HANDBOOK OF SYSTEMATIC MALACOLOGY

PARTS 3 AND 4

JOHANNES THIELE

Johannes Thiele (1860-1935) was one of the most productive systematists of his time. His probably best-known work, the *Handbuch der systematischen Weichtierkunde* (1929-1935), completed only months before his death, has become an indispensable source of information for any worker in the field. Few other works have subsequently reached the breadth and depth of information that Thiele had accumulated on the phylum Mollusca.

The *Handbuch* was originally issued in four parts by Gustav Fischer Verlag in Jena. It was subsequently combined in two cloth-bound volumes and sold as a hard-cover edition. With each subsequent part after 1929, Thiele supplied extensive additions and corrections to the earlier text. As these additions and corrections have different dates of publication, they are included in this translation as footnote on appropriate pages rather than merged into the main body of the text.

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Handbook of Systematic Malacology

Parts 3 and 4

Handbook of Systematic Malacology

Part 3
(Scaphopoda / Bivalvia / Cephalopoda)

and

Part 4
(Comparative Morphology / Phylogeny / Geographical Distribution)

Johannes Thiele

Scientific Editors of Translation:
Rüdiger Bieler and Paula M. Mikkelsen

Foreword to the English-language Edition

Johannes Thiele (1860–1935) was one of the most productive systematists of his time. Between 1886 and 1935, Thiele, who was originally based at the Dresden Museum and later at the Zoological Museum in Berlin, published more than 150 scientific publications (for biographies and bibliographies, see Rensch, 1930, Winckworth, 1938, and Bieler & Boss, 1989). Although a considerable number of his works dealt with sponges and crustaceans, he is best known for his extensive contributions to malacology. These contributions range from smaller review articles to major monographs (e.g., as part of the VALDIVIA German Deep-Sea Expedition series) to handbooks that have become standards in the field of malacology. His probably best-known work, the **Handbuch der systematischen Weichtierkunde** (1929–1935) has become an indispens-- able source of information for any worker in the field. Few other works have subsequently reached the breadth and depth of information that Thiele had accumulated on the phylum Mollusca. His now 'traditional' systematic arrangement of taxa in the **Handbuch** has been followed by thousands of workers and has become the basis for the arrangement of scientific collections throughout the world. Although many parts are now outdated due to subsequent work, the **Handbuch** is still an important source of information and of great taxonomic significance as it comprises more anatomical data than the other major handbooks in use, i.e., Wenz's work as part of the *Handbuch der Paläozoologie*, or the *Treatise on Invertebrate Paleontology*, and because it contains a large number of new taxa described by Thiele. To meet the demand, the **Handbuch** was reprinted in its original form in 1963 (by A. Asher & Co., Amsterdam). Workers less familiar with the German language have had to resort to translation services, and there is likely hardly a page in the **Handbuch** that has not been translated at least once. Dr. Joseph Rosewater, Curator of Mollusks at the National Museum of Natural History in Washington,

D.C., initiated a request for a full English translation of Thiele's **Handbuch**, shortly before his untimely death in 1985.

We have verified and modified this translation word by word. Thiele's original text has its difficulties, such as awkward terminology and frequent ambiguous statements. Special care has been taken to retain these kinds of text problems, to provide a translation which is as literal as possible, while still furnishing readable copy. A limited number of technical terms have been used where Thiele employed common German terms without modern English equivalents, but no attempt has been made to update or correct the original, except in the case of the few obvious printer's errors in the text. Many geographical names have been translated to make them more accessible to English readers; again, to remain as close as possible to Thiele's concept of these places, we did not modernize the names according to political boundaries. 'Stirps' or 'Sippe' was used by Thiele for taxa equivalent to the modern category superfamily. Because he frequently used non-standard endings (rather than -acea or -oidea) we have retained 'stirps' in the translation. Where we used informal endings for taxonomic group names we found a likewise informal ending in the translation (e.g., -aceans, -ids). In instances involving complex systematic or zoogeographical problems, or at any time when the English translation seems unclear, the reader is advised to refer back to the original Germany text for clarification.

One problem with terminology deserves special mention here. Thiele's terminology for radular teeth was somewhat different from that in modern use. He referred to plates (Platten) instead of teeth (Zähne) and to teeth instead of cusps. His arrangement of central plate (Mittelplatte) intermediate plate (Zwischenplatte), and marginal or lateral plate (Randplatte or Seitenplatte) is in most cases equivalent to the modern rachidian, lateral and marginal teeth, respectively. We have decided however to use the literal translations of the original terms, in order to avoid implications of homology not stated by Thiele, and to allow for the possibility that a 'plate' does not necessarily carry a tooth-like structure.

The **Handbuch** was originally issued in four parts, in orange paperbacks by Gustav Fischer Verlag in Jena. It was subsequently combined in two cloth-bound volumes and sold as a hard-cover edition. With each subsequent part after 1929, Thiele supplied extensive additions and corrections to the earlier text. The original **Handbuch** contains 24 pages of such additions. Another often-overlooked oddity of Thiele's work is the fact that he made major nomenclatural statements in the index and errata sections, such as the introduction of replacement names for homonyms subsequently discovered (see also Tomlin, 1936). As these

additions and corrections have different dates of publication, they are included in this translation as footnotes on appropriate pages rather than merged into the main body of the text.

Throughout the text, the start of each original page as well as the original figure placement is signified by an original page number in the left margin. Names of new genera and species introduced in the **Handbuch** have been printed in *boldface* in the main body of the text and in the index (new names were unclearly indicated by s p a c e d font in the original index). A number of new taxa that were clearly introduced as such by Thiele but missed by the compiler of the original index have also been included. As in-depth account of Thiele's publications and new genus-group taxa can be found in a series of papers by Bieler and Boss (1989, 1991).

As the dates of publication of the four original parts (Teile) are not readily obtainable from the hard-bound original volumes (Bände), a compilation of the dates follows below:

Erster Band ("1931"):

Teil 1. (Loricata; Gastropoda: Prosobranchia), pp. 1–376 (1929; published between 4 September and 22 October).

Teil 2. (Gastropoda: Opisthobranchia and Pulmonata; Additions; Index for Teil 1–2), pp. 377-788 (1931; published before 1 November).

Zweiter Band "1935"):

Teil 3. (Scaphopoda; Bivalvia; Cephalopoda; Additions and Corrections for Teile 1–2; Index for Teil 3), pp. 779–1022 (1934; published before 20 January).

Teil 4. (General Part and Corrections for Teile 1–3), pp. 1023–1154, pp. i–vi (for Erster Band, 1.–2. Teil), unnumbered divider pages for 1. and 2. Teil, pp. i-v for Zweiter Band, unnumbered divider pages for 3. and 4. Teil (1935; published before 28 March).

Literature cited:

Bieler, R., & K. J. Boss. 1989. Johannes Thiele and his contributions to zoology. Part 1. Biography and bibliography. *Nemouria, Occasional Papers of the Delaware Museum of Natural History, 34*: 1–30.

Boss, K. J., & R. Bieler. 1991. Johannes Thiele and his contributions to zoology. Part 2. Genus group names (Mollusca). *Nemouria, Occasional Papers of the Delaware Museum of Natural History, 39*: 1–77.

viii

Rensch, B. 1930. Johannes Thiele zum 70. Geburtstage. *Archiv für Molluskenkunde, 62(6)*: 201–209, pl. 11.
Tomlin, J. R. le B. 1936. Book notes: Thiele's "Handbuch der Systematischen Weichtierkunde." *Proceedings of the Malacological Society of London, 22(3)*: 136–137.
Winckworth, R. 1938. Obituary: Johannes Thiele, 1860–1935. *Proceedings of the Malacological Society of London, 23(1)*: 9–11.

This Volume:

This third and final part of the English edition comprises 'Teile' 3 and 4 (the second volume of the original).

Teil 3 is a continuation of the systematic treatment of the Mollusca, covering Scaphopoda, Bivalvia and Cephalopoda (Aplacophora were not included in the **Handbuch**; Thiele, who published extensively on Solenogastres, did not consider them part of the Mollusca). Whereas the first three parts provide an indispensable resource for taxonomic and anatomical research, the fourth part is the highlight of Thiele's work. In this final part, completed only a few months before his death, Thiele summarizes in great detail his thoughts on molluscan phylogeny and zoogeography. He probably was the last malacologist who had a near-complete overview of the known extant molluscan taxa based on personal work involving shells *and* anatomy. Certain of his hypotheses have been replaced by others — it would, after all, be a major embarrassment to our field of science if we had not made some progress in the past 60 years. More recent evidence, for instance, no longer supports the position of the Pleurotomariidae as the most primitive living gastropods and the Patellidae as closely related with the Fissurellidae, but rather places the Patellidae as a much earlier offshoot of the gastropod clade. And the Juliidae, placed in the Bivalvia by Thiele based on the then available shell characters, are now recognized as highly derived bivalved gastropods. Nevertheless, much of this work remains surprisingly up-to-date, and much what he already inferred has been painstakingly rediscovered in subsequent decades. In the gastropods, for instance, this includes his statements about the special anatomical conditions and systematic position of the neritaceans and some of his hypotheses concerning the phylogenetic origin of the opisthobranchs.

In the first part of the **Handbuch**, Thiele arranged his taxa — possibly influenced by his strong collection management background — in linear sequence that is reminiscent of a *scala naturae*: family A stands next to family B which then connects to family C. In the fourth part he broke this mold and much of his concentration was placed on finding

morphological homologies. He carried it to the next level by often focusing on the distinction between primitive and special characters of the groups under study, foreshadowing in part today's cladistic approach to molluscan phylogeny.

We hope that this pro-bono translation will make Thiele's work more widely known and accessible to malacologists world-wide.

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Contents

iii

PART 4

PART 3

Scaphopoda/Bivalvia/Cephalopoda

Class SCAPHOPODA

Shell bilaterally symmetrical, more or less elongated, in most cases weakly curved, tube- or spindle-shaped, as a rule posteriorly narrowed, exteriorly smooth or ribbed, open at both ends. The animal in repose is completely enclosed by the shell. The mantle is ventrally closed and, with the body, forms an anteriorly and posteriorly open tube, the posterior part of which forms a shovel-shaped appendage. The head is an oral cone without eyes, with a rosette of lobe-shaped appendages at the oral opening, at its base are found a pair of small skin folds, from which arise several long, terminally thickened, extensile cirri (captacula). The anteriorly produced, distensible foot is protruded from the anterior opening and serves in burrowing. The nervous system is of similar arrangement to that in bivalves, but differs in the presence of buccal ganglia. Gills are absent; instead of these, the function of respiration may be performed by the mantle and an organ (aquatic lung) consisting of several finger-shaped tubes on the rectum. The oral tube leads into a buccal mass, which contains a horseshoe-shaped jaw, a radula, the rows of which consist of five plates, and a subradular sense organ as in Loricata; the short esophagus has a wide glandular sack on either side; the digestive gland opens into the loop-shaped stomach; the coiled intestine opens into the mantle cavity behind the foot. The somewhat lobed kidney sacks lie beside the rectum, without connection with one another and with the pericardium; they open somewhat behind the anus. The heart is rudimentary, without auricles; it consists of a dorsal invagination of the pericardium, true blood vessels are absent; the blood sinus surrounding the rectum is connected with the mantle cavity by 1 pair of small cleft-shaped pores. The sexes are separate, special exit ducts and copulatory organs absent; at the time of maturity, the gonad fuses with the right kidney, through which the germ cells are released into the mantle cavity, from where they are expelled through the posterior opening by contraction of the animal.

The scaphopods live in the sea and burrow into the substratum with their foot, so that in most cases their posterior end alone projects out; their food consists of small organisms, mainly foraminiferans.

The posterior end of the shell corresponds to the embryonic shell only in very young animals; later it is repeatedly truncated and then frequently shows indentations or a more or less long slit or a series of perforations.

1. Family SIPHONODENTALIIDAE

Shell more or less small, smooth, colorless, often narrowed at the anterior end. Foot simply worm-shaped or with a disk-shaped, denticulate terminal disk, in the center of which a finger-shaped process occasionally is situated; the anterior end of the foot is introvertible; the central plate of the radula is a cutting-edge-less plate, which is about as long as broad; the intermediate plate forms a fairly strong, somewhat cuspidate, medially directed cutting edge; the marginal plate is broader than long, without cutting edge.

Cadulus Philippi, 1844

Shell circular or oval in cross section, more or less swollen in the center or nearer the narrowed anterior end.

Several species in various seas.

Section *Cadulus* s. s. Shell short, distinctly swollen in the center, spindle-shaped; both openings simple, the posterior one with an interior thickening of the margin. *C. (C.) ovulum* Philippi (Fig. 784). —Section *Gadila* Gray, 1847 (synonyms *Helonyx* Stimpson, 1865; *Gadus* (Rang, 1829) Conrad, 1866, non Linné, 1758; *Loxoporus* Jeffreys, 1869). Shell more or less slender, curved, dorsally concave, somewhat swollen in the center or nearer the anterior end; at the posterior margin without callous thickening and without incisions. *C. (G.) gadus* (Montagu). —Section *Dischides* Jeffreys, 1867. Shell fairly slender, posteriorly on either side with a deep incision. *C. (D.) politus* (S. Wood).—Section *Platyschides* Henderson, 1920. Shell posteriorly with 2 or 4 very shallow indentations. *C. (P.) grandis* Verrill.—Section *Polyschides* Pilsbry & Sharp, 1898. Shell posteriorly with a few, in most cases 4, distinct incisions, which divide the margin into lobes. *C. (P.) tetraschistus* (Watson) (Fig. 785).

Fig. 784. Shell of *Cadulus cyathoides* Jaëckel.
Length about 3 mm.

Fig. 785. Shell of *Cadulus (Polyschides) tetraschistus* (Watson) var. *quadridentata* (Dall). Length nearly 1 cm (after Pilsbry).

Siphonodentalium M. Sars, 1859

Synonyms *Siphonodontum* + *Tubidentalium* Locard, 1886.

Shell curved, nearly or completely circular in cross section, smooth, widest at the anterior opening; posterior end with or without incisions; foot with a disk-shaped thickening.

Few species, mostly in the deep sea.

