three subclasses, Prosobranchia, Opisthobranchia, and Pulmonata. The accompanying diagrams (Figs. 87, 88) show the distinctive anatomical features of these groups, a primitive and a more advanced prosobranch being both illustrated. In Thiele's classification, currently adopted by most neontologists, the subclass Prosobranchia is divided into three orders, Archaeogastropoda, Mesogastropoda, and Stenoglossa. Only the first of these is dealt with in the

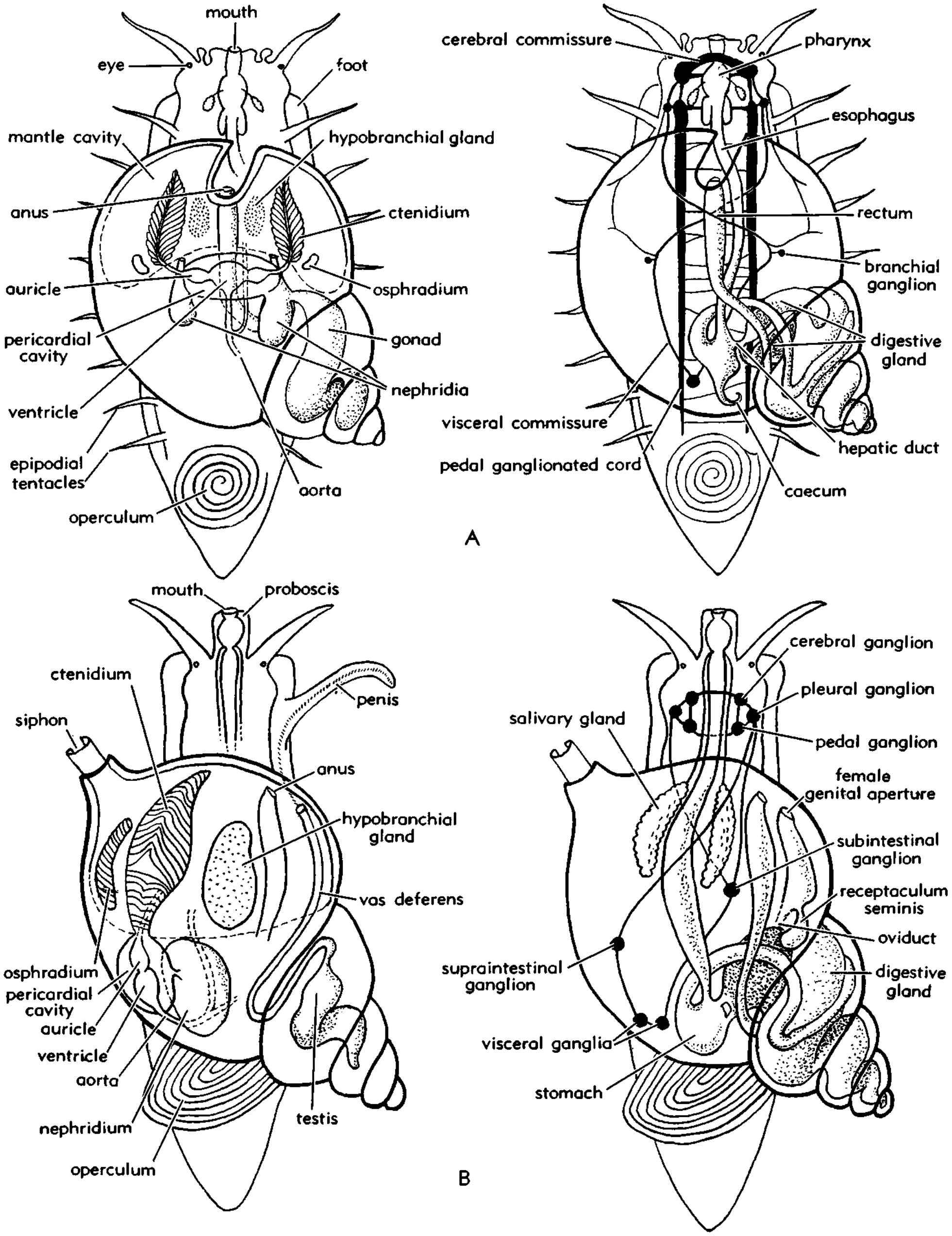

Fig. 87. Schematic representation of *(A)* a zygobranch archaeogastropod and *(B)* a siphonostomatous caenogastropod (122).

present part of the *Treatise* (except for the Supplement). The name Archaeogastropoda is here adopted as being preferable to any of the earlier names (Scutibranchia, Aspidobranchia and Diotocardia) which it replaced, as there has been some inconsistency in their use and it does not in itself imply the existence of any particular anatomical condition in the groups, many extinct, to which it is applied. This taxon is

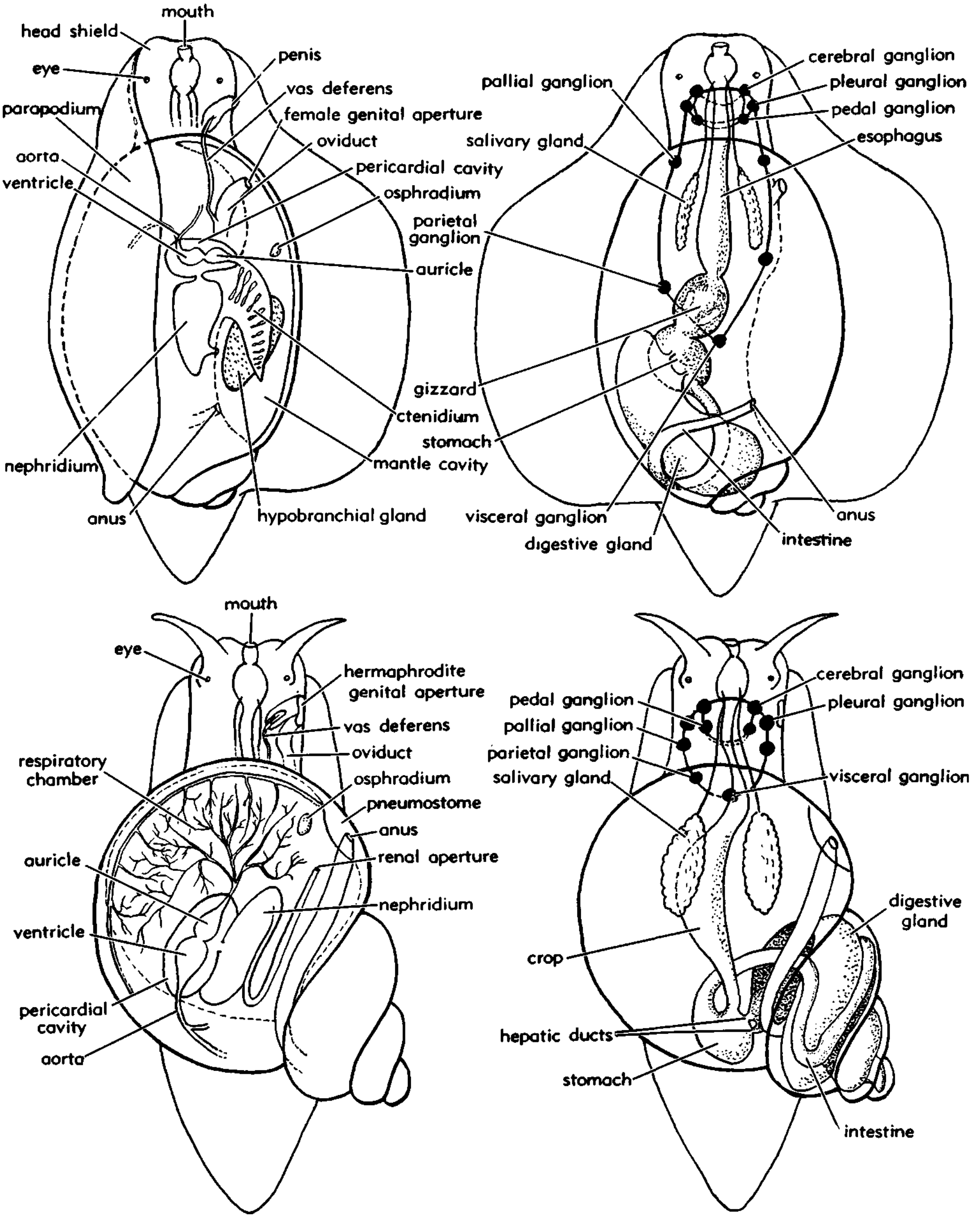

FIG. 88. Schematic representation of *(A)* a tectibranch opisthobranch with parapodia folded back on one side in left-hand diagram and on both sides in right-hand diagram, and *(B)* a fresh-water (basommatophoran) pulmonate (122).

a diverse assemblage, comprising gastropods in which the primitive features attributed to the hypothetical newly torqued ancestral form are retained to a varying extent. It has been subdivided in several ways by past authorities; by GRAY (1850) into Podophthalma and Edriophthalma; by TROSCHEL (1857) into Rhipidoglossa and Docoglossa; by BOUVIER (1887) into *zygobranches* and *azygobranches* (although SPENGEL's Azygobranchia had included monotocardian prosobranchs also); by PERRIER (1889) into *diotocardes (s.s.)* and *hétérocardes* (=Docoglossa). NAEF (1911) recognized four distinct orders, Belleromorpha, Zygobranchia, Trochomorpha and Docoglossa, among the forms now termed Archaeogastropoda. While there is no strong objection to some such arrangement, it has been decided here to recognize only a single order, and to divide this into suborders.

The first of these, the Bellerophontina, constitutes the most primitive group, in which the shell has complete bilateral symmetry and bears clear evidence that the ctenidia were paired and equal. Had we full knowledge of the soft anatomy of this group we might find good grounds for its recognition as a distinct order, but the available evidence does not justify this procedure.

Much might be said for the union of all asymmetrical gastropods in which there is clear evidence of the retention of two ctenidia in a second suborder. As already explained, however, there are reasons for thinking that the Murchisoniacea, although dibranchiate, were much more advanced in other characters than the Pleurotomariacea. The group has, therefore, been elevated to the rank of a suborder, reference of which to the Archaeogastropoda is queried. The Pleurotomariacea and a newly erected superfamily Fissurellacea, both of which have modern representatives clearly retaining many primitive features, form the essential constituents of another suborder, the Pleurotomariina (Zygobranchia of some neontological classifications). With them it has been decided to associate provisionally the long extinct superfamily Trochonematacea.

A further suborder Macluritina has been erected for the inclusion of the Macluritacea, a peculiar Lower Paleozoic group characterized by a hyperstrophically coiled shell, together with the apparently derivative superfamily, the Euomphalacea. In these groups the shell has a spiral ridge representing an anal channel, but its position suggests that the right ctenidium had been lost.

The next suborder, the Trochina, is constituted by the numerous monobranchiate archaeogastropods with ordinary orthostrophic, mainly conispiral shells and simple outer lips. Its many modern representatives belong to the superfamily Trochacea, but it also includes the extinct Platyceratacea, Microdomatacea, Anomphalacea, and Oriostomatacea.

C. M. YONGE (112) has expressed the opinion that the Neritacea should constitute a distinct order on account of their peculiar combination of anatomical characters; in particular, they have a very complex pallial genital system, although in many features they have not advanced beyond the archaeogastropod stage of evolution. They are here recognized as a distinct suborder, the Neritopsina.

The last archaeogastropod suborder here recognized is the Patellina (formerly the Docoglossa), which most previous workers have recognized as a well-characterized group on account of the peculiar radula of the Recent representatives and of the simple patelliform shell.

The remaining prosobranchs have been considerd by many authorities to constitute a single major taxon, to which the name Pectinibranchiata was restricted by GRAY in 1850. This group, which it is proposed to regard as an order, has been renamed Caenogastropoda, for consistency with the decision to adopt THIELE's name Archaeogastropoda for the more primitive order. It has been subdivided in different ways by different workers: into Zoophaga and Phytophaga by GRAY (1850); Proboscidifera and Rostrifera by GRAY (1853); Proboscidifera, Toxifera and Rostrifera by ADAMS & ADAMS (1853-4); Holostomata and Siphonostomata by a number of authorities; Taenioglossata, Rhachiglossata and Toxoglossata by MÖRCH (1865); and *ténioglosses* and *sténoglosses* by BOUVIER (1887). These last two subdivisions have been latterly assigned the rank of orders with the names

Mesogastropoda and Neogastropoda, but the division of caenogastropod taxa among them has to some extent been decided in a very arbitrary manner. It is not here proposed to make a taxonomic division of the Caenogastropoda which will be binding on contributors who will be dealing with this order in Part J of the present *Treatise.* Classification of the opisthobranchs and pulmonates will also be discussed in that Part.

## Summary of Classification[1]

As in previously published *Treatise* volumes, it is thought to be desirable to furnish in tabular form an outline of classification down to subfamily level as formulated by the authors contributing to this section on Gastropoda. The numbers of genera and subgenera assigned to each family and higher-rank taxa are given in parentheses following the name of the taxon, a single number signifying genera and two numbers signifying genera and subgenera. For example, "Coreospiridae (3)" indicates that 3 genera are included in this family, none divided into subgenera; "Sinuitinae (4;1)" indicates that this subfamily contains 4 genera and 1 subgenus (additional to a nominotypical subgenus not counted), or in other words, the subfamily contains 5 differently named taxa of generic-subgeneric rank. This method of making a census differs from that previously employed in *Treatise* tabulations (as p. L7-L10 and p. O160-O167) wherein nominotypical subgenera were included, thus enlarging in somewhat spurious manner the reported numbers of generic taxa.