Section *Siphonodentalium* s. s. Shell with posterior incisions; foot without finger-shaped process. *S. (S.) lobatum* (Sowerby).—Section *Pulsellum* Stoliczka, 1860 (synonym *Siphonentalis* G.O. Sars, 1878). Shell without posterior incisions; foot with a finger-shaped process. *S. (P.) lofotense* M. Sars.

Entalina Monterosato, 1872

Shell widest anteriorly, in the posterior part strongly ribbed, angulate. Foot as in *Pulsellum* with a finger-shaped process.

E. quinquangularis (Forbes). Few species in various seas.

781

2. Family DENTALIIDAE

Shell elongated, curved, smooth or ribbed, widest anteriorly. Foot not introvertible, on either side with a lobe near the end; central plate of the radula about twice as broad as long (Fig. 786).

Fig. 786. Half radular row of *Dentalium octangulatum* Donovan.

Dentalium Linné, 1758

Characters of the family.

Numerous species in all seas.

The genus is divided into a few groups, the anatomy of which is partly unknown.

Section *Compressidens* Pilsbry & Sharp, 1897. Shell small and thin, nearly smooth, dorsoventrally compressed, without posterior slit. *D. (C.) pressum* Sharp & Pilsbry.—Section *Fustiaria* Stoliczka, 1868 (synonym *Pseudantalis* Monterosato, 1884). Shell smooth or with regular annular furrows; oral opening circular; posterior opening round or oval, with a very long slit on the ventral side. *C. (F.) circinatum* Sowerby. —Section *Bathoxiphus* Pilsbry & Sharp, 1897. Shell nearly or completely smooth, laterally compressed, posteriorly with a broad ventral slit. *D. (B.) ensiculus* Jeffreys.—Section *Episiphon* Pilsbry & Sharp, 1897. Shell small and very slender, only slightly curved, thin, smooth, posteriorly sometimes with a small tube-shaped prolongation, without slit. *D. (E.) sowerbyi* Guilding.—Section *Rhabdus* Pilsbry & Sharp, 1897. Shell scarcely curved, very thin, smooth and shiny; both openings simple. *D. (R.) rectius* Carpenter.—Section *Laevidentalium* Cossmann, 1888. Shell of moderate to considerable size, smooth, round or somewhat oval; posterior end in most cases simple, occasionally with a short ventral indentation. *D. (L.) incertum* Deshayes.—Section *Graptacme* Pilsbry & Sharp, 1897. Shell with fine, dense, deeply incised, longitudinal furrows at the posterior end or throughout the length, small or medium-sized, cylindrical, posteriorly sometimes with incisions. *D. (G.) semistriatum* Turton.—Section *Dentalium* s. s. Shell ribbed or angulate; ribs often posteriorly strengthened; posterior end without slit. *D. (D.) elephantinum* Linné (Fig. 787). *Coccodentalium* Sacco, 1896, is distinguishable by the presence of ring-shaped ribs or lamellae. *D. (C.) radula* Schröter †.—Section *Tesseracme* Pilsbry, 1894. Posterior end quadrangular. *D. (T.) quadrapicale* Sowerby.—Section *Antalis* H. & A. Adams, 1854 (synonyms *Entalis* Gray, 1847, non Sowerby, 1839;

Fig. 787. *Dentalium elephantinum* Linné.
Length about 8 cm.

Entaliopsis Newton & Harris, 1894). Shell cylindrical or angulate, in the young state or permanently with longitudinal ribs or striae, posteriorly with an angular indentation or a small short tube. *D. (A.) entalis* Linné. —Section *Heteroschisma* Simroth, 1895. Shell longitudinally ribbed, posteriorly with a dorsal slit. *D. (H.) subterfissum* Jeffreys.—Section *Fissidentalium* P. Fischer, 1885 (synonym *Schizodentalium* Sowerby, 1894). Shell large and strong, with many longitudinal ribs, posteriorly simple or with a long slit or a series of perforations. *D. (F.) ergasticum* P. Fischer. A few species mainly in the deep sea.

782

Class BIVALVIA

The bivalves (Bivalvia, Acephala, Pelecypoda) are as a rule bilaterally symmetrical mollusks, the shell of which consists of 2 lateral halves, which are nearly always articulated with one another by an elastic ligament and in most cases enclose the entire animal. The form of the shell shows important variations; in most cases it is more or less compressed and transversely oval, sometimes roundish or higher than long; on the other hand, it is occasionally greatly elongated; the anterior and posterior ends are often distinctly dissimilar, sometimes the former is pointed, the latter not seldom truncated. The exterior side is smooth or more or less distinctly sculptured; besides the concentric growth lines, there may be stronger rings or radial ribs, seldom oblique ridges, sometimes also small scales or thorns or long spines. The two valves are as a rule identical mirror images or only slightly dissimilar, but are sometimes strikingly unequal, especially when one valve is attached to the substratum or when the byssus emerges asymmetrically from the shell.

The beaks (umbones), from which the growth of both valves begins, are seldom far apart from one another, resulting in a broad dorsal surface; in most cases they lie close together, separating the anterior and posterior halves; the former is then known as lunule, the latter as escutcheon; one or both of these may be distinctly delimited from the lateral parts.

The ligament joining the two valves is sometimes completely external, sometimes partly or completely internal. When the external ligament continues anteriorly between the umbones, it is said to be amphidetic; it is opisthodetic when it lies completely posterior to the umbones. The internal ligament may be continuous with the external one or may be separated from the latter; it is called the cartilage (resilium). In most cases it is short, situated below the umbones, often it is borne on the more or less large downwardly projecting processes of the dorsal

margins. Occasionally it contains a calcified part (lithodesma). In Adesmacea alone, which bore into solid structures by rasping movements of the rough shell valves, is the ligament completely reduced, so that the valves are joined together only by muscles.

In most cases the shell is able to enclose the entire animal without gaping. However, in byssate mussels a narrow cleft, seldom an asymmetric indentation, remains open for emergence of the byssus. In very few groups the shell remains wide open on the ventral side. If the mantle has large siphons, the posterior end gapes more or less broadly, very much as in *Pinna*, which sticks into the substratum with its pointed anterior end.

The dorsal margin of the two valves, which is as a rule expanded into a hinge plate, is in most cases supplied with tooth-shaped processes fitting into one another; in taxodonts, a more or less large number of such hinge teeth is present, which are usually transversely disposed, but occasionally the outer ones are arranged obliquely or parallel to the margin. In heterodonts, the number of teeth is reduced; the tooth below the umbo of the right valve is designated as the central tooth with the numeral 1; it fits into both, in most cases separated, halves of an arch-shaped, lamellar-tooth-structure of the left valve (2), which is joined by the two branches of lamella 3 of the right valve; the anterior half of lamella 4 of the left valve is in most cases absent. Some of these teeth may be reduced, such as the posterior branches, when the ligament is sunken. Besides these teeth, called cardinal teeth, there may be anterior and posterior lateral teeth parallel to the margin. Occasionally there are tooth-like structures of another kind. In some, in most cases small, shells, the hinge margin is transversely finely grooved, and, mainly in thin shells, it is smooth.

The inner surface of the shell more or less distinctly shows the scars of muscle attachments, of which those of the adductor muscles are the most conspicuous. In most cases, 2 of them are present, one anterior and one posterior; however, in various groups the anterior one has become diminished or completely reduced, whereas the posterior one has come closer to the center of the shell. As a rule these two muscles together close the shell, but in Adesmacea the anterior one has become displaced outward from the interior, and attaches to an outwardly reflected part; therefore its contraction results in gaping of the posterior part of the shell, antagonistic to contraction of the posterior muscle. The protractors and retractors of the foot attach on the dorsal part of the inner side. Running parallel to the lower shell margin is the so-called pallial line, at which the musculature of the mantle edge attaches; it is seldom interrupted and is indicated by a series of punctures. In bivalves with

large siphons, more or less elongated retractors are formed, at the attachment of which the pallial line has acquired an embayment, the pallial sinus (sinupalliates).

The broad mantle folds, interiorly covering the lateral parts of the shell and bringing about its growth, primitively have free margins throughout their length, which are sometimes provided with tentacles or eyes. Parts of the two margins are often fused together, mainly at the posterior end where an upper, excurrent opening is separated from a lower one, and on the ventral side where a more or less large opening for protrusion of the foot is separated from the posterior incurrent opening. The two posterior openings are often produced into more or less long tubes (siphons), which remain separate or fuse with one another. Occasionally they reach considerable length, so that they greatly surpass the body covered by the shell. Sometimes they have a membranous or calcareous covering; such a calcareous tube either remains separate from the shell or fuses with one valve or with both; in *Brechites* the shell has become rudimentary as a result of such fusion.

Because the body of bivalves is as a rule completely enclosed by the shell, a distinctly recognizable head has become reduced. Nevertheless in a few groups, small cup-shaped eyes are present in front of the anterior end of the inner gill lamina; these may be homologous with the cephalic eyes of snails. Besides these and the sense organs at the margin of the mantle and the siphons, statocysts are developed, which in some groups connect with the surface of the body by fine canals and contain small sand grains instead of statoconia or statoliths; there are also epithelial sense organs (osphradia, abdominal and adoral sense organs).

784   The body epithelium has glandular structures in various places, such as often in the posterior part of mantle cavity, at the mantle margin, or occasionally also on the inner side of the mantle lobes, as in *Lithophaga*, in which an acidic secretion is produced by a gland, used by the animals for boring into limestone rock. The skin glands are most strongly developed in the foot, the ventral surface of which is often pulled into a groove anteriorly, a deeper groove posteriorly, and produces a secretion (byssus) that hardens, by which the animals attach themselves to solid substrata.

The muscular foot, which is protrusible by swelling, assumes various forms; it seldom has a distinct sole as in snails, which is nevertheless not a creeping sole; the sole corresponds with the byssus cavity, which however is very often reduced. In most cases the foot is hatchet-, tongue-, or finger-shaped, more seldom pestle- or worm-shaped; occasionally it is very small or completely lost.

The mouth opening of bivalves lies at the base of a groove, formed by an anterior and a posterior lip, which continue on either side into more or less broad lobes (oral lobes or palps), the sides of which facing one another are as a rule beset with transverse ridges; in most cases they extend to the anterior end of the gills. In *Lima* species the two lip margins are fused together, forming a tube open at both ends. Sometimes the labial palps have become rudimentary. In nuculaceans they have a long process on either side, which is groove-shaped on one side.

The gills in nuculaceans and *Solenomya* have a form similar to those in zeugobranch snails, each consisting of an axis with 2 rows of short leaflets. As a rule these leaflets have become attenuated to form long filaments which are flexed outward, so that each filament has two limbs, the filaments altogether forming 2 lamellae on either side. The successive filaments are initially joined to one another only by brush-like cilia; moreover, there are often firm fusions, mainly at their ends, which then enclose a longitudinal exit vessel. Further fusions may take place not only between successive filaments but also between their two limbs, so that each gill has the appearance of 2 lamellae pierced by clefts. In other groups the rows of filaments become plicated, and the filaments in the interior and exterior edges may become very large (border filaments). Sometimes the exterior gill lamella is distinctly smaller than the interior; it is occasionally upwardly directed; it may form only a simple lamella or may disappear completely. When the free margins of the interior lamella fuse with the visceral sack and posterior to it with one another, those of the exterior lamella with the mantle, the mantle cavity is divided into a lower and an upper chamber; water entering the lower chamber passes into the upper chamber through the gill clefts and then to the exterior through the excurrent opening. In the Poromyacea, the gill lamellae become narrowed and finally assume the form of small sieves or rows of simple pores in the horizontal septum. Bivalves seldom have accessory gills, as small folds over the upper margin of exterior lamella, or as folds of the partition extending between the two gills behind the foot, or as folds on the interior side of the mantle.

The central nervous system of bivalves as a rule consists of 3 pairs of ganglia, the cerebropleurals, pedals, and viscerals. The first in most cases lie in front of or beside the esophagus; in *Lima* they are displaced far backward and are close to the viscerals, to which they are always connected by the visceral commissure. Below these lie sometimes small palpal ganglia, which mainly innervate the labial palps. The pedal ganglia are also joined with the cerebropleurals by connectives. The visceral ganglia supply the gills, the posterior adductor muscle, and the major part of the mantle margin, and, especially when sense organs are present, may be strongly developed on the latter.

785

Along with the head, the buccal mass is also reduced; the foregut is short, the digestive gland often opens asymmetrically into the sack-shaped stomach. A gelatinous structure (crystalline style) sticks into the initial part of the intestine or into a blind sack; the intestine is more or less coiled; its terminal part runs above the posterior adductor muscle, below which it opens in most cases with an anal papilla.

The heart of bivalves is similar to that of zeugobranch snails; the ventricle in most cases is traversed by the intestine, seldom lying above or below the latter and is very seldom symmetrically paired as are the auricles. The pedal sinus is separated from a sinus lying below the kidneys by a closable, sometimes paired opening (Keber's valve) which allows the swelling of the foot. A muscular thickening at the beginning of the posterior aorta, in siphonate bivalves separated from the ventricle by a valve, serves for swelling of the siphons.

The pericardium, which only in some *Arca* species consists of two completely separated, symmetrical halves, has glandular epithelium at various places. It is connected to the surface by 2 kidney ducts, which have the basic form of a two-limbed tube, with ciliated proximal limb and excretory distal limb; the glandular area may increase by folding or coiling. The primitively completely separated ducts frequently join together.

In most cases bivalves have separate sexes, although hermaphroditism has developed in various groups. The gonads lie paired symmetrically in the visceral sack, occasionally they extend into the mantle. Their exit ducts are nearly always short and simple, and as a rule open next to the kidney openings; copulatory organs are always absent. Occasionally there is brood care, wherein the eggs develop inside the mantle cavity, in most cases within the gill laminae.

The phylogenetically oldest bivalves are the taxodonts, originating from which on the one hand are the anisomyarians with straight hinge margin and open mantle, and on the other the long series of groups which nearly always have 2 adductor muscles, and in which often more or less long siphons are developed.

1. Order TAXODONTA

Hinge margin with more or less numerous, identical teeth; nearly always 2 adductor muscles present.

I. STIRPS NUCULACEA

Shell roundish to elongated; ligament sometimes completely external, sometimes with internal cartilage. Hinge margin more or less arched or

angulate, as a rule with several small teeth; mantle open or with posterior siphons; gills with 2 rows of short leaflets; foot with a broadened and scalloped terminal disk, suited for burrowing, without byssus; labial palps on either side with an in most cases long tentacle-like appendage.