The stratigraphic occurrence of each cited suprafamilial and familial taxon is given and the authorship of systematic descriptions belonging to it is indicated by code letters enclosed in parentheses. With reference to this statement of authorship, explanation needs to be given that whereas indicated authorship of any unit invariably covers preparation of the diagnosis of that unit, it does not necessarily include authorship of all constituent taxonomic divisions. For example, the diagnosis and general discussion of the suborder Pleurotomariina was prepared by Cox and KNIGHT, therefore being recorded by code letters as "(CX, KN)." Family-group divisions of this suborder, however, were organized in diverse manner, some by KNIGHT, BATTEN, and YOCHELSON, some of these authors with collaboration of Cox, some by Cox alone, and some by KEEN. The summary of classification affords a convenient means of explicit statement of the authorship of systematic descriptions; for this purpose, adopted code letters for the names of authors are as follows.

*Authorship of Systematic Descriptions*

| | |
|---|---|
| BATTEN, R. L. | BA |
| COX, L. R. | CX |
| KEEN, A.M. | KE |
| KNIGHT, J. B. | KN |
| ROBERTSON, ROBERT | RO |
| YOCHELSON, E. L. | YO |

The sequence of taxa recorded in the following tabulation, according to preference of most authors, is determined mainly by order of appearance in the geologic record, proceeding from oldest to youngest. Stratigraphic and geographic distribution are shown graphically in Figures 88A to 88E, inclusive.

*Main Divisions of Gastropoda Described in Treatise Part I*

Gastropoda *(class)* (794;414).[2] *L.Cam.-Rec.* (CX)

Prosobranchia *(subclass)* (789;414).[2] *L.Cam.-Rec.* (CX)

Archaeogastropoda *(order)* (732;407). *L.Cam.-Rec.* (CX)

Bellerophontina *(suborder)* (54;6). *L.Cam.-L.Trias.* (CX-KN)

Helcionellacea *(superfamily)* (4). *L.Cam.-U.Cam.* (KN-BA-YO)

Helcionellidae (1). *L.Cam.-U.Cam.* (KN-BA-YO)

Coreospiridae (3). *L.Cam.-U.Cam.* (KN-BA-YO)

Bellerophontacea *(superfamily)* (50;6). *U.Cam.-L.Trias.* (KN-BA-YO)

Cyrtolitidae (6). *U.Cam.-L.Sil.* (KN-BA-YO)

Sinuitidae (12;2). *U.Cam.-M.Perm.* (KN-BA-YO)

Sinuitinae (4;1). *U.Cam.-M.Dev.* (KN-BA-YO)

Bucanellinae (5;1). *U.Cam.-M.Perm.* (KN-BA-YO)

Euphemitinae (3). *?Dev., L.Carb.(Miss.)-Perm.* (KN-BA-YO)

Bellerophontidae (29;4). *U.Cam.-L.Trias.* (KN-BA-YO)

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[1] This section, with accompanying diagrams designed to show graphically the recorded stratigraphic and geographic distribution of gastropod family-group taxa, has been prepared by R. C. MOORE.

[2] Contains additional generic-rank taxa not described in this volume.

Tropidodiscinae (4). *U.Cam.-Dev.* (KN-BA-YO)
Bucaniinae (8). *L.Ord.-Dev.* (KN-BA-YO)
?Carinaropsinae (5). *?L.Ord., M.Ord.-Dev.* (KN-BA-YO)
Pterothecinae (4). *M.Ord.-M.Dev.* (KN-BA-YO)
Bellerophontinae (6;2). *M.Ord.-L.Trias.* (KN-BA-YO)
Knightitinae (2;2). *Dev.-M.Perm.* (KN-BA-YO)
Family Uncertain (3). *U.Ord.-U.Carb.(U. Penn.).* (KN-BA-YO)

Macluritina *(suborder)* (50;9). *U.Cam.-Trias., ?U.Cret.* (CX-KN)
Macluritacea *(superfamily)* (15;2). *U.Cam.-Dev.* (KN-BA-YO)
Onychochilidae (10). *U.Cam.-L.Dev.* (KN-BA-YO)
Onychochilinae (5). *U.Cam.-L.Dev.* (KN-BA-YO)
Scaevogyrinae (5). *U.Cam.-M.Ord.* (KN-BA-YO)
Macluritidae (5;2). *L.Ord.-Dev.* (KN-BA-YO)
Euomphalacea *(superfamily)* (35;7). *L.Ord.-Trias., ?U.Cret.* (KN-BA-YO-CX)
Helicotomidae (8). *L.Ord.-M.Jur.* (KN-BA-YO-CX)
Euomphalidae (22;7). *L.Ord.-Trias., ?U.Cret.* (KN-BA-YO-CX)
Omphalotrochidae (5). *Dev.-M.Perm., ?U. Trias.* (KN-BA-YO-CX)