1. Family NUCULIDAE

Shell nacreous, trigonal to oval; posterior part shortened, not gaping; hinge margin angulate, the ligamental cartilage is sunken between the two limbs, in most cases more or less interiorly projecting. Mantle completely open, without siphons; foot ventrally directed; gills directed anteriorly and ventrally; labial palp tentacles fairly large; statocysts open, with sand grains; kidneys fairly short, with two limbs, lobed, connected with one another; apertural part communicating with the pericardial funnel and with the gonoduct.

Nucula Lamarck, 1799

Synonym *Nuculana* Link, 1807.
Characters of the family.
The genus includes numerous species distributed in all seas.
Subgenus **Brevinucula** n. subgen. Shell small and relatively strong, short trigonal, exteriorly smooth and shiny; hinge margin strongly angulate, the small ligamental cartilage not or only slightly interiorly projecting and separating the anterior and posterior tooth rows; posteriorly the shell is flattened. *N. (B.) guineensis* Thiele (Fig. 788). Few species on the African coasts and on the east coast of North America, in the deep sea.
Subgenus **Lionucula** W. Quenstedt, 1930 (*Leionucula*) (synonym *Ennucula* Iredale, 1931). Shell small to medium-sized, in most cases fairly thin, roundish to oval, exteriorly smooth; the ligament projects obliquely forward below the hinge margin and above it lie the posterior teeth of the anterior row; the structure is uniform without radial trabeculae. *N. (L.) albensis* Orbigny †; many living species in various seas.

Fig. 788. Hinge margin of *Nucula (Brevinucula) guineensis* Thiele, enlarged.

Subgenus *Acila* H. & A. Adams, 1858. Surface of the more or less strong shell with anteriorly and posteriorly diverging or zig-zag-shaped ridges or rows of tubercles, which sometimes appear somewhat serrated at the margin; hinge margin and ligament as in *Lionucula*. Section *Truncacila* Grant & Gale, 1931. Shell posteriorly not beaked. *N.* (*T.*) *castrensis* Hinds.—Section *Acila* s. s. Shell posteriorly short beaked. *N.* (*A.*) *divaricata* Hinds.

Subgenus *Nucula* s. s. Exterior shell layer formed of peculiar radial prism-like trabeculae, which are interiorly overlain with nacre and at the margin project as small denticles; surface in most cases smooth, sometimes distinctly concentrically or characteristically sculptured; the ligament is similar in most cases to that in *Lionucula*, in small species only slightly or not inwardly projecting (*Pronucula* Hedley, 1902). *N.* (*N.*) *nucleus* (Linné) (Fig. 789). Several species in all seas.

787
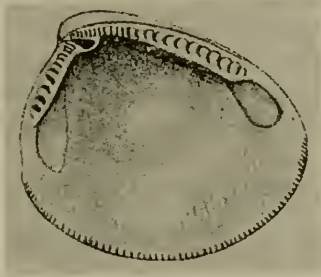
786   Fig. 789. Internal side of the left shell valve of *Nucula nucleus* (Linné), enlarged.

Deminucula Iredale, 1931, does not seem to be different.

Just as Verrill and Dall have assumed, I have no doubt that Link did not propose *Nuculana* as a new genus, but had only somewhat changed the Lamarkian name.

2. Family MALLETIIDAE

Shell roundish or longish, sometimes posteriorly truncated or pointed, not nacreous; hinge margin not distinctly angulate, with more or less numerous teeth; ligament completely external; an incurrent siphon and a pallial sinus absent in *Tyndaria*. Statocysts open, with sand gains.

Tyndaria Bellardi, 1875 (*Tindaria*)

Shell roundish or oval, smooth or concentrically sculptured; umbo elevated, in most cases situated a little in front of the center; pallial line

without indentation; mantle open ventrally, only an excurrent aperture differentiated with marginal papillae, without siphons. A few species, mainly in the deep sea.

Section *Pseudoglomus* Dall, 1896. Shell thin, smooth, roundish; ligament short, somewhat sunken; hinge margin with few teeth separated by a small space. *T. (P.) pompholyx* (Dall).—Section *Tyndaria* s. s. Shell oval, in most cases strong, concentrically sculptured; hinge margin with several teeth which are continuous or with short interruption. *T. (T.) arata* Bellardi †. *Protonucula* Cotton, 1930, is not substantially different from *Tyndaria*.

Neilonella Dall, 1881

Synonyms *Saturnia* Seguenza, 1877 (non Schrank, 1802); *Tindariopsis* Verrill & Bush, 1897.

Shell exteriorly concentrically sculptured, fairly small and strong, anteriorly rounded, posteriorly angular; pallial line with a small indentation; siphons short, ventrally open and openly joined with one another.

N. corpulenta (Dall). A few species, mainly in deep water.

Malletia Desmoulins, 1832

Synonyms *Solenella* Sowerby, 1832; *Ctenoconcha* Gray, 1840.

Shell longish, posteriorly rounded or truncate, medium-sized, in most cases fairly thin, smooth or striated; tooth row with short interruption; pallial line distinctly indented; animal with long, closed and completely united siphons.

A few species in cold or deep water.

Subgenus *Minormalletia* Dall, 1908. Shell longish, thin, smooth, fairly small, posteriorly rounded; umbo situated in front of the center; tooth row interrupted. *M. (M.) arciformis* Dall. Few species on the west coast of Central America.

Subgenus *Neilo* H. & A. Adams, 1854. Shell posteriorly truncated, with an edge descending posteriorly from umbo and an indistinct beak; surface sometimes distinctly concentrically sculptured, sometimes fairly smooth or with weak, somewhat oblique furrows; umbo situated somewhat in front of the center; hinge margin well-developed, with numerous small teeth. *M. (N.) australis* (Quoy & Gaimard).

788 Subgenus *Malletia* s. s. (synonym *Pseudomalletia* P. Fischer, 1887). Shell posteriorly rounded or blunt, without sculpture; hinge margin short, in front of the umbones with few small teeth. *M. (M.) chilensis* Desmoulins.

3. Family LEDIDAE

Shell not nacreous, transversely oval or more or less elongated, often posteriorly pointed; hinge margin more or less angulate, denticulate; ligament with a smaller or larger cartilage between the teeth; mantle with posterior siphons and a tentacle; labial palp tentacles long; statocysts closed, with a statolith; kidneys tube-shaped, anteriorly directed, interconnected and emptying together with the gonoducts.

A. Subfamily Sareptinae

Shell small, thin, transversely oval, smooth or concentrically striated; ligament with sunken or interior cartilage; hinge margin in most cases fairly short; animal without siphons.

Microyoldia Verrill & Bush, 1897

Shell small, transversely oval; umbo situated somewhat in front of the center; ligament with a relatively large cartilage on the upper side of the hinge margin somewhat posterior to the umbones; hinge margin fairly strong, arched.

M. regularis (Verrill), on the North American east coast.

Pristigloma Dall, 1900

Synonym *Glomus* Jeffreys, 1876, non Gistel, 1848.

Shell small, roundish; umbo at or near the center; ligament elongated and posteriorly extending from the umbones to below the beginning of the posterior tooth row; hinge margin fairly weak and in most cases short.

P. nitens (Jeffreys). Few species in the North Atlantic, near the West Indies and Japan.

Sarepta A. Adams, 1860

Synonym *Ovaleda* Iredale, 1925.

Shell transversely oval; umbo situated in the center, only slightly projecting; ligamental cartilage situated below umbones, short, between the two halves of the weak and short hinge margin, which bears a few small denticles.

S. speciosa A. Adams (Fig. 790). Few species in the Pacific Ocean.

The hinge of *S. tellinaeformis* Hedley, for which Iredale proposed a genus *Ovaleda*, is so similar to the typical species that it undoubtedly belongs to the same genus.
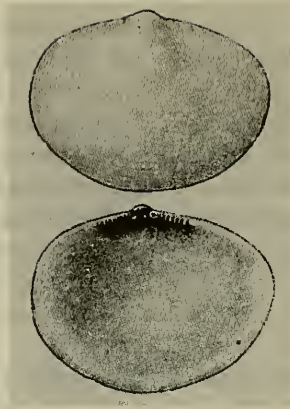
Fig. 790. External and internal side of a shell valve of *Sarepta speciosa* A. Adams, enlarged.

B. Subfamily Ledinae

Shell more or less elongated and posteriorly rostrate; ligamental cartilage not closely joined with the external ligament; animals as a rule with pallial indentation and with siphons.

789   *Ledella* Verrill & Bush, 1897

Synonyms *Junonia* Seguenza, 1877, non Hübner, 1816; *Comitileda* Iredale, 1924.

Shell small, transversely oval, in most cases smooth, with small, in most cases somewhat blunt rostrum which is set off below by a shallow indentation; area not sunken; cartilage in most cases small, but distinct; siphons separate.

A few species in various seas.

Magaleda Iredale, 1929, for *Leda inopinata* Edg. Smith, differs only by the presence of a few radial ridges.

Phaseolus Monterosato, 1875

Shell very small, transversely oval, smooth; hinge margin with few denticles parallel to the margin.

P.·ovatus Seguenza (Fig. 791), in the Mediterranean Sea and Atlantic Ocean.
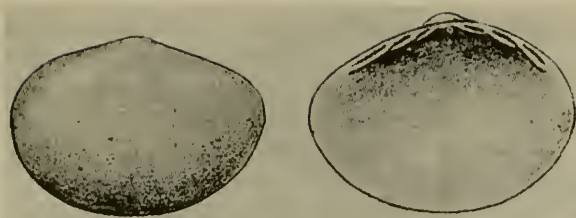
Fig. 791. External and internal side of a shell valve of *Phaseolus ovatus* Seguenza, enlarged (after Seguenza).

Leda Schumacher, 1817

Shell with a more or less long, sometimes pointed, sometimes truncated rostrum, as a rule concentrically sculptured; ligamental cartilage short, situated below the umbones, sometimes obliquely posteriorly directed; siphons partly or completely fused with one another.

Numerous species in all seas.

Section *Jupiteria* Bellardi, 1875 (synonyms *Ledina* Sacco, 1898, non Dall, 1898; *Saccella* Woodring, 1925; *Teretileda* Iredale, 1929). Shell in most cases fairly small, inflated, with short, pointed rostrum, which is concave above, exteriorally more or less distinctly concentrically sculptured; ligamental cartilage not elongated. *L. (J.) concava* Bronn †. Several living species.—*Scaeoleda* Iredale, 1929 (*L. crassa* Hinds) is scarcely different; the concentric sculpture is distinct and forms an edge below the rostrum.—Section *Spinula* Dall, 1908. Shell smooth, with a pointed rostrum, which is straight above and distinctly demarcated below; ligamental cartilage triangular; siphons long, completely fused, without pallial indentation; without labial palp tentacles. *L. (S.) calcar* Dall, on the east coast of South America.—Section *Lembulus* Risso, 1826. Shell with oblique sculpture and short rostrum, delimited below by an edge, straight above. *L. (L.) pella* (Linné), in the Mediterranean Sea and Atlantic Ocean. —Section *Leda* s. s. (synonym *Thestyleda* Iredale, 1929). Shell with a more or less long rostrum, truncated at the end, and with more or less distinct concentric sculpture; hinge teeth angular; ligamental cartilage straight or somewhat oblique. *L. (L.) pernula* (Müller) (Fig. 792). A few species in various seas. *Poroleda* Tate, 1893, is scarcely different; rostrum long.—Section *Propeleda* Iredale, 1924 (synonym *Lamellileda* Cotton, 1930). Shell with long rostrum, truncated at the end, with obliquely posteriorly ingressing ligamental cartilage, and thin hinge teeth which are almost parallel to the margin. *L. (P.) ensicula* Angas. Few species in the southern seas.

790
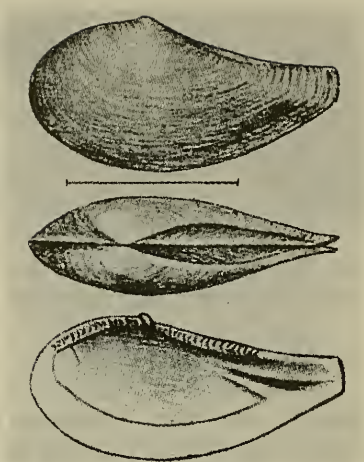
Fig. 792. Shell of *Leda pernula* (Müller) after Sars.

Silicula Jeffreys, 1879

Shell elongated, compressed, thin; umbo close to the rounded anterior end; posterior end blunt; ligament obliquely ingressing; hinge margin with few teeth which are parallel to the margin; pallial indentation broad, moderately deep.

S. *fragilis* Jeffreys. Few species in the northern Atlantic Ocean and near Patagonia. This group is probably related to *Propeleda*, and may only deserve the rank of a section.

Portlandia Mörch, 1857

Shell small to medium-sized, in most cases with smooth periostracum, completely closed; umbo small, close to the center; outline oval, in most cases with short rostrum which is demarcated by a shallow indentation; ligamental cartilage situated below the umbones; hinge margin not very long; siphons largely fused.

A few species, mainly in cold seas.

? Subgenus *Adranella* Verrill & Bush, 1898. Shell small, concentrically striated, oval, posteriorly somewhat broadened, not rostrate; hinge margin fairly strong. *P. (A.) casta* (Verrill & Bush).

Subgenus *Yoldiella* Verrill & Bush, 1897. Shell small; pallial indentation more or less shallow. *P. (Y.) lucida* Lovén.

Subgenus *Portlandia* s. s. Shell medium-sized; pallial indentation distinct. *P. (P.) arctica* (Gray).

<div align="center">*Yoldia* Möller, 1842</div>

Shell in most cases fairly large and flat, more or less elongated, smooth or weakly sculptured, gaping; umbo close to the center, only slightly projecting; external ligament weak; cartilage more or less projecting interiorly; pallial indentation deep. Mantle with long, fused siphons and a long posterior tentacle.

Several species in various seas.