Pleurotomariina *(suborder)* (168;51). *U.Cam.-Rec.* (CX-KN)
Pleurotomariacea *(superfamily)* (136;20). *U. Cam.-Rec.* (KN-BA-YO-CX)
Sinuopeidae (13). *U.Cam.-M.Perm.* (KN-BA-YO)
Sinuopeinae (3). *U.Cam.-U.Sil.* (KN-BA-YO)
Platyschismatinae (5). *L.Ord.-M.Perm.* (KN-BA-YO)
Turbonellininae (5). *U.Sil.-L.Perm.* (KN-BA-YO)
Raphistomatidae (19;2). *U.Cam.-M.Perm.* (KN-BA-YO)
Ophiletinae (5;1). *U.Cam.-L.Ord.* (KN-BA-YO)
Raphistomatinae (6). *M.Ord.-U.Dev., ?L. Carb.(Miss.).* (KN-BA-YO)
Liospirinae (3;1). *?L.Ord., M.Ord.-M.Perm.* (KN-BA-YO)
Omospirinae (5). *M.Ord.-L.Jur.* (KN-BA-YO-CX)
Eotomariidae (25;1). *U.Cam.-L.Jur.* (KN-BA-YO-CX)
Eotomariinae (17;1). *U.Cam.-L.Jur.* (KN-BA-YO-CX)
Agnesiinae (3). *L.Dev.-U.Trias.* (KN-BA-YO-CX)
Neilsoniinae (5). *L.Carb.(Miss.)-U.Trias.* (KN-BA-YO-CX)
Lophospiridae (5;2). *Ord.-M.Trias.* (KN-BA-YO-CX)
Lophospirinae (3;2). *Ord.-Sil.* (KN-BA-YO)
Ruedemanniinae (2). *M.Ord.-M.Trias.* (KN-BA-YO-CX)
Luciellidae (5). *Ord.-U.Carb.(Penn.).* (KN-BA-YO)
Phanerotrematidae (3). *M.Ord.-L.Dev.* (KN-BA-YO)
Gosseletinidae (14). *M.Ord.-Trias.* (KN-BA-YO-CX)
Gosseletininae (7). *M.Ord.-Trias.* (KN-BA-YO-CX)
Coelozoninae (7). *M.Ord.-L.Dev.* (KN-BA-YO)
Euomphalopteridae (2;1). *M.Sil.-U.Sil.* (KN-BA-YO)
Portlockiellidae (4). *Dev.-M.Perm.* (KN-BA-YO)
Catantostomatidae (1). *M.Dev.* (KN-BA-YO)
Porcelliidae (3). *Dev.-M.Jur.* (KN-BA-YO-CX)
Rhaphischismatidae (1). *L.Carb.(Miss.)* (KN-BA-YO)
Phymatopleuridae (9;1). *L. Carb.(Miss.)-Trias.* (KN-BA-YO-CX)
Polytremariidae (2). *L.Carb.(Miss.)-M.Perm.* (KN-BA-YO)
Laubellidae (1). *M.Trias.* (CX)
Schizogoniidae (2). *M.Trias.-U.Trias.* (CX)
Zygitidae (1). *M.Trias.* (CX)
Kittlidiscidae (1). *M.Trias.* (CX)
Temnotropidae (1). *M.Trias.-U.Trias.* (CX)
Pleurotomariidae (11). *Trias.-Rec.* (CX)
Trochotomidae (2;1). *U.Trias.-U.Jur.* (CX)
Scissurellidae (3;2). *U.Cret.-Rec.* (KE)
Haliotidae (1;10). *?U.Cret., Mio.-Rec.* (CX)
Family Uncertain (7). *L.Ord.-U.Trias.* (KN-BA-YO-CX)

Trochonematacea *(superfamily)* (5;2). *M. Ord.-M.Perm.* (KN-BA-YO)
Trochonematidae (5;2). *M.Ord.-M.Perm.* (KN-BA-YO)

Fissurellacea *(superfamily)* (27;29). *Trias.-Rec.* (CX)
Fissurellidae (27;29). *Trias.-Rec.* (CX-KE)
Emarginulinae (14;20). *?Trias., Jur.-Rec.* (CX-KE)
Diodorinae (4;2). *Jur.-Rec.* (CX-KE)
Fissurellinae (9;7). *Eoc.-Rec.* (KE)

Patellina *(suborder)* (32;37). *?M.Sil., M.Trias.-Rec.* (CX-KN)

Patellacea *(superfamily)* (23;32). *?M.Sil., M. Trias.-Rec.* (CX-KN)
Metoptomatidae (3). *M.Sil.-M.Perm.* (KN-BA-YO)

    - Symmetrocapulidae (2). *Trias.-Jur., ?Cret.* (CX)
    - Acmaeidae (10;19). *M.Trias.-Rec.* (CX-KE)
    - Patellidae (4;12). *?Jur., Eoc.-Rec.* (KE-CX)
      - Patellinae (2;11). *?Jur., Rec.* (KE-CX)
      - Nacellinae (2;1). *Eoc.-Rec.* (KE)
    - Lepetidae (4;1). *Mio.-Rec.* (KE)
  - Cocculinacea *(superfamily)* (5;5). *Mio.-Rec.* (KE)
    - Cocculinidae (1;3). *Mio.-Rec.* (KE)
    - Lepetellidae (4;2). *Rec.* (KE)
  - Superfamily and family Uncertain (4). *L.Jur.-U.Cret.* (CX)
- Trochina *(suborder)* (232;214). *L.Ord.-Rec.* (CX-KN)
  - Platyceratacea *(superfamily)* (19;7). *L.Ord.-M.Perm.* (KN-BA-YO)
    - Holopeidae (13). *L.Ord.-M.Perm.* (KN-BA-YO)
      - Holopeinae (6). *L.Ord.-U.Dev.* (KN-BA-YO)
      - Gyronematinae (7). *M.Ord.-M.Perm.* (KN-BA-YO)
    - Platyceratidae (6;7). *M.Ord.-M.Perm.* (KN-BA-YO)
  - Microdomatacea *(superfamily)* (10). *M.Ord.-M.Perm.* (KN-BA-YO)
    - Microdomatidae (5). *M.Ord.-M.Perm.* (KN-BA-YO)
    - Elasmonematidae (5). *U.Sil.-U.Carb.(Penn.).* (KN-BA-YO)
  - Anomphalacea *(superfamily)* (9). *Sil.-M.Perm.* (KN-BA-YO)
    - Anomphalidae (9). *Sil.-M.Perm.* (KN-BA-YO)
  - Oriostomatacea *(superfamily)* (8;1). *U.Sil.-L.Dev., ?Trias.* (KN-BA-YO)
    - Oriostomatidae (3). *U.Sil.-L.Dev.* (KN-BA-YO)
    - Tubinidae (5;1). *L.Dev., ?Trias.* (KN-BA-YO-CX)
  - Trochacea *(superfamily)* (192;207). *Trias.-Rec.* (KE)
    - Trochidae (96;136). *Trias.-Rec.* (KE-CX)
      - Proconulinae (12). *Trias.-U.Cret.* (CX)
      - Chilodontinae (5;1). *M.Trias.-U.Cret.* (CX)
      - Margaritinae (20;14). *Trias.-Rec.* (KE-CX)
      - Angariinae (5;1). *Trias.-Rec.* (KE-CX)
      - Monodontinae (17;31). *?Trias., M.Jur.-Rec.* (KE-CX)
      - Gibbulinae (11;18). *U.Jur.-Rec.* (KE-CX)
      - Calliostomatinae (9;27). *L.Cret.-Rec.* (KE-CX)
      - Trochinae (3;19). *U.Cret.-Rec.* (KE-CX)
      - Umboniinae (16;6). *U.Cret.-Rec.* (KE-CX)
      - Solariellinae (5;9). *U.Cret.-Rec.* (KE)
      - Halistylinae (1). *Pleist.-Rec.* (KE)
      - Subfamily Uncertain (2). *M.Trias.-U.Cret.* (CX)
    - Ataphridae (5;2). *Trias.-U.Cret.* (CX)
    - Stomatellidae (8;4). *Trias.-Rec.* (KE-CX)
    - Turbinidae (39;51). *M.Trias.-Rec.* (KE-CX)
      - Astraeinae (4;15). *Trias.-Rec.* (KE-CX)
      - Liotiinae (10;5). *Trias.-Rec.* (KE-CX)
      - Helicocryptinae (1). *M.Jur.-L.Cret.* (CX)
      - Petropomatinae (1). *L.Cret.* (CX)
      - Turbininae (3;17). *L.Cret.-Rec.* (KE-CX)
      - Colloniinae (7;4). *U.Cret.-Plio.* (KE)
      - Homalopomatinae (10;10). *Paleoc.-Rec.* (KE)
      - Subfamily Uncertain (3). *L.Jur.-U.Cret.* (CX)
    - Cyclostrematidae (37;9). *U.Jur.-Rec.* (KE-CX)
      - Skeneinae (27;6). *U.Jur.-Rec.* (KE-CX)
      - Cyclostrematinae (9;3). *U.Cret.-Rec.* (KE)
    - Phasianellidae (4;5). *Paleoc.-Rec.* (KE-RO)
    - Velainellidae (1). *Eoc.* (KE)
    - Orbitestellidae (2). *Rec.* (KE)
- Neritopsina *(suborder)* (83;82). *M.Dev.-Rec.* (CX-KN)
  - Neritacea *(superfamily)* (83;82). *M.Dev.-Rec.* (CX-KN)
    - Plagiothyridae (3). *M.Dev.-L.Carb.(Miss.).* (KN-BA-YO)
    - Neritopsidae (14;3). *M.Dev.-Rec.* (KN-BA-YO-CX)
      - Naticopsinae (8;2). *M.Dev.-U.Cret.* (KN-BA-YO-CX)
    - Dawsonellidae (1). *U.Carb.(Penn.).* (KN-BA-YO)
    - Neritidae (26;41). *Trias.-Rec.* (KE-CX)
      - Neritinae (21;39). *M.Trias.-Rec.* (KE-CX)
      - Neritiliinae (2). *Rec.* (KE)
      - Smaragdiinae (3;2). *Mio.-Rec.* (KE)
    - Helicinidae (28;32). *U.Cret.-Rec.* (KE)
      - Dimorphoptychiinae (1). *U.Cret.-Paleoc.* (KE)
      - Helicininae (10;14). *?Paleoc., Mio.-Rec.* (KE)
      - Hendersoniinae (3). *?Paleoc., Pleist.-Rec.* (KE)
      - Proserpininae (1;1). *?Oligo., Rec.* (KE)
      - Stoastomatinae (7;11). *Pleist.-Rec.* (KE)
      - Ceratodiscinae (3;5). *Rec.* (KE).
      - Proserpinellinae (3;1). *Pleist.-Rec.* (KE)
    - Deianiridae (1). *U.Cret.* (CX)
    - Phenacolepadidae (2;3). *Eoc.-Rec.* (KE)
    - Hydrocenidae (1;3). *Pleist.-Rec.* (KE)
    - Titiscaniidae (1). *Rec.* (KE)
    - Family Uncertain (6). *L.Carb.(Miss.)-Perm.* (KN-BA-YO)
- Murchisoniina *(suborder)* (49;6). *?U.Cam., L.Ord.-U.Trias.* (CX-KN)
  - Murchisoniacea *(superfamily)* (29;6). *?U.Cam., L.Ord.-U.Trias.* (KN-BA-YO)
    - Murchisoniidae (21;6). *?U.Cam., L.Ord.-U.Trias.* (KN-BA-YO-CX)
    - Plethospiridae (8). *L.Ord.-U.Trias.* (KN-BA-YO)

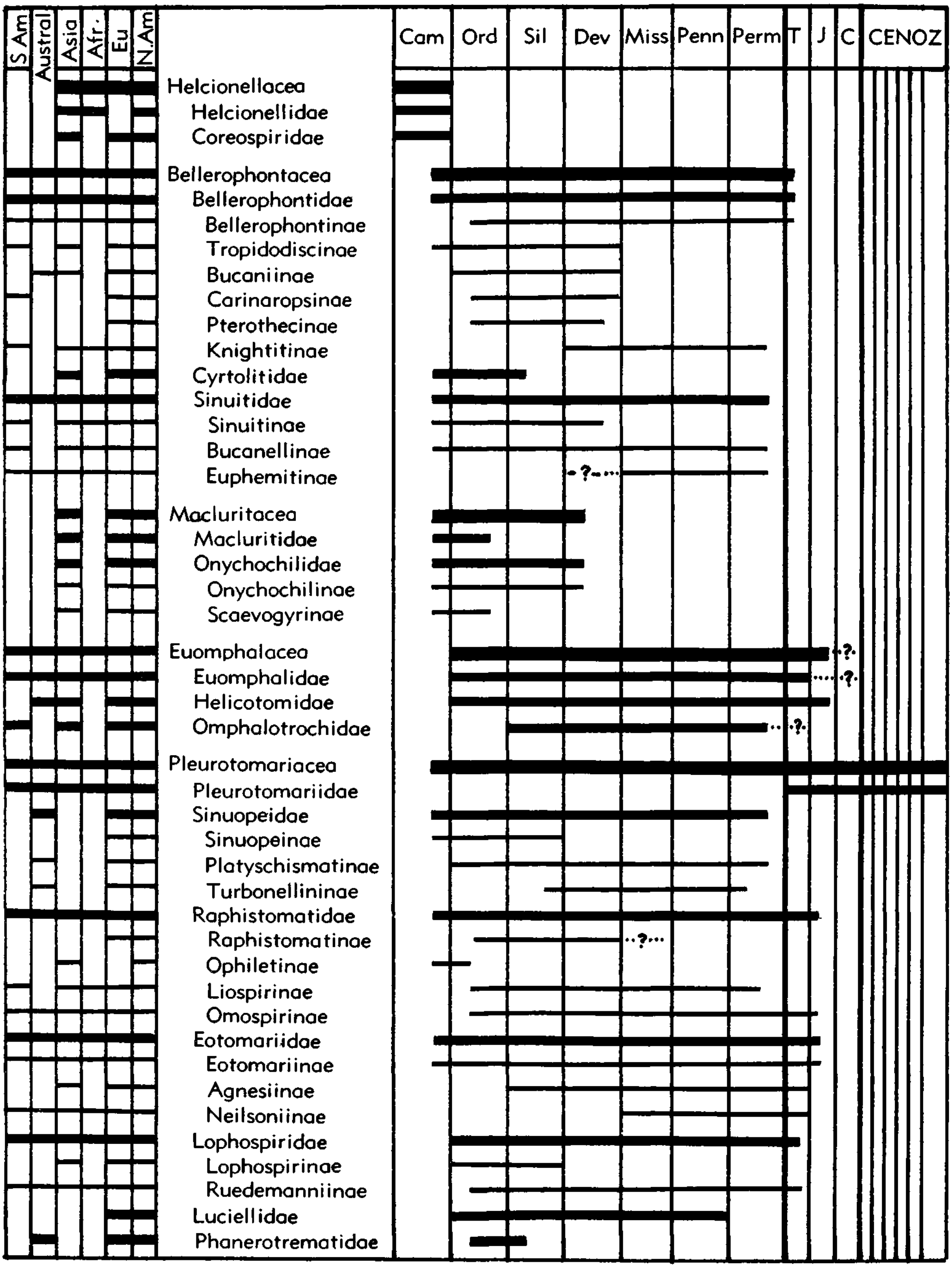

FIG. 88A. Stratigraphic and geographic distribution of gastropod family-group taxa described in *Treatise* Part I (MOORE, n).