Section *Katadesmia* Dall, 1908. Shell smooth and shiny, moderately elongated; umbo situated somewhat anterior to the center, posterior end with a short, rounded point; external ligament situated posterior to the umbones; cartilage trigonal. *Y. (K.) vincula* Dall, on the west coast of Central America.—Section *Megayoldia* Verrill & Bush, 1897. Shell posteriorly broadly truncated; external ligament anterior and posterior to the umbones; cartilage strong. *Y. (M.) thraciaeformis* (Storer). Few species in the northern seas.—Section *Orthoyoldia* Verrill & Bush, 1897. Shell elongated, anteriorly and posteriorly rounded. *Y. (O.) scapania* Dall. Few species near Central America and Brazil.—Section *Yoldia* s. s. Shell smooth, elongated and posteriorly narrowed, with rounded point. *Y. (Y.) hyperborea* (Lovén).—Section *Cnesterium* Dall, 1898. Shell similar to *Yoldia* s. s., but with oblique furrows which cut the growth lines at sharp angles. *Y. (C.) scissurata* Dall. *Scissula* Dall, 1909, in which the furrows are confined to the median part of the shell, was later synonymized with *Cnesterium* by Dall.—Section *Kalayoldia* Grant & Gale, 1931. Shell elongated; rostrum concave above; surface concentrically furrowed. *Y. (K.) cooperi* Gabb.—Section *Adrana* H. & A. Adams, 1858. Shell greatly elongated, without strong periostracum; anterior and posterior sides sometimes scarcely different; umbo scarcely projecting, exterior side with weak, somewhat oblique furrows. *Y. (A.) elongata* (Sowerby). Few Central American species.

791

<div align="center">## 4. Family SOLENOMYIDAE</div>

Shell elongated, anteriorly and posteriorly rounded, thin, composed of characteristic prisms, with very strong, smooth, elastic periostracum surpassing the calcareous shell at the margin which contains several weaker radial striae; the ligament, situated far posteriad, has a more or less sunken cartilage, borne on strengthened ridges of the calcareous shell; a ridge also lies anterior to the attachment of the posterior adductor muscle; the hinge margin is completely toothless.

The animals have an elongated burrowing foot, the anteriorly directed end of which bears a disk which is serrate at the margin, as in nuculids; gills bipectinate, laterally directed; labial palps with short tentacles; mantle margin fused, leaving an anterior opening for the foot and a narrow, posterior opening surrounded by tentacles; statocysts open as in nuculids; intestine with only a weak coil behind the stomach; ventricle elongated, traversed by the intestine; kidneys sack-shaped, with 2 short anterior limbs which contain the pericardial funnel and the renal apertures; the gonads open into the kidneys.

Solenomya Lamarck, 1818 (*Solemya*)

Synonym *Stephanopus* Scacchi, 1833.

Characters of the family.

A few species in various seas; they burrow in sand in most cases.

Section *Solenomya* s. s. Ligament extending more or less far forward, mainly internal. *S.* (*S.*) *australis* Lamarck.—Section *Petrasma* Dall, 1908. Ligament situated posterior to the umbones, internal. *S.* (*P.*) *borealis* Totten.—Section *Acharax* Dall, 1908. Ligament situated posterior to the umbones, completely external. *S.* (*A.*) *johnsoni* Dall.

It is not clear how *Solemyarina* Iredale, 1931 (*S. velesiana* Iredale), can be separated.

II. STIRPS ARCACEA

Shell not nacreous, nearly always equivalve; mantle completely open; gills with 2 rows of identical filaments, in most cases with two limbs, sometimes more or less broadened on the side facing the ascending limb, interconnected only by cilia; labial palps without appendages.

1. Family ARCIDAE

Shell nearly always ribbed, with elevated umbones, between which lies in most cases rhomboidal ligament on a more or less broad dorsal field; the hinge margin bears several denticles, the outermost of which are often placed obliquely, sometimes parallel to the margin; the periostracum often bears bristles or lamellae. The foot as rule has a simple byssus stem; the heart and pericardium are sometimes double, bilaterally symmetrical, sometimes simple, in the latter case the ventricle either lies below the intestine or is pierced by it; the sack-shaped kidneys are completely separated from each other; the pericardial branch is more or less short, sometimes ending close to the kidney aperture.

792

Arca Linné, 1758

Characters of the family.

Numerous species in all seas.

Subgenus *Navicula* Blainville, 1825 (synonyms ? *Daphne* + *Daphnoderma* Poli, 1795; ? *Cyphoxis* Rafinesque, 1819; *Byssoarca* Swainson, 1833; *Thyas* Gray, 1857 (non Koch, 1835); *Cibota* Mörch, 1853; *Arcoptera* Heilprin, 1886). Shell elongated, boat-shaped, with strong umbones which are separated from one another; a broad dorsal surface; a large rhomboidal ligament with a few oblique reinforcements; a long, straight hinge margin with numerous small teeth; somewhat gaping ventrally for the passage of the byssus. *A. (N.) noae* Linné (Fig. 793). This species was named as genotype of *Arca* by Gray and again later by Lamy, 1907, in his monograph of the genus; however, Schumacher, 1817, had already designated *A. antiquata* as the type of the genus. A few species in warm seas.
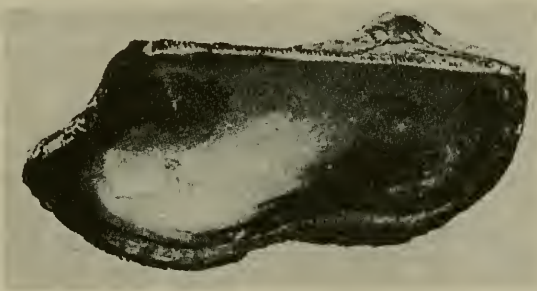
Fig. 793. Internal side of the left shell valve of *Arca (Navicula) noae* Linné. Length about 7 cm.

Subgenus *Litharca* Gray, 1842. Shell with high umbones situated behind the center, from which a very sharp edge descends to the posterior corner, whereas the anterior part gradually narrows and ends in a rounded point; surface with radial, scaly ribs; dorsal surface deeply grooved, with large ligament which is posteriorly rounded and anteriorly gradually pointed, containing a few oblique bands; somewhat gaping ventrally; hinge margin straight with numerous small denticles. *A. (L.) lithodomus* Sowerby, on the west coast of Colombia.

Subgenus *Scaphula* Benson, 1834. Shell small, broad and low, boat-shaped; umbo situated far forward, with sharp edge to the posterior corner, flattened below; surface weakly sculptured; dorsal surface fairly

broad; ligament rhomboidal, situated between the umbones, leaving the posterior part of the dorsal surface free; hinge margin weak, median denticles small or absent, outer ones oblique. *A. (S.) celox* Benson. Few species in Indian rivers.

Subgenus *Barbatia* Gray, 1842 (synonym *Savignyarca* Jousseaume, 1891). Shell laterally compressed, elongated oval or somewhat angular; umbo close to the center; dorsal surface and ligament narrow; surface in most cases with bristles or small scales; hinge margin with numerous teeth, the median of which are weaker or reduced, whereas the outer ones are larger and more or less oblique. *A. (B.) barbata* Linné. A few species in warmer seas.

Subgenus *Trisidos* (Bolten) Röding, 1789 (synonyms *Trisis* Oken, 1815; *Parallelepipedum* (Klein) Mörch, 1853). Shell strong and large, peculiarly twisted; umbo situated anterior to the center, moderately elevated; dorsal surface and ligament long and narrow; anterior end rounded; posterior end truncated; surface finely ribbed; ventral side not gaping; hinge margin long and straight; median teeth weak, outer ones oblique. The byssus consisting of a few threads. *A. (T.) tortuosa* Linné. 2 species in the Indo-Pacific region.

Subgenus *Acar* (Gray) H. & A. Adams, 1857 (synonym *Calloarca* (Gray) H. & A. Adams, 1857). Shell fairly small, in most cases elongated; umbo situated in front of the center; dorsal surface fairly narrow; ligament restricted to its posterior part; surface more or less finely ribbed; ventral side not gaping; median hinge teeth weak or rudimentary, outer ones oblique; byssus weak. Section *Acar* s. s. Shell with a posterior edge, medium-sized; ribs often tuberculate. *A. (A.) plicata* Chemnitz.—Section *Bentharca* Verrill, 1898. Shell small, lower anteriorly, without posterior edge. *A. (B.) asperula* Dall.—Section *Bathyarca* Kobelt, 1891 (synonym *Microcucullaea* Iredale, 1929). Shell in most cases small, scarcely ribbed, without edge, more or less high, ventrally rounded. *A. (B.) pectunculoides* Scacchi. A few deep-sea species.

Subgenus *Arcopsis* Koenen, 1885 (synonym *Fossularca* Cossmann, 1887). Shell fairly small, short; surface in most cases finely ribbed; umbo close to the center; the more or less short ligament lies between the umbones and leaves the anterior and posterior part of the dorsal surface free; it has densely placed transverse thickenings; the median hinge teeth are small, the outer ones oblique. *A. (A.) quadrilatera* Lamarck †. Cossmann, 1912, proposed a section *Galactella* for the Recent *A. lactea* Linné.

Subgenus *Noetia* (Gray) H. & A. Adams, 1857. Shell colorless, longish or fairly short, with a more or less distinct posterior edge; ligament with several transverse thickenings. Section **Paranoetia** n. sect. Shell longish, fairly thin, with smooth ribs, without distinct edge; umbo only slightly elevated, situated in front of the center; median hinge teeth small, outer ones oblique. *A. (P.) lateralis* Reeve.—Section *Noetiella* Thiele, 1931. Shell rounded trapeze-shaped; umbo situated slightly behind the center; posterior edge weak; surface finely latticed, with brown periostracum; area narrow; hinge margin fairly short, weakly curved; median denticles small, outer ones oblique; ventral margin smooth, not gaping. *A. (N.) pectunculiformis* Dunker, near Java.—Section *Noetia* s. s. Shell strong, triangular, strongly ribbed; umbo greatly elevated and posteriorly directed, with distinct posterior edge; hinge margin broad; anterior teeth angular, posterior ones oblique; ventral margin strongly denticulate; periostracum scaly. *A. (N.) reversa* Gray. Few species near Central America.

Subgenus *Arca* s. s. Shell strong, strongly ribbed, with large umbones close to the center and a posterior edge; dorsal surface fairly broad, with strong ligament, which in most cases contains a few oblique bands; hinge margin straight, with numerous teeth which differ only slightly in size; ventral margin strongly denticulate, not gaping. Foot with shallow groove, without byssus. Several species in warm seas. Section *Arca* s. s. (synonyms *Anadara* Gray, 1847; *Anomalocardia* (Klein) Mörch, 1853, non Schumacher, 1817). The two valves not distinctly different. *A. (A.) antiquata* Linné.—Section *Scapharca* Gray, 1847. Right valve somewhat smaller than the left. *A. (S.) inaequivalvis* Bruguière.—Section *Cunearca* Dall, 1898. Size and sculpture of the two valves differ. *A. (C.) incongrua* Say (? = *brasiliana* Lamarck). *Imparilarca* Iredale, 1929 (*hubbardi* Iredale), is probably not separable.—Section *Senilia* Gray, 1842. Shell very large and strong; periostracum smooth. *A. (S.) senilis* Lamarck.

Subgenus *Argina* Gray, 1842. Shell roundly oval, ribbed; umbo situated far forward; area and ligament very narrow; hinge margin with many denticles posterior to the umbones and very few anterior to it; margin folded, not gaping. *A. (A.) campechiensis* Gmelin = *pexata* Say. Few species near Central America. *Lunarca* Gray, 1842, is probably identical.

Subgenus *Cucullaea* Lamarck, 1801. Shell strongly bulging, trapeze-shaped, finely and densely ribbed, with a posterior edge; umbo situated in the center; area and ligament moderately broad; hinge margin straight, anteriorly and posteriorly demarcated by distinct corners; hinge teeth in the center short, anteriorly and posteriorly longer, very oblique, nearly parallel to the margin; anterior margin of the posterior adductor muscle scar elevated lamella-like; ventral shell margin finely denticulate, not gaping. *A. (C.) concamerata* Martini, in the Indo-Pacific region.

794

2. Family GLYCYMERIDAE

Shell strong, of variable size, roundish; umbo in most cases situated in the center, more or less projecting; ligament external, with oblique thickenings; hinge margin curved; median teeth sometimes reduced, outer ones oblique; surface ribbed or smooth; adductor muscle scars only slightly differing, toward the center more or less elevated; the pallial line distinctly delineated from the posterior scar; shell margin denticulate, not gaping ventrally. Mantle and gills similar to those in *Arca*; foot large, deeply cleft ventrally, without byssus; pericardium and heart unpaired, the ventricle traversed by the intestine; kidneys separated from one another, situated outside the foot muscles.

Glycymeris Da Costa, 1778

Characters of the family.
Several species, mainly in warm seas, at moderate depths.
Section *Glycymeris* s. s. (synonyms *Axinaea* + *Axinaeoderma* Poli, 1795; *Tuceta* (Bolten) Röding, 1798; *Veletuceta* Iredale, 1931). Shell smooth or finely radially striated. *G. (G.) glycymeris* (Linné). —Section *Pectunculus*[1] Lamarck, 1799. Shell with more or less broad and high ribs. *G. (P.) pectunculus* (Linné). *Tucetona flabellata* (Tenison-Woods)] and *Grandaxinaea* Iredale, 1931 (*magnificens* Iredale) are scarcely different.—Section *Melaxinaea* Iredale, 1930. Shell with narrow ribs and concentric threads. *G. (M.) labyrintha* (Iredale).

3. Family LIMOPSIDAE

Shell in most cases small, often with bristly surface, white or more seldom brown colored, usually roundish or oval and somewhat inclined; ligament more or less sunken, short; the hinge margin sometimes bearing several teeth, sometimes only few or none at all; inner shell margin smooth or denticulate. the anterior adductor muscle is smaller and situated higher than the posterior one and may disappear completely; the foot is fairly small, often with a posterior tip and has a fairly weak byssus; gills fairly broad, with separate filaments, occasionally without ascending limb. In the deep sea and colder seas.

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[1] Addition from Part 3 (1934) : 1010.
Because the name *Pectunculus* is preoccupied by Da Costa, 1778, (see p. 1348), this should be replaced by *Tucetona* Iredale.