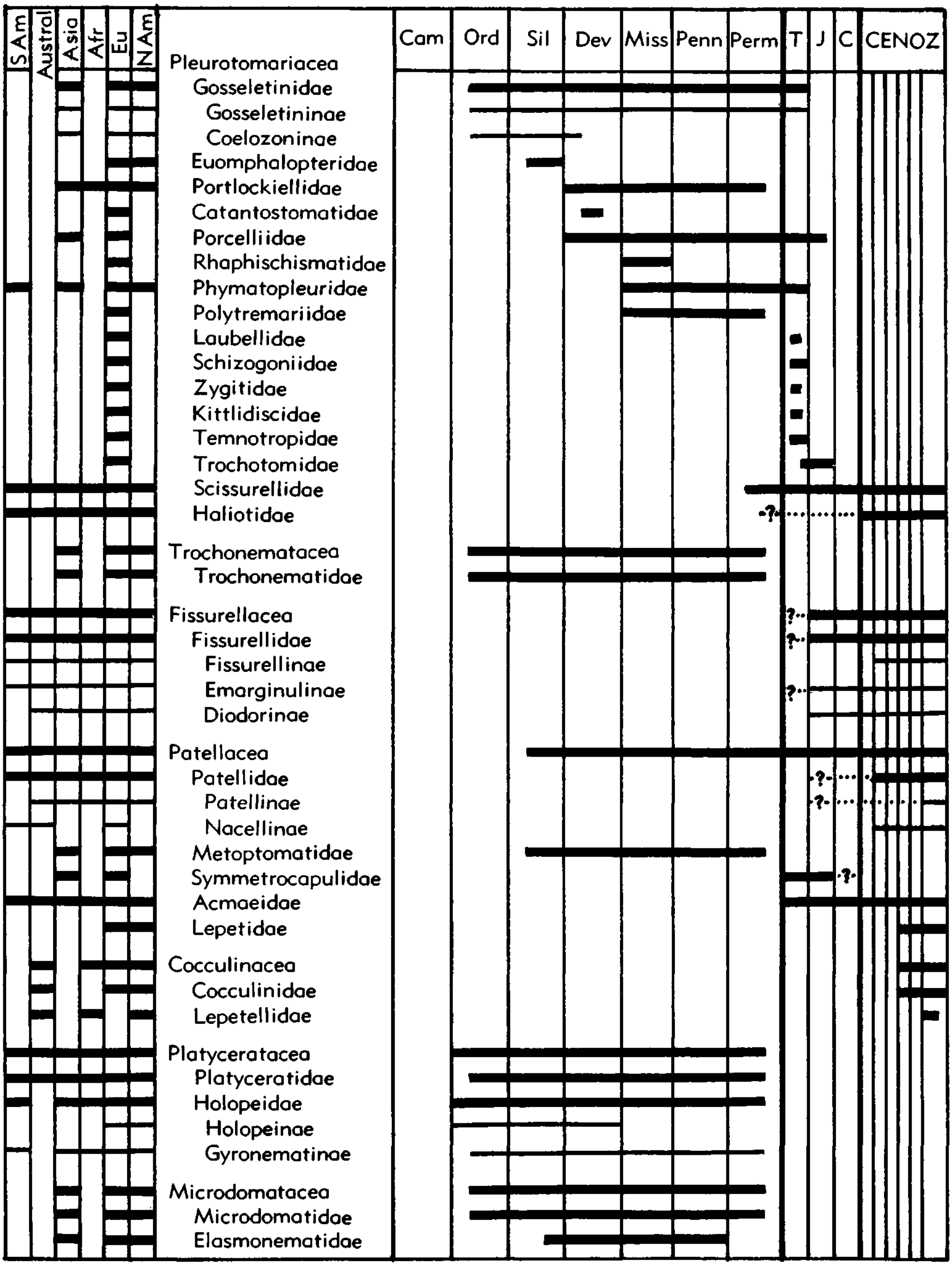

Fig. 88B. Stratigraphic and geographic distribution of gastropod family-group taxa, continued from Fig. 88A, (Moore, n).

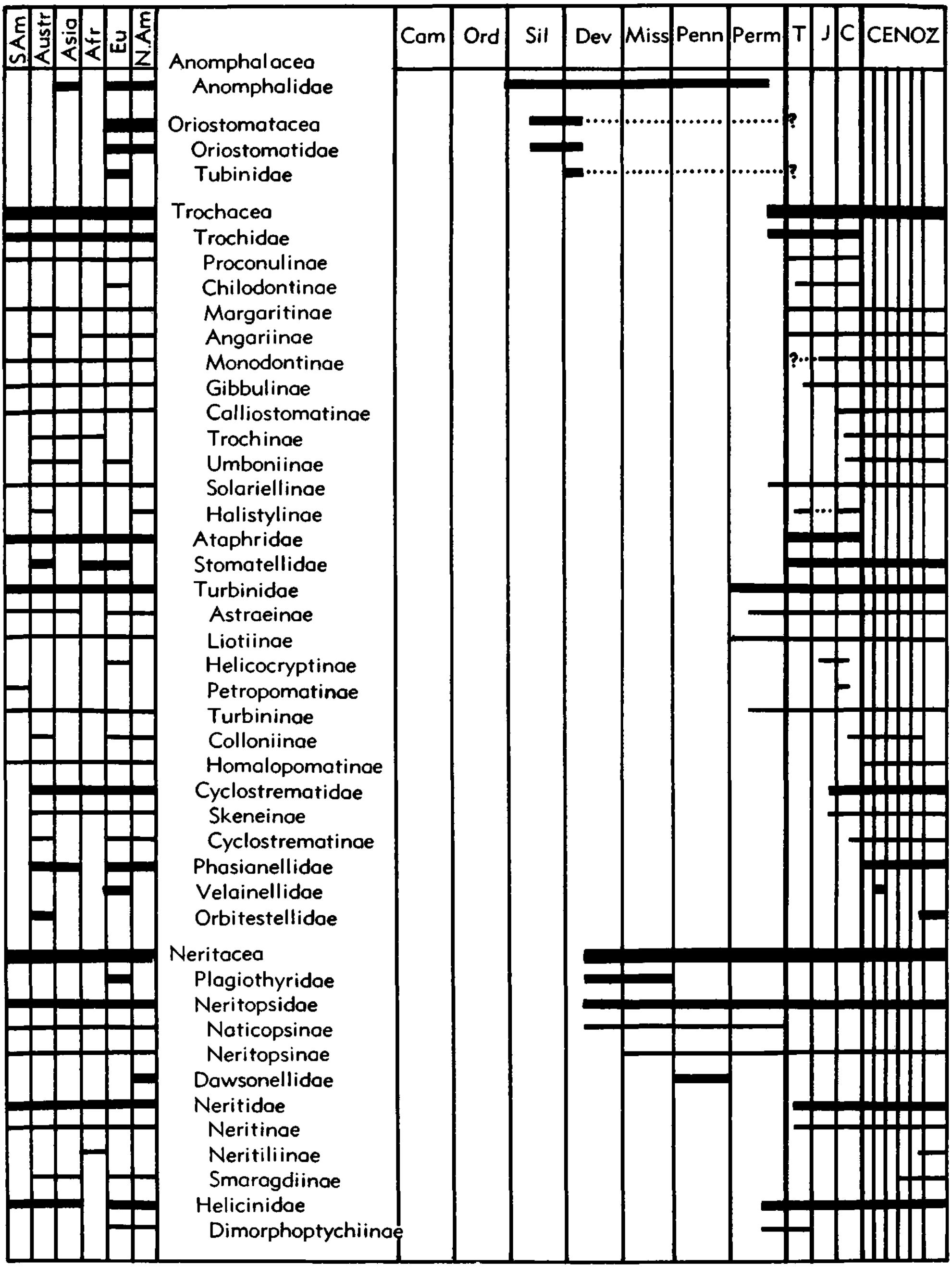

FIG. 88C. Stratigraphic and geographic distribution of gastropod family-group taxa, continued from Fig. 88B, (MOORE, n).

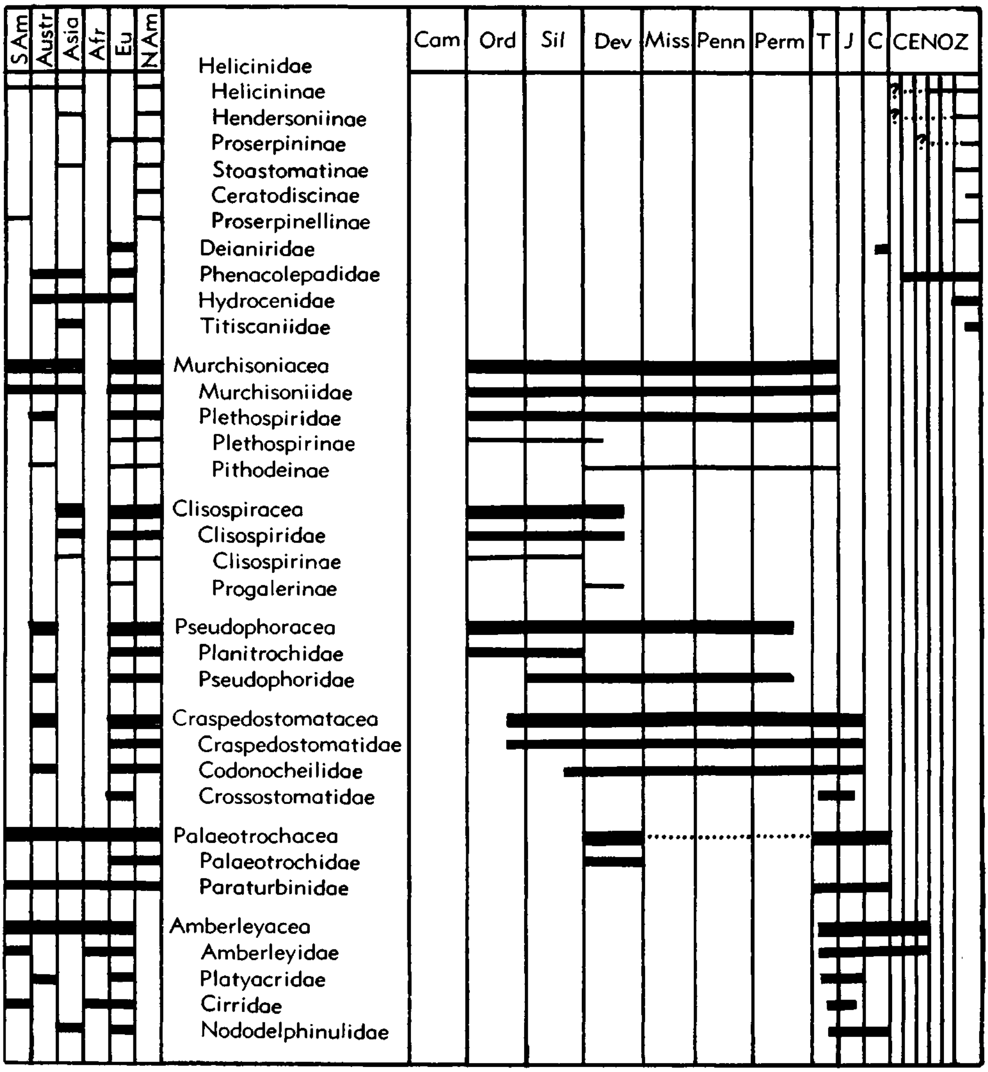

FIG. 88D. Stratigraphic and geographic distribution of gastropod family-group taxa, continued from Fig. 88C,(MOORE, n).

Plethospirinae (3). *L.Ord.-L.Dev.* (KN-BA-YO)

Pithodeinae (5). *Dev.-U.Trias.* (KN-BA-YO-CX)

Suborder Uncertain (84;2). *?L.Cam., L.Ord.-Oligo.* (KN-BA-YO-CX)

Clisospiracea *(superfamily)* (5). *L.Ord.-M. Dev.* (KN-BA-YO)

Clisospiridae (5). *L.Ord.-M.Dev.* (KN-BA-YO)

Clisospirinae (2). *L.Ord.-Sil.* (KN-BA-YO)

Progalerinae (3). *L.Dev.-M.Dev.* (KN-BA-YO)

Pseudophoracea *(superfamily)* (15). *L.Ord.-L. Carb.(Miss.).* (KN-BA-YO)

Planitrochidae (6). *L.Ord.-U.Sil.* (KN-BA-YO)

Pseudophoridae (9). *Sil.-M.Perm.* (KN-BA-YO)

Craspedostomatacea *(superfamily)* (16). *U. Ord.-Jur.* (KN-BA-YO-CX)

Craspedostomatidae (8). *U.Ord.-Jur.* (KN-YO-CX)

Codonocheilidae (6). *U.Sil.-M.Jur.* (KN-BA-YO-CX)