Limopsis Sasso, 1827

Synonyms *Trigonocaelia* Nyst & Galeotti, 1835; *Pectunculina* Orbigny, 1844; *Felicia* Mabille & Rochebrune, 1889; *Cosmetopsis* Rovereto, 1898; *Loringella* + *Phrynelima* + *Aspalima* Iredale, 1929; *Versipella* + ? *Senectidens* + ? *Glycilima* Iredale, 1931.

Shell small to medium-sized, roundish, in most cases more or less inclined and colorless, with bristle-bearing periostracum; external surface with weak radial or concentric sculpture; umbo only slightly projecting, situated in the center of the hinge margin; ligament with triangular cartilage often somewhat ingressing into the hinge margin, which is arched or angular; the tooth row interrupted in the center; posterior adductor muscle scar larger than the anterior one; ventral shell margin smooth or denticulate.

L. aurita (Brocchi). Several species, mainly in the deep sea and in cold seas.

A few groups may be accepted as sections, such as *Loringella*, for the thick-shelled *L. loringi* Angas with distinct concentric sculpture; *Aspalima* (*erecta* Hedley & Petterd) is similar; it seems doubtful whether *Glycilima* (*paradoxa* Iredale) can be accepted.

Section *Empleconia* Dall, 1908. Upper part of the anterior margin deeply indented, forming an exterior excavation. *L. (E.) vaginata* Dall, in the northern Pacific Ocean.

Pleurodon S. Wood, 1840

Synonyms *Nuculina* Orbigny, 1845; *Nucinella* S. Wood, 1850; *Huxleyia* A. Adams, 1860; *Cyrilla* A. Adams, 1862; *Diabolica* Jousseaume, 1897; *Cyrillista* + *Cyrillona* Iredale, 1929.

Shell small, inclined oval, smooth with concentric furrows; ligamental cartilage very small; hinge margin fairly broad and short, with a few, in most cases strong teeth; on the posterior side with an elongated lateral tooth; shell margin smooth.

P. ovalis S. Wood †. Few living species (Fig. 794) in various seas.

Cratis Hedley, 1915

Shell small, somewhat inclined oval, with demarcated, low hat-shaped embryonic shell, externally with finely net-like sculpture; ligamental cartilage situated in the center; hinge margin strong, with few (5) distinct teeth; with a few wart-shaped teeth on the lower part of anterior margin and on the posterior margin.

Fig. 794. Internal and external sides of a shell valve of *Pleurodon pretiosus* (Gould), enlarged. — a, hinge margin, more strongly enlarged.

C. progressa Hedley, near east Australia.

Denticosa Iredale, 1930, proposed for "*Philobrya*" *cuboides* Verco, seems to be scarcely different.

Lissarca Edg. Smith, 1879

Synonym *Austrosarepta* Hedley, 1899.

796   Shell small, inclined oval or rounded rhomboid, externally concentrically striated, with small ligamental cartilage below the umbones and weak hinge margin, which bears few small anterior and posterior denticles; with a few small tubercles on the posterior margin and in most cases also on the anterior margin.

L. rubrofusca Edg. Smith. About a dozen species in southern seas.

Limopsilla Thiele, 1923

Shell small, thick-walled, roundly triangular, with demarcated embryonic shell, below it with a very small ligamental cartilage; hinge margin transversely grooved, with a few denticles in front of and behind the center; ventral margin smooth.

L. pumilio (Edg. Smith), near South Africa.

Lissarcula Thiele, 1923

Shell exteriorly with concentric and radial threads; embryonic shell hat-shaped, situated in front of the center; anterior margin arched, posterior margin only slightly arched; hinge margin transversely grooved, anteriorly and posteriorly with 2 denticles; ventral margin with a few small tubercles.

L. australis Thiele, near Australia.

Hochstetterina nom. nov.

Synonym *Hochstetteria* Vélain, 1877, part.
Shell roundish, inclined; embryonic shell more or less demarcated, close to the center of the hinge margin, which has only transverse grooves but no teeth; ligament below the umbones, sometimes asymmetrical; surface more or less distinctly concentrically striated; shell margin denticulate to a greater or lesser extent.

H. crenella (Vélain). Few species in southern seas.

Because Kobelt, 1884, designated *Hochstetteria aviculoides* Vélain as the typical species, which Bernard has included in *Philobrya*, the generic name must be changed.

Adacnarca Pelseneer, 1903

Shell roundish, somewhat inclined, thin, weakly radially striated, shiny; embryonic shell not demarcated, close to the center of the transversely grooved hinge margin; shell margin finely denticulate; anterior adductor muscle very small; inner gill lamina without ascending lamella.

A. nitens Pelseneer, in the Antarctic Sea and one Australian species.

Philobrya Carpenter, 1872

Shell with nearly or completely anterior, often distinctly demarcated, embryonic shell, from the center of which the ligament extends obliquely more or less far backward, separating a short anterior part from a longer posterior part of the in most cases transversely grooved hinge margin; the shell is sometimes distinctly, sometimes only indistinctly, ribbed with rows of bristles or unribbed; sometimes ridge-like marginal teeth are present, especially below the posterior end of hinge margin; an anterior adductor muscle absent.

Several species, mainly in southern seas.

Section *Hochstetteria* Vélain, 1877. Anterior shell margin convex; ligament short. *P.* (*H.*) *aviculoides* (Vélain). —Section *Philobrya* s. s. (synonyms) *Byrophila* Carpenter, 1864 (non Treitschke, 1825); *Briophila* P. Fischer, 1886; *Philippiella* Pfeffer, 1886; *Stempelleria* Clasing, 1918; *Stempellia* N. Odhner, 1922). Anterior margin straight or concave; shell not distinctly ribbed, often with radial rows of bristles; ligament distinctly elongated. *P.* (*P.*) *setosa* (Carpenter). The Antarctic species, for which Hedley recognized the group *Philippiella*, are so similar to the above mentioned Californian species, that they can scarcely be separated.

—Section *Cosa* Finlay, 1927. Shell with distinct radial ribs. *P. (C.) costata* Bernard.—Section *Notomytilus* Hedley, 1916. Shell brown, with nearly or completely terminal, not demarcated umbones; posterior margin with a few small tubercles. *P. (N.) rubra* (Hedley). *Micromytilus* Cotton, 1931 [*P. crenatulifera* (Tate)] (Fig. 795) is scarcely different.—Section *Verticipronus* Hedley, 1904. Shell similar to *Notomytilus*; embryonic shell flattened, with radial sculpture, brown; anterior part of the hinge margin elevated tooth-like, below the posterior end of which there is a bifurcated ridge. *P. (V.) mytilus* (Hedley).—Section *Neocardia* Sowerby, 1892. Shell with concentric and radial sculpture or smooth, colorless, with a double ridge below the posterior part of the hinge margin. *P. (N.) angulata* (Sowerby). A couple of South African species.

Fig. 795. Interior side of a shell valve of *Philobrya (Micromytilus) crenatulifera* (Tate), enlarged.

2. Order ANISOMYARIA

Anterior adductor muscle reduced or completely lost. True hinge teeth scarcely present, but sometimes small tubercles or special tooth formations are developed; embryonic shell with grooved hinge margin. Mantle open, without siphons; gill lamellae smooth with identical filaments or folded with nonidentical filaments.

I. STIRPS MYTILACEA

Shell in most cases with umbones near the anterior end of terminal; equivalve, often elongated or anteriorly narrowed to pointed, sometimes oval; interior side in most cases nacre-like shiny, occasionally external or internal not very conspicuous prismatic layers are developed; ligament nearly always external, situated posterior to the umbones; hinge margin toothless, but sometimes with a few small tubercles in front of or behind the ligament, primitively corresponding to the ends of external radial ribs. The mantle forms a closed, sometimes elongated excurrent siphon;

a retractor is as a rule developed in the posterior part of the mantle; the gills consist of separate filaments, similar to those in arcids; the anterior adductor muscle is sometimes well developed, but in most cases small, seldom completely lost; foot finger-shaped, with a byssus in most cases consisting of several threads; statocysts open, with small sand grains; the kidneys lie outside the foot retractors beside the pericardium, they are sack-shaped with posterior opening; in a few groups the gonads extend into the mantle.

1. Family MYTILIDAE

Characters of the stirps.
The animals live in the sea, with the exception of a few which have invaded freshwater.

798

Idasola Iredale, 1915

Synonym *Idas* Jeffreys, 1876, non Mulsant & Verreaux, 1876.
Shell small, anteriorly rounded, posteriorly obliquely truncated, longish; umbo close to the anterior end; hinge margin transversely grooved; ligament external; surface finely latticed; inner margin smooth.
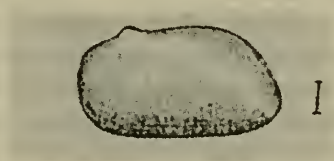
Fig. 796. *Idasola argentea* (Jeffreys).

I. argentea (Jeffreys) (Fig. 796), in the Bay of Biscay (deep sea).

Dacrydium Torell, 1859

Shell small, colorless, smooth, thin, obliquely oval; umbo small, close to the anterior end; hinge margin transversely grooved; ligament obliquely ingressing below the umbones; anterior adductor muscle attached close to the margin. The gonad lies in the body.
D. vitreum Holböll. Few species in most cases in cold seas and in the deep sea. They make nests with their byssus.

Crenella T. Brown, 1827

Synonyms *Stalagmium* Conrad, 1833; *Hippagus* + *Myoparo* Lea, 1833; *Nuculocardia* Orbigny, 1845; ? *Crenellodon* Edwards, 1891.

Shell small, oval or rhomboidal, in most cases with radial sculpture and with small tubercles at the inner margin; ligament short. Excurrent siphon not elongated; foot thickened at the end, with a byssus thread.

Few species in various seas.

Subgenus *Rhomboidella* Monterosato, 1884. Shell obliquely rhomboidal, similar to *Dacrydium*, but differing in sculpture and the tuberculate margin. *C. (R.) rhombea* (Berkeley).

Subgenus *Crenella* s. s. Shell oval, with distinct sculpture and tuberculate margin. *C. (C.) decussata* (Montagu).

Subgenus *Solamen* Iredale, 1924. Shell oval, with weak sculpture and smooth margin. *C. (S.) rex* Iredale. It seems doubtful whether this group is related to *Arcoperna* (*filosa* Conrad) from the Eocene; Dall placed the latter near *Botula* as a section of *Modiolus*. *Exosiperna* Iredale, 1929, for *Scapha* Verco, is smaller and stronger.

Modiolus Lamarck, 1799

Synonym *Modiola* Lamarck, 1801.

Shell with blunt umbones which are more or less close to the anterior end but not terminal; surface smooth or bristly; ligament fairly long, external; hinge margin toothless. The anterior adductor muscle distinct, fairly close to the anterior margin; the gonads not or only slightly extending into the mantle.

Several species in various seas.

Subgenus *Adipicola* Dautzenberg, 1927 (synonym *Myrina* H. & A. Adams, 1857, non Fabricius, 1808). Shell long, anteriorly distinctly elongated and rounded, somewhat lower than the posterior part; surface smooth; ligament sunken. *M. (A.) pelagicus* (Forbes).

Subgenus *Modiolus* s. s. Umbo close to the anterior end, which forms a short, rounded corner; posterior end significantly elevated, inflated in the line extending posteriorly from the umbo. Section *Modiolus* s. s. (synonym *Eumodiolus* Jhering, 1900). Shell hairy or not hairy. *M. (M.) modiolus* (Linné).—*Limnoperna* Rochebrune, 1882, proposed for small freshwaters of east Asia, is scarcely different. *M. (L.) siamensis* (Morelet). For the small Australian "*Modiolaria*" *subtorta* Dunker, Iredale, 1924, proposed a genus *Fluviolanatus*, the systematic position of which is uncertain; the shell is fairly long and low, without distinct sculpture; umbo close to the anterior end.

Subgenus *Amygdalum* Megerle von Mühlfeld, 1811. Shell thin and smooth, pale, often with colored pattern; the animals build nests with their byssus. Section *Modiolula* Sacco, 1898 (synonym *Nudiola* Monterosato, 1917). Shell moderately long, inflated, in most cases hairy. *M. (M.) phaseolinus* (Philippi).—Section *Amygdalum* s. s. (synonym *Modiella* Monterosato, 1884). Shell elongated, not inflated. *M. (A.) arborescens* (Chemnitz).

Volsella was proposed by Scopoli, 1777, for bivalves with denticulate hinge margin, and his inclusion of *Mytilus modiolus* Linné indicates that he misidentified this species, which has toothless hinge margin; because the other included species are likewise not recognizable, included this genus name may be rejected because of insufficient substantiation.

Brachyodontes Swainson, 1840 (*Brachidontes*)

Shell in most cases with radial sculpture, anteriorly somewhat rounded or pointed; umbo nearly or completely terminal; ligament fairly short; the dorsal line sometimes forming a rounded corner posterior to the hinge margin; a few small tubercles are developed anterior and posterior to the ligament.

Several species in various seas.

Subgenus *Brachyodontes* s. s. Shell anteriorly rounded or blunt; umbo nearly terminal; surface radially ribbed; an anterior adductor muscle present. Section *Brachyodontes* s. s. Ventral margin anteriorly curved. *B. (B.) sulcatus* (Lamarck). A few small species live in freshwater in South and East Asia.—Section *Hormomya* Mörch, 1853 (synonyms *Stavelia* Gray, 1858; *Trichomya* Jhering, 1900). Ventral margin elongated. *B. (H.) exustus* (Linné).

Subgenus *Ischadium* Jukes-Browne, 1905. Umbo terminal, pointed; ventral margin somewhat concave; surface radially ribbed; an anterior adductor muscle absent; posterior foot retractor broadly fused with the adductor muscle. *B. (I.) hamatus* (Say).

Subgenus *Septifer* Recluz, 1848. Shell with pointed terminal umbo and a plate on either side in the interior of the anterior corner, at which the anterior adductor muscle attaches; the posterior adductor muscle posteriorly surrounds the attachment of the posterior foot retractors; the gonad branches in the mantle. *B. (S.) bilocularis* (Linné) (Fig. 797).

Subgenus *Mytilaster* Monterosato, 1883. Umbo nearly terminal; surface with only growth lines or zig-zag-shaped wrinkles, with a few small tubercles posterior to the ligament and few anterior ones. *B. (M.) lineatus* (Gmelin).
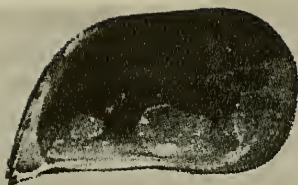
Fig. 797. Interior side of the right shell valve of *Brachyodontes (Septifer) bilocularis* (Linné).
Length about 46 mm.

Musculus (Bolten) Röding, 1798

Synonyms *Modiolaria* Beck, 1838; *Lanistes* Swainson, 1840; *Modiolarca* Gray, 1843; *Lanistina* Gray, 1847.

800   Shell more or less long, in most cases transversely oval; umbo close to the anterior end; outer side anteriorly and posteriorly radially ribbed, smooth in-between; inner margins with small tubercles; ligament moderately long; attachment of the anterior adductor muscle close to the ventral margin. The excurrent siphon is more or less elongated, and as a rule, closed tube-shaped; the lower one is ventrally open; the gonads penetrating the mantle.

Several species in most seas; they are absent in the Antarctic.

Subgenus *Gregariella* Monterosato, 1884. Shell elongated, in most cases hairy on the posterior part. Section *Gregariella* s. s. Shell anteriorly distinctly lower than posteriorly. *M. (G.) petagnae* (Scacchi).—Section *Botulina* Dall, 1889 (synonym *Trichomusculus* Iredale, 1924). Anteriorly not lower than posteriorly; posterior edge in most cases beset with bristles. *M. (B.) opifex* (Say).

Subgenus *Musculus* s. s. Shell transversely oval, not hairy. *M. (M.) discors* (Linné).

Lithophaga (Bolten) Röding, 1798

Synonyms *Lithophagus* Megerle von Mühlfeld, 1811; *Lithodomus* Cuvier, 1817.

Shell more or less elongated, cylindrical; umbo close to the rounded anterior end or terminal; surface smooth or wrinkled; hinge margin elongated, smooth; ligament more or less long, sunken; scar of the anterior adductor muscle close to the ventral margin. Mantle with shorter or longer siphons; an acid-secreting gland lies in its anterior part, by which the animals bore into limestone.

A few species in various seas.

Subgenus *Lioberus* Dall, 1898. Shell inflated, smooth, moderately elongated, fairly thin, anteriorly very shortly rounded, somewhat lower than posteriorly; beak anteriorly inclined; mantle with long incurrent and excurrent siphons.

L. (L.) castanea (Say). *Leiosolenus* Carpenter, 1856 (*spatiosus* Carpenter) may represent a related group.

Subgenus *Botula* Mörch, 1853. Shell similar to *Lioberus*, but with anteriorly located beaks. *L. (B.) fusca* (Gmelin).

Subgenus *Adula* H. & A. Adams, 1857. Shell long and low, smooth or transversely grooved; umbo not situated close to the anterior end, with a posteriorly extending edge. *L. (A.) soleniformis* (Orbigny). *Zelithophaga* Finlay, 1927 [*truncata* (Gray)] is scarcely different.
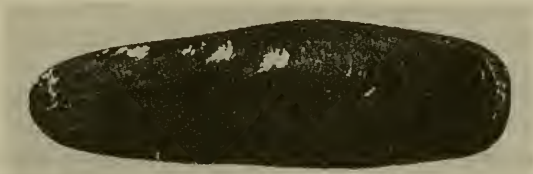
Fig. 798. Shell of *Lithophaga lithophaga* (Linné).
Length about 8 cm.

Subgenus *Lithophaga* s. s. Shell long, cylindrical; umbo close to the anterior end. Section *Lithophaga* s. s. Without calcareous deposition. *L. (L.) lithophaga* (Linné) (Fig. 798).—Section *Myoforceps* P. Fischer, 1886. With a smooth calcareous deposit posteriorly ending in a projecting point. *L. (M.) caudigera* (Lamarck). *Labis* Dall, 1916, is scarcely different.—Section *Diberus* Dall, 1898. Calcareous deposition with peculiar feather-shaped sculpture. *L. (D.) plumula* (Hanley).

801   *Mytilus* Linné 1758

Shell anteriorly pointed, with nearly or completely terminal umbones, anteriorly in most cases with few small denticles; anterior adductor muscles small, sometimes absent.

Several species in various seas.

Subgenus *Mytilus* s. s. (synonym *Eumytilus* Jhering, 1900). Shell smooth, anteriorly below the umbo with a small ribbed expansion, the margin of which bears 2–5 small denticles; anterior adductor muscle present. *M. (M.) edulis* Linné.

Subgenus *Chloromya* Mörch, 1853. Shell smooth; umbo terminal, in the interior of the anterior end with an inflection of the margin, which forms a small plate similar to a septum; without anterior adductor muscle. Section *Chloromya* s. s. With 1 or 2 hinge teeth at the anterior end; marine. *M.* (*C.*) *perna* Linné.—Section **Sinomytilus** n. Shell thin, fairly small; umbo very pointed, interiorly toothless; ventral side concave, delimited by a sharp edge. *M.* (*S.*) *crosseanus* (Morlet). A couple of species in freshwater from China and Indochina, which have been described as *Dreissena*.

Subgenus *Aulacomya* Mörch, 1853. Shell large, radially ribbed; umbo terminal, projecting over the inner margin; with a ridge on one side corresponding to a furrow of the other valve; anterior adductor muscle in most cases absent. *M.* (*A.*) *magellanicus* Chemnitz.

II. STIRPS PTERIACEA

Shell laterally compressed, variably formed; ostracum formed completely of prisms, in most cases thin at the margin; hypostracum weak and considerably smaller than the ostracum, nacreous; hinge margin straight, toothless; mantle open, joined with the gills by ciliary junctions; anterior adductor muscle small or reduced; foot in most cases with byssus; the mantle cavity posteriorly extending far upward.

1. Family VULSELLIDAE

Ligament sometimes with several cartilages, sometimes with only one; gill lamellae as a rule smooth, filaments identical.

Crenatula Lamarck, 1804

Hinge margin fairly long; ligament with several small cartilages posterior to the somewhat elevated umbones; anterior margin curved, posterior margin obliquely truncated; mantle margin with papillae; foot without byssus.

C. viridis Lamarck. Few species in the Indian Ocean and Red Sea, in sponges.

Pedalion (Solander) Huddesford, 1770

Synonyms *Isognomon* (Klein) Solander, 1786; *Melina* Retzius, 1788; *Perna* Bruguière, 1792; *Vulsella* Mus. Calonn., 1797 *Isogonum* (Bolten) Röding, 1798; *Sutura* Megerle von Mühlfeld, 1811; *Isognomum* (Klein) Mörch, 1853.

Shell nearly equivalve, externally often scaly; umbo at the anterior end of the sometimes short, sometimes posteriorly elongated hinge line; ligament with several strong cartilages situated in pits; anterior margin retracted and somewhat gaping. Foot tongue-shaped, with byssus; gill lamellae smooth.

A few species in warm seas.

802   Section *Pedalion* s. s. Hinge margin not strikingly elongated. *P. (P.) ephippium* (Linné).—Section *Isognomum* Mörch, 1853. Shell high and short, with elongated hinge margin. *P. (I.) isognomum* (Linné).

Foramelina Hedley, 1914

Shell strong; hinge margin fairly short, with several cartilages; right valve with a hole below the umbo, from which a suture extends to the anterior end of the hinge margin; the byssus emerges through the hole, it consists of a bundle of threads; the byssus muscle is stronger than the adductor muscle and attaches to the left valve above the latter.

F. exempla Hedley, near Australia.

Vulsella (Bolten) Röding, 1798

Synonym *Reniella* Swainson, 1840.

Shell tall and short, often gaping; hinge margin short, with a strong cartilage in an oblique, triangular pit, inclined posteriorly; posterior end often somewhat concave. Foot without byssus and without retractors; heart chambers paired; gill lamellae smooth or somewhat pleated.

A few species living in sponges, in the Indo-Australian region.

Section *Vulsella* s. s. (synonym *Abisa* Gregorio, 1884). Shell medium-sized; gills folded (?). *V. (V.) lingulata* Lamarck.—Section *Madrela* Gregorio, 1884. Shell fairly small; gills smooth (?). *V. (M.) spongiarum* Lamarck.

Malleus Lamarck, 1799

Synonyms *Pinctada* (Bolten) Röding, 1798 part.; *Tudes* Oken, 1815; *Himantopoda* Schumacher, 1817.

Shell tall and short, often with folded margins and more or less elongated hinge margin; ligament similar to that in *Vulsella* with a strong cartilage in an oblique, triangular pit; umbo only slightly projecting. The foot consisting of 2 parts, the larger anterior one is long finger-shaped, with ventral glandular groove, the smaller posterior one tongue-shaped with byssus and groove; the posterior byssus muscle attaches to the shell below the adductor muscle; gill lamellae smooth; heart asymmetrical.

A few species in warm seas.

Section *Parimalleus* Iredale, 1931. Shell fairly small, with wrinkled nucleus, without prolongation of the hinge margin. *M. (P.) cursator* Iredale. —Section *Malvufundus* Gregorio, 1885. Hinge margin without anterior prolongation. *M. (M.) anatinus* Lamarck.—? Section *Fundella* Gregorio, 1884 (non Zeller, 1848). Without anterior prolongation of the hinge margin internally with a median constriction. *M. (F.) lioyi* Gregorio. —Section *Malleus* s. s. Hinge margin prolonged anteriorly and posteriorly. *M. (M.) vulgaris* Lamarck (Fig. 799).
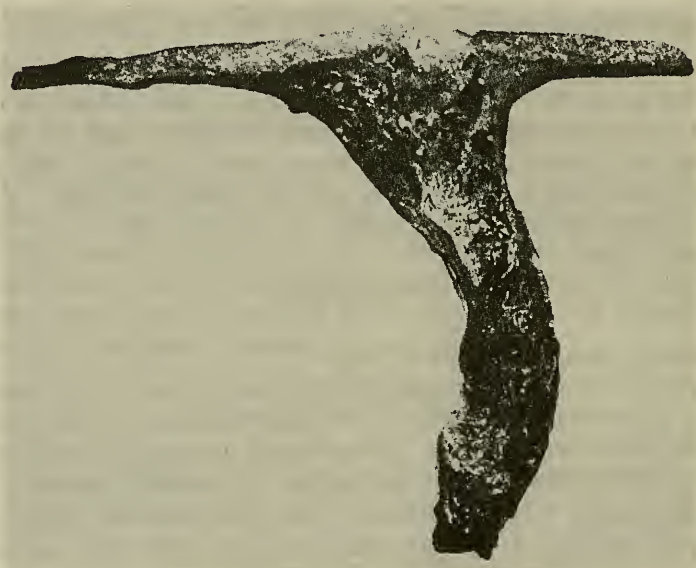
Fig. 799. Shell of *Malleus vulgaris* Lamarck.
Length about 18.5 cm.

803

2. Family PTERIIDAE

Hinge margin straight, posteriorly angularly demarcated or elongated; ligament somewhat sunken, fairly long, posterior to the only slightly projecting, anteriorly inclined umbones; hinge margin with 1 or 2 inconspicuous tooth-like thickenings below the umbones; anterior corner demarcated ear-like by the byssus notch; surface often scaly; left valve somewhat more bulging than the right. The single adductor muscle attaches in the center; the anterior foot retractors attaching below the umbones; gill lamellae folded, with large inner border filaments, they are

attached to the mantle by ciliary tufts; foot with byssus; kidneys triangular, sack-shaped, situated below the pericardium; ciliated funnel short, connected with one another in the upper and posterior corners.

Pteria Scopoli, 1777

Synonyms *Avicula* (Klein) Bruguière, 1792; *Glaucoderma* + *Glaucus* Poli, 1795 (non Forster, 1777, nec Gmelin, 1791); *Anonica* Oken, 1815.

Characters of the family.

Several species in the warmer seas.

Section *Electroma* Stoliczka, 1871. Shell fairly small and thin; hinge margin posteriorly slightly elongated, below it obliquely truncated; foot retractors symmetrical. *P. (E.) smaragdina* (Reeve).—Section *Pteria* s. s. Hinge margin posteriorly greatly prolonged; foot retractors asymmetrical. *P. (P.) hirundo* (Linné) (Fig. 800). Separation of *Austropteria* Iredale, 1931 (*saltata* Iredale), from *Pteria* is not clear. —Section *Pinctada* (Bolten) Röding, 1798 (synonyms *Unionium* Link, 1807; *Margaritiphora* Megerle von Mühlfeld, 1811; *Meleagrina* Lamarck, 1812; *Margarita* Leach, 1814; *Perlamater* Schumacher, 1817). Shell only slightly inclined, nearly equivalve; posterior corner slightly elongated. *P. (P.) margaritifera* (Linné).
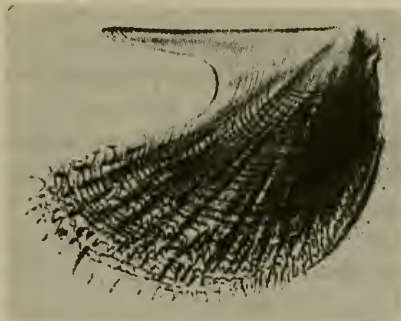
Fig. 800. Shell of *Pteria hirundo* (Linné)
(after Dunker).

3. Family PINNIDAE

Shell large and fairly thin, anteriorly pointed with terminal umbones, posteriorly gradually becoming higher, posteriorly gaping; ligament long, situated in a groove; hinge margin toothless. Anterior adductor muscle small, posterior one large, close to center of the shell; mantle margin fringed; oral lobes elongated, a peculiar gland of dubious

function is present over the upper lip; byssus strongly developed; gill lamellae folded, with large inner and outer border filaments; a long worm-shaped process located over the anal papilla at the posterior end; proximal limb of the kidney fairly long, outer sacks somewhat elongated, with abundant folds, completely separated from one another.

Pinna Linné, 1758

Synonym *Chimaera* Poli, 1791, non Linné, 1758.
Characters of the family. Shell often with groove-shaped scales.
A few species in the warmer seas.

804 Subgenus *Atrina* Gray, 1842. Shell without median edge; hypostracum undivided. Section *Atrina* s. s. Shell regular, in most cases not very long. *P. (A.) nigra* Chemnitz.—Section *Streptopinna* Martens, 1880. Shell more or less irregularly formed; ventral margin lobed. *P. (S.) saccata* Linné.