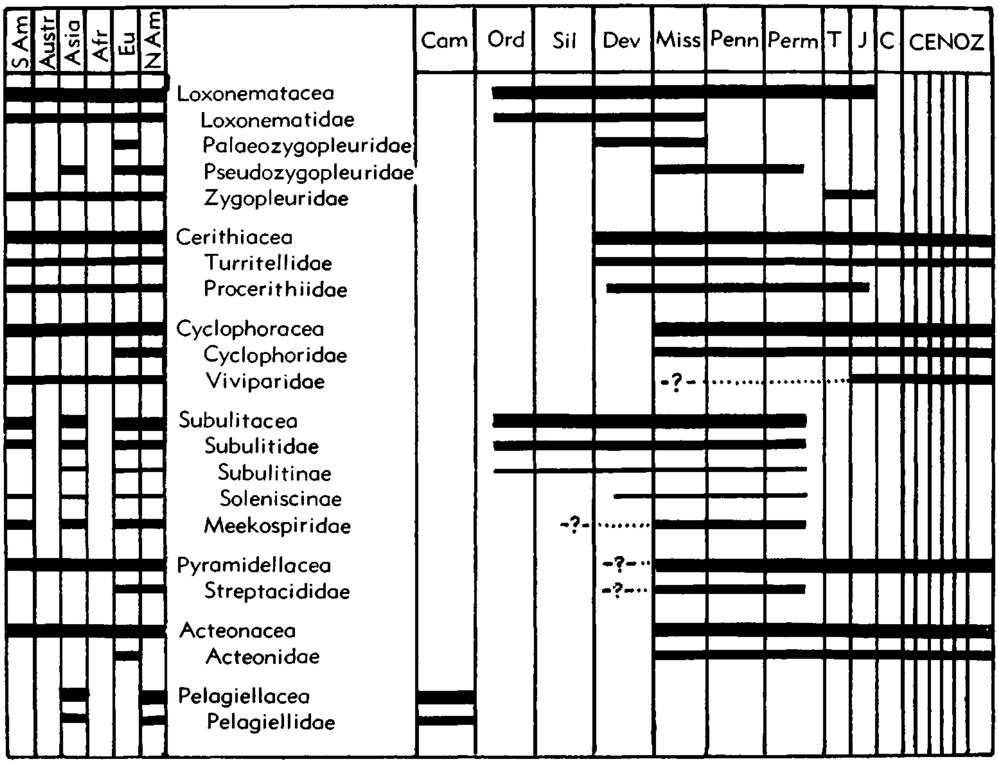

FIG. 88E. Stratigraphic and geographic distribution of gastropod family-group taxa, continued from Fig. 88D, (MOORE, n).

Crossostomatidae (2). *M.Trias.-M.Jur.* (CX)

Palaeotrochacea *(superfamily)* (7). *L.Dev.-U.Cret.* (KN-BA-YO)

Palaeotrochidae (4). *L.Dev.-U.Dev.* (KN-BA-YO)

Paraturbinidae (3). *Trias.-U.Cret.* (CX)

Amberleyacea *(superfamily)* (26;2). *M.Trias.-Oligo.* (CX)

Platyacridae (5). *M.Trias.-U.Jur.* (CX)

Cirridae (7;1). *U.Trias.-M.Jur.* (CX)

Amberleyidae (9;1). *M.Trias.-Oligo.* (CX)

Nododelphinulidae (5). *U.Trias.-U.Cret.* (CX)

Superfamily and family Uncertain (15). *?L.Cam., L.Ord.-U.Trias.* (KN-BA-YO-CX)

Caenogastropoda *(order)* (57;7).[3] *Ord.-Rec.* (CX)

Loxonematacea *(superfamily)* (31;5). *M.Ord.-U.Jur.* (KN-BA-YO-CX)

Loxonematidae (7). *M.Ord.-L.Carb.(Miss.).* (KN-BA-YO)

Palaeozygopleuridae (2). *Dev.-L.Carb.(Miss.).* (KN-BA-YO)

Pseudozygopleuridae (9;5). *L.Carb.(Miss.)-M.Perm.* (KN-BA-YO)

Zygopleuridae (12). *Trias.-U.Jur.* (CX)

Family Uncertain (1). *Perm.* (KN-BA-YO)

Cerithiacea *(superfamily)* (7).[3] *L.Dev.-Rec.* (KN-BA-YO-CX)

Turritellidae (4).[3] *L.Dev.-Rec.* (KN-BA-YO-CX)

Procerithiidae (3).[3] *M.Dev.-U.Jur.* (KN-BA-YO-CX)

Cyclophoracea *(superfamily)* (6).[3] *L.Carb.(Miss.)-Rec.* (KN-BA-YO-CX)

Cyclophoridae (4).[3] *L.Carb.(Miss.)-Rec.* (KN-BA-YO-CX)

Dendropupinae (4). *L.Carb.(Miss.)-L.Perm.* (KN-BA-YO)

Viviparidae (2).[3] *?L.Carb.(Miss.), Jur.-Rec.* (KN-BA-YO-CX)

Rissoacea *(superfamily)* (1). *Perm.-Rec.* (CX)

Hydrobiidae (1).[3] *Perm.-Rec.* (CX)

Subulitacea *(superfamily)* (13;2). *M.Ord.-M.Perm.* (KN-BA-YO)

Subulitidae (10;2). *M.Ord.-M.Perm.* (KN-BA-YO)

Subulitinae (5;2). *M.Ord.-M.Perm.* (KN-BA-YO)

Soleniscinae (5). *M.Dev.-M.Perm.* (KN-BA-YO)

Meekospiridae (3). *?U.Sil., L.Carb.(Miss.)-M.Perm.* (KN-BA-YO)

Opisthobranchia *(subclass)* (4).[3] *?Dev., L.Carb.(Miss.)-Rec.* (KN-BA-YO)

Order Uncertain (3).[3] *?Dev., L.Carb.(Miss.)-Rec.* (KN-BA-YO)

Pyramidellacea *(superfamily)* (3).[3] *?Dev., L.Carb.(Miss.)-Rec.* (KN-BA-YO)

Streptacididae (3). *?Dev., L.Carb.(Miss.)-Perm.* (KN-BA-YO)

Pleurocoela *(order)* (1).[3] *L.Carb.(Miss.)-Rec.* (KN-BA-YO)

Acteonacea *(superfamily)* (1).[3] *L.Carb.(Miss.)-Rec.* (KN-BA-YO)

Acteonidae (1).[3] *L.Carb.(Miss.)-Rec.* (KN-BA-YO)

?Gastropoda Incertae Sedis (1). *Cam.* (KN-BA-YO)

Pelagiellacea *(superfamily)* (1). *Cam.* (KN-BA-YO)

Pelagiellidae (1). *Cam.* (KN-BA-YO)

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[3] Contains additional generic-rank taxa not described in this volume.

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# SYSTEMATIC DESCRIPTIONS

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