Subgenus *Pinna* s. s. Shell with a median longitudinal bulge or an edge corresponding to a deep cleft of the hypostracum. *P. (P.) rudis* Linné. *Pennaria* (Browne) Mörch, 1853 (*muricata* Linné), and *Cyrtopinna* Mörch, 1853 (*incurvata* Chemnitz), are slightly different; the latter is very elongated, posteriorly obliquely truncated.

These clams protrude into the substratum with the pointed anterior end, the gaping posterior end upwardly directed, so that they cannot change their location.

III. STIRPS PECTINACEA

Shell often inequivalve and with radial ribs; hinge margin moderately long, without true hinge teeth; ligament with a median cartilage in a pit. Mantle lobes separate, sometimes with eyes, often with thread-shaped appendages; gills and foot variously developed; an anterior adductor muscle in most cases absent.

1. Family DIMYIDAE

Shell small, with silvery shine, inequivalve, cemented with the right valve; left valve somewhat smaller and flatter; surface with weak radial sculpture; hinge margin straight, fairly short, with weak external and small internal ligament; outline somewhat inclined oval; umbo scarcely projecting; pallial line arch-shaped; anterior adductor muscle fairly small, close to the anterior margin; posterior one larger, distinctly bipartite; mantle completely open; margin with papillae, without eyes; gills with identical filaments without ascending limbs; foot and labial palps rudimentary; sexes separate.

Dimya Rouault, 1848

Synonym *Margariona* (Dall) Kobelt, 1882.
Characters of the family.
D. deshayesiana Rouault †; living *D. argentea* Dall, in the West
Indies, *D. corrugata* Hedley, near South and East Australia, and *D.
radiata* Kawamoto, near Japan.
The fossil group *Dimyodon* Munier-Chalmas, 1886, has a hinge
similar to that in *Plicatula*.

2. Family PECTINIDAE

Shell of variable form and size, in most cases inequivalve, often with
radial ribs or folds; hinge margin occasionally with diverging lamellae
or strong, identical teeth anteriorly and posteriorly; an anterior adductor
muscle absent; mantle margin in most cases with a broad internal fold
and with tentacles, frequently also with eyes; lip margins folded; foot
often without byssus, sometimes rudimentary; gill lamellae smooth or
pleated; the cerebral ganglia are displaced more or less far backward, and
may even be fused with the visceral ganglia.
The habits are variable; a few groups are cemented by one valve,
others are able to swim by opening and closing the shell.

A. Subfamily Plicatulinae

805

Shell somewhat irregularly formed, in most cases with radial folds,
cemented by the right valve; hinge margin short, without projecting
corners, with 2 strong, articulating teeth on either side, which in the right
valve lie next to ligamental cartilage and are clasped by teeth of the left
valve; pallial line not far from shell margin; attachment of the adductor
muscle in posterior half. Mantle margin with short tentacles and a narrow
interior fold, without eyes; foot rudimentary; gill lamellae with identical
two-limbed filaments which are connected by ciliary tufts only at the
lower corners and the ends of the ascending limbs; the inner ascending
limb sometimes absent; visceral ganglia of simple structure; cerebral
ganglia at the base of the labial palps; kidneys with long pericardial
ducts, connected with one another; sexes separate.

Plicatula Lamarck, 1801

Characters of the subfamily.
Synonyms *Harpax* Parkinson, 1811; *Ostrenomia* Conrad, 1873.
P. plicata (Linné). A few species in warmer seas.

B. Subfamily Amussiinae

Shell in most cases small and thin, often transparent, more seldom colored, smooth or with weak sculpture, without distinct radial folds, sometimes with internal radial ridges; hinge margin short or moderately long, sometimes transversely grooved, with median ligamental cartilage, at the ends with projecting corners, which are distinctly delimited from the main part of shell, in the right valve often with a deep incision below it. Mantle margin with few eyes or without such; gill lamellae with identical filaments, similar to those in *Plicatula*; the major part of the adductor muscle with transversely striated fibers extending obliquely and crossing the part with smooth fibers; the foot either has a distinct groove and a small anterior pit similar to that in mytilids or the groove is rudimentary and the anterior part of the foot has a large funnel-shaped invagination, the edges of which probably serve for burrowing, similar to that in nuculids.

The species live in most cases in the mud of the deep sea or in cold seas.

Propeamussium Gregorio, 1883

Shell thin and small, roundish below; right shell with a deep incision below the anterior ear-shaped part. The animals are poorly known; the foot in most cases seems to have a groove and a small anterior pit; sexes separate (always?).

Several species in various seas.

Subgenus *Palliolum* Monterosato, 1884. Shell without internal radial ribs. Section *Pectinella* Verrill, 1897. Shell thin, bulging, somewhat inequivalve, smooth; anterior ear of the right valve fairly large, smooth-margined, considerably larger than the posterior corner. *P. (P.) sigsbeei* (Dall).—Section *Hyalopecten* Verrill, 1897. Shell compressed, very thin, transparent, with concentric wave-shaped folds, sometimes with fine radial lines; ears small, unequal. *P. (H.) undatum* (Verrill). —Section *Cyclopecten* Verrill, 1897. Shell thin, inequivalve; right valve flattened, somewhat upwardly curved at the margin, in most cases with regular concentric borders; left valve variously sculptured, net-like or with scales or smooth. *P. (C.) pustulosum* (Verrill). *Chlamydella* Iredale, 1929 (*Cyclopecten favus* Hedley) is scarcely different.—Section *Similipecten* Winckworth, 1932. Shell small and thin, without distinct sculpture; posterior ears poorly delimited; only the right valve has a thin prismatic outer layer. *P. (S.) simile* (Laskey). —Section *Arctinula* n. Shell

806

very thin, colorless, smooth, roundish; right valve somewhat smaller and flatter than the left; ears of the left valve equal in size, obtusely angled, the anterior ones of the right valve rounded at the end; the structure of the valves variable, the right one consists of prisms, which are vertical to the surface, the left one shows fine radial lines parallel to the surface. *P. (A.) groenlandicum* (Sowerby).—? Section *Cyclochlamys* Finlay, 1926. Shell small, rhomboid; ears only slightly delimited; surface with strongly tuberculate ribs. *P.* ? *(C.) transenna* (Suter) (position doubtful).—Section *Lissopecten* Verrill, 1897. Shell shiny, speckled brown and white, exteriorly nearly smooth with very weak radial folds, interiorly with many thread-shaped radial ribs; byssus notch ventrally denticulate. *P. (L.) hyalinum* (Poli).—Section *Palliolum* s. s. Shell colorless or vividly colored, nearly equivalve; posterior ears smaller than the anterior ones; surface with microscopic radial sculpture. *P. (P.) testae* (Philippi). *Camptonectes* Meek, 1864 (*lens* Sowerby †) has been considered by Verrill as closely related to *Palliolum*; he includes the Recent species *Pecten striatus* Müller and *tigrinus* Lamarck with small posterior ears and denticulate byssus notch, the latter with several radial pleats, but these species have pleated gills and do not belong here.

Subgenus *Propeamussium* s. s. Shell with internal radial accessory ridges as in *Amussium*; right valve flatter, with concentric sculpture; left valve with radial or reticulate sculpture. *P. (P.) fenestratum* (Forbes). The separation of *Ctenamusium* Iredale, 1929 [*P. thetidis* (Hedley)], is not understandable.

Amussium (Klein, Bolten) Röding, 1798 (*Amusium*)

Synonym *Pleuronectia* Swainson, 1840.

Shell smooth or indistinctly sculptured, often somewhat inequivalve, thin, anteriorly and posteriorly somewhat gaping; hinge margin short; ears only slightly different, without byssus notch; the remaining shell roundish, internally with more or less numerous radial reinforcement ridges. Mantle margin without eyes; gill lamellae with identical filaments having two limbs; foot with anterior funnel-shaped expansion, without retractors; gonad hermaphroditic.

A few species in most cases living in mud in the deep sea.

A. pleuronectes (Linné) (Fig. 801). *Paramusium* Verrill, 1897, is based mainly on the erroneous description of the gills of *A. dalli* Edg. Smith, but may perhaps be used as a subgroup for the very thin-shelled deep-sea species.
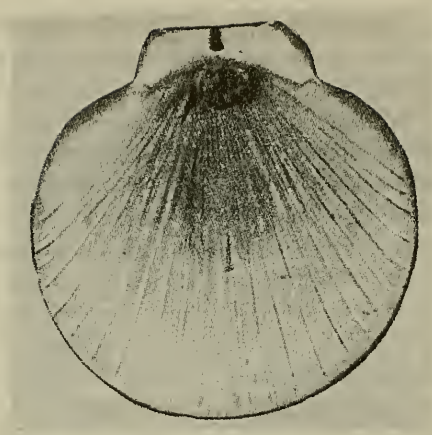
Fig. 801. Internal side of the shell of *Amussium pleuronectes* (Linné).
Length about 8 cm.

807
Adamussium n. gen.

Shell very thin, roundish, with flat radial folds, exteriorly with densely-placed concentric borders and microscopic radial lines, brownish, anteriorly and posteriorly gaping; hinge margin short; ears of the left valve obtusely angled; anterior ear of the right valve rounded and shallowly indented. Animal unknown.

A. *colbecki* (Edg. Smith) in the Antarctic Ocean. This species has such great similarity to *Amussium*, mainly in the form of the ears, that it probably belongs here, although the radial ridges are absent.

C. Subfamily Pectininae

Shell in most cases fairly thin, often with distinct radial folds; ears more or less large, the anterior one of the right valve in most cases delimited by a strong incision; the two valves often differently bulging; interior side porcelaneous. Mantle margins with numerous eyes and tentacles, and with a broad inner fold; gill lamellae pleated; foot with byssus, pedal groove and anterior glandular pit, or with an anterior funnel-shaped expansion and more or less rudimentary byssal gland; the unilaterally developed left retractor is sometimes strong, sometimes very weak or completely lost; lips with interlocking processes; visceral ganglia highly developed as the main center for innervation of the sense organs of the mantle margin, often asymmetrical; sexes in most cases separate, more seldom hermaphroditic.

Many species are able to swim by clapping the shell.

Pecten (Klein) Osbeck, 1765

Shell roundish, in most cases with distinct radial folds; ear distinctly demarcated; byssal notch variable; valves sometimes only slightly, sometimes very differently bulging.

Several species mainly in warmer seas.

Subgenus *Chlamys* (Bolten) Röding, 1798. Shell valves only slightly differing, in most cases fairly flatly bulging, and with radial folds, often rough; anterior ears often distinctly larger than the posterior ones; lower margin of the byssal notch of the right valve denticulate. ? Section *Veprichlamys* Iredale, 1929. Shell very thin, smooth, inclined. *P.* ? (*V.*) *perillustris* (Iredale).—Section *Camptonectes* Meek, 1864 (synonym *Eburneopecten* Conrad, 1865). Shell fairly small and thin; both valves similarly bulging and sculptured, smooth or with weak radial sculpture and as a rule with fine oblique lines; posterior ears small. *P.* (*C.*) *lens* Sowerby †. As stated earlier, a few living species are included here. *Belchlamys* Iredale, 1929 (*aktinos* Petterd) is characterized by the peculiarly infolded posterior ear; *Talochlamys* Iredale, 1929 (*famigerator* Iredale) appears to be similar to *Camptonectes*.—Section *Pseudamussium* (Klein) Mörch, 1853. Shell fairly thin, with a few flat radial folds and fine dense, occasionally indistinct striae; right anterior ear ribbed. *P.* (*P.*) *septemradiatus* (Müller).—Section *Aequipecten* P. Fischer, 1887 (synonym *Mimachlamys* Iredale, 1929). Shell roundish, nearly equivalve, with distinct radial folds and rows of small scales; anterior ears more or less larger than the posterior ones. *P.* (*A.*) *opercularis* (Linné).—Section *Chlamys* s. s. Shell with numerous narrow, scaly or spiny small radial folds, nearly equivalve; anterior ears in most cases distinctly larger than the posterior ones. *P.* (*C.*) *islandicus* Müller (Fig. 802). *Scaeochlamys* Iredale, 1929 (*lividus* Lamarck) is only slightly different.—Section *Plagioctenium* Dall, 1898. Both valves more or less strongly bulging, with a few strong radial folds and fine concentric lines; anterior and posterior ears nearly equal in size. *P.* (*P.*) *ventricosus* Sowerby. —Section *Pallium* (Martini) Schumacher, 1817 (synonyms *Decadopecten* (Rüppell) Swainson, 1840; *Dentipecten* (Rüppell) Gray, 1847). Shell only slightly bulging, with few strong radial folds and fine scaly ribs; ears more or less differing; at the hinge margin with a few tubercles. *P.* (*P.*) *plica* Lamarck. Scarcely differing are *Manupecten* Monterosato, 1872 = *Felipes* (Locard) Carus, 1889 [*P. pesfelis* (Linné)]; *Peplum* Bucquoy, Dautzenberg & Dollfus, 1889 [*clavatus* (Poli)]; *Flexopecten* Sacco, 1897 [*flexuosus* (Poli)]; *Mesopeplum* Iredale, 1929 (*caroli* Iredale); and *Notochlamys* Cotton, 1930 (*anguineus* Finlay).—Section *Nodipecten* Dall, 1898. Shell with many fine and a few strong radial folds which form a few hollow tubercles; ears unequal. *P.* (*N.*) *nodosus* (Linné).

808
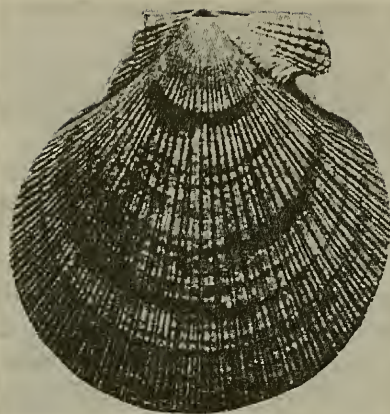
Fig. 802. Shell of *Pecten (Chlamys) islandicus* Müller.
Height almost 9 cm.

Subgenus *Placopecten* Verrill, 1897. Shell large, roundish, nearly equivalve, flatly bulging, without radial folds, with only dense, fine ribs; ears nearly equal in size; anterior ear of the right valve with weak, smooth indentation. *P. (P.) clintonius* Say, on the east coast of North America.

Subgenus *Equichlamys* Iredale, 1929. Shell fairly large, roundish; both valves moderately bulging, with a few radial folds flattening out toward the margin and with fine ribs; ears nearly equal in size, the anterior one weakly indented. *P. (E.) bifrons* Lamarck, near Australia.

Subgenus *Patinopecten* Dall, 1898. Shell very large; right valve somewhat more bulging than the left, with several radial folds, which are broader on the right; ears nearly equal in size, on the right with a weak anterior indentation. *P. (P.) caurinus* Gould.

Subgenus *Pecten* s. s. (synonyms *Janira* Schumacher, 1817; *Vola* (Klein) Mörch, 1853). Shell inequivalve; ears nearly equal in size, without deep byssal notch; left valve bulging, the right one flat or somewhat concave. Section *Pecten* s. s. Both valves with distinct radial folds, which are in most cases finely ribbed and rough. *P. (P.) adscensionis* Osbeck. *Notovola* Finlay, 1927 (*P. novaezelandiae* Reeve) is scarcely different.—Section *Euvola* Dall, 1897. Left shell greatly bulging, smooth or with flat folds, not rough; right valve flat or concave, with or without ribs. *P. (E.) ziczac* (Linné).

Subgenus *Hinnites* Defrance, 1821. Shell initially similar to that in *Chlamys*; both valves only slightly bulging, with several rough small radial folds; right valve with a ventrally denticulate byssal notch; later

809 the animals cement to the substratum with the right valve and become more or less inequivalve, sometimes thick and heavy, with irregularly formed ears; the byssus is no longer produced. *P. (H.) cortessi* (Defrance) †. Few living species.

Semipecten Adams & Reeve, 1848 (*Hemipecten*)

Shell small, translucent, smooth, inequivalve, irregularly roundish, without distinctly delineated ears, but with a deep byssal notch of the flat right valve, which is ventrally denticulate as in *Chlamys*; left valve bulging; ligamental cartilage small. Mantle margins with tentacles and eyes; foot with byssus and small anterior pit; byssal muscle present only on the left; gill lamellae folded, the ascending arms becoming gradually smaller posteriorly and finally end; sexes separate.

S. forbesianus Adams & Reeve (Fig. 803), in the Indo-Australian sea.

Fig. 803. Shell of *Semipecten forbesianus* Adams & Reeve, weakly enlarged.

Pedum Bruguière, 1792

Shell greatly compressed, fairly thin, high triangular, with weak radial sculpture; ligamental surface large, with deeply ingressing cartilage which is internally borne by a fold; left valve flat, anteriorly and posteriorly enclosed by the margins of the right valve, which has a deep byssal notch delineated above by a sharp margin to the umbo. Mantle margins with tentacles and eyes; foot with byssus.

P. spondyloideum (Gmelin), in the Indo-Pacific area, in coral reefs.

D. Subfamily Spondylinae

Shell inequivalve, cemented to substratum by the deeper right valve, as a rule with strong folds or thorns; ligamental surface of the right valve

larger than that of the left valve, with median cartilage; hinge margin on either side with 2 articulating teeth and corresponding pits; the teeth of the right valve situated beside the cartilage, those of the left valve more lateral. Animal similar to that in *Pecten*; mantle margins with eyes; gill lamellae folded, with large interior border filaments; foot with anterior funnel-shaped expansion, without byssus and without retractors; the cerebral ganglia approach the viscerals and may touch them.

Spondylus Linné, 1758

Characters of the subfamily.
S. gaederopus Linné. Several species in warm seas.

3. Family LIMIDAE

Shell colorless, higher than long, in most cases oval, straight or inclined, more or less bulging, closed or gaping, exteriorly with coarser or finer radial ribs or folds, sometimes with tubercles or scales; umbo situated above the center of the triangular ligamental surface of shifted forward; correspondingly the pit of the cartilage is straight or inclined; hinge margin smooth or denticulate, sometimes there are weak tubercles or ridges in the upper corners. Animal often reddish colored; mantle margins nearly always with numerous, more or less long glandular threads and with a broad interior fold; open pitted eyes are present in only few species; gill lamellae folded, with strong interior border filaments; the foot has its point directed backward; it has a' byssal groove, whereas a byssus may be sometimes present, sometimes absent; the lips in *Mantellum* are fused along their margins to form a tube which is open on both sides, smooth-margined in other groups; the large adductor muscle lies high and close to the posterior margin; the visceral commissure is in most cases greatly shortened and the cerebral ganglia approach or adjoin the visceral ganglia; the interconnected kidneys lie anterior to the adductor muscle; the pericardial limbs, before opening into the distal limbs, receive the exit ducts of the gonads; the ventricle is often cleft.

Like some Pectinidae, species of limids are able to swim by rapid opening and closing of the shell; some build nests.

Lima Chemnitz, 1784

Synonyms *Limaria* Link, 1807; *Glaucion* Oken, 1815.
Characters of the family.
Many species in various seas.

810

Subgenus *Notolimea* Iredale, 1924. Shell small, more or less thick-walled, straight or only slightly inclined, not gaping, bulging, in most cases with strong, frequently tuberculate or scaly radial folds; ligamental cartilage small; hinge ridge more or less broadened and denticulate on its underside; these denticles are sometimes short, sometimes considerably elongated, parallel to one another; only in *L. opulenta* Thiele are they thickened at the lower ends and therefore arranged fan-shaped in 2 groups interrupted by the cartilage. In *L. crassa* Forbes, the mantle cirri are said to be absent; in *L. opulenta* they are present; the anatomy is unknown. *L. (N.) australis* Edm[1]. Smith. Iredale, 1929, proposed the subgroups; *Gamellima*, for *L. austrina* (Tate), with weak denticles, and *Isolimea*, for *L. parvula* Verco, with thinner shell and stronger denticles.

So far this group has been almost always called *Limea* Bronn, 1831, the typical species of which the Tertiary *L. strigilata* Brochi, however the various figures of this species, especially one by Hörnes, show that it has a few small radial folds in the corners, as in *L. murrayi* Edg. Smith, but the hinge margin does not have parallel denticles; therefore this group must be called by the name given by Iredale.

Subgenus *Limatula* S. Wood, 1839. Shell in most cases small and fairly thin, distinctly higher than long, strongly bulging, straight or only slightly inclined, with weak, more seldom strong radial folds; umbo somewhat projecting, situated above the center of the smooth hinge margin; ligamental cartilage fairly broad and thin. Mantle lobes only slightly fused with one another; cirri in most cases few in number; foot without byssus and retractors; lips not fused with each other. *L. (L.) subauriculata* (Montagu). A few species in all seas.

Subgenus *Lima* s. s. Shell in most cases of medium, sometimes considerable, size, fairly thick-walled and only slightly gaping; lips not fused with one another. Section *Radula* (Klein) Mörch, 1835. Shell distinctly inclined, fairly thick, only slightly bulging, scarcely gaping, anteriorly flattened or somewhat concave; ligamental surfaces only slightly diverging; cartilage strong; exterior side with strong scaly radial ribs; animal with byssus and posterior foot retractors; gill rachis weak. *L. (R.) lima* (Linné). *Austrolima* Iredale, 1929, is scarcely different. —Section *Lima* s. s. (synonym *Ctenoides* (Klein) Mörch, 1853). Shell fairly thick, weakly bulging, only slightly inclined; upper part of the anterior margins outwardly curved and gaping; surface with numerous, more or less fine, small radial ribs, somewhat diverging in the center, in most cases tuberculate or spiny; in most cases with an oblique ridge in

811

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[1] This is a typographical error in the original; read Edg. Smith. —Editors.

the upper corners of one of the valves; foot with byssus and posterior retractors, behind it with a large process; gill rachis moderately strong. *L. (L.) scabra* (Born) = *aspera* Chemnitz (Fig. 804).—Section *Acesta* H. & A. Adams, 1858. Shell of medium to very considerable size and fairly thin, somewhat inclined; upper part of the anterior margin infolded; anterior corner only slightly or not projecting; umbo displaced far forward, correspondingly the cartilage pit very oblique; surface with low ribs which are sometimes absent in the median part; foot without byssus and posterior retractors; process behind the foot weak; gill rachis broad. *L. (A.) excavata* (Fabricius). *Callolima* Bartsch, 1913 (*rathbuni* Bartsch) is scarcely different; the ligament is more superficial.

Fig. 804. Shell of *Lima scabra* (Born).
Height 8 cm.

Subgenus *Limea* Bronn, 1831 (synonyms *Limoarca* Münster, 1832; *Escalima* Iredale, 1929). Shell obliquely oval, thin, not gaping, finely radially ribbed, bulging; ligamental cartilage fairly broad; hinge margin smooth, in the upper corners with a few small radial folds. *L. (L.) strigilata* (Brocchi) †, the living *L. (L.) murrayi* Edg. Smith. This group is perhaps closest to *Limatulella* Sacco, 1898, which is very similar in form and sculpture, differing only by the absence of small folds in the corners. Animal similar to that in *Mantellum*. *L. (L.) loscombi* Sowerby.

Subgenus *Mantellum* (Bolten) Röding, 1798. Shell fairly thin, inclined, ventrally more or less forwardly produced, in most cases distinctly gaping, more or less bulging; ligamental surfaces greatly diverging, so

that the shell can be widely opened; surface with weaker or stronger radial ribs which are sometimes somewhat tuberculate; inner folds of the mantle margin very broad, anteriorly in the center broadly fused with one another; foot without byssus and retractors; lip margins fused with one another to form a tube, which is open at both ends; the process behind the foot small. *L. (M.) inflata* (Chemnitz).

IV. STIRPS ANOMIACEA

Shell inequivalve, cemented to the substratum permanently or only during early life by a calcified byssus, which emerges through a deep indentation of the right valve; this indentation is more or less completely surrounded by the lower margin, so that it often appears as a perforation; the structure of the two valves is often different, that of the left valve 812 nacre-like, that of the right at least in the outer layer, prismatic (similar to that in the pectinid group *Arctinula*); hinge margin toothless, in most cases asymmetrical, that of the right valve short or with 2 prolongations, enclosed by the margin of the left valve. Animal highly asymmetrical, the right gill is downwardly displaced by the byssus, the lamellae consisting of identical two-limbed filaments; the small foot has a groove and an anterior pit connected with it; it is affixed to the left valve by a very strong byssal muscle and often, in addition, by a smaller retractor; the moderately strong roundish adductor muscle lies more ventrally; the heart projects out freely, without pericardium, into the mantle cavity; the kidneys are highly asymmetrical, the left one ring-shaped around the byssal musculature, the right one between the adductor and byssal muscles, they are interconnected anterior to the heart; branched ciliated processes are considered to represent the ciliated funnel; the sexes are separate, the gonads asymmetrical, the right one lying largely in the mantle.

When the byssus is reduced, the retractors are absent.

1. Family ANOMIIDAE

Shell in most cases irregularly roundish, often translucent and thin, smooth or sculptured; interior side in most cases nacreous shiny; the byssal aperture of the right valve is closed in a few groups.

Anomia (Linné) Müller, 1776

Shell as a rule in the right valve with a deep indentation, which is sometimes completely surrounded by the lower margin and is only

seldom reduced; left valve with the scar of one or 2 byssal muscles; ligament short or somewhat elongated by process of the hinge margin of the right valve, covered by the left valve.

Several species in various seas.

Subgenus *Isomonia* Dautzenberg & H. Fischer, 1897. Left valve with straight hinge margin, which forms corners at the ends, thin, roundish; ligamental pit very small; scar of the byssal muscle simple, joined with that of the adductor muscle; right valve unknown. *A. (I.) alberti* (Dautzenberg & H. Fischer), near the Azores.

Subgenus *Heteranomia* Winckworth, 1922. Shell small, thin and transparent, smooth or spiny; umbo marginal; byssal muscle simple, lying over the small adductor muscle; gill filaments without ascending limbs. *A. (H.) squamula* Linné, in the northern Atlantic Ocean.

Subgenus *Monia* Gray, 1849. Shell of variable size and strength; hinge margin of the right valve sometimes prolonged by processes; the end of the process enclosing the byssal aperture may be fused with the upper margin; byssal muscle simple; gill filaments with two limbs. *A. (M.) zelandica* Gray.

Subgenus *Anomia* s. s. (synonym *Fenestella* (Bolten) Röding, 1798). Shell in most cases fairly thin; hinge margin short, without processes; byssal aperture without fused margins; byssal musculature bipartite. Section *Anomia* s. s. Muscle scars situated close together, the uppermost being the largest; byssal aperture fairly large. *A. (A.) ephippium* Linné. —Section *Patro* Gray, 1849. Scar of adductor muscle larger than that of the upper byssal muscle, the central one small; byssal aperture fairly small. *A. (P.) elyros* Gray.—Section *Enigmonia* Iredale, 1918 (synonym *Aenigma* Koch, 1846, non Newman, 1836). Shell thin, often transversely oval, umbo of the left valve not positioned marginally; scar of the large byssal muscle away from the other two. *A. (E.) aenigmatica* (Chemnitz) (Fig. 805).

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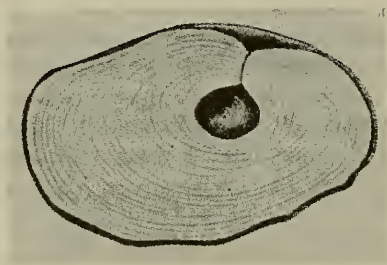
Fig. 805. Shell of *Anomia (Enigmonia) aenigmatica* (Chemnitz).

Subgenus *Pododesmus* Philippi, 1837 (synonym *Tedinia* Gray, 1851). Byssal aperture small, sometimes fused with the byssus; hinge margin only slightly elongated; byssal muscle simple. *A. (P.) rudis* Broderip.

Subgenus *Placunanomia* Broderip, 1832. Shell with few strong zig-zag-shaped folds; byssal aperture closed; right valve with 2 ridges, diverging at an acute angle, separated by a pit; corresponding to these are furrows in the left valve, as bearers of the ligament; byssal muscle simple. *A. (P.) cumingi* Broderip.

Placenta Retzius, 1788

Shell greatly compressed, disk-shaped, often large, more or less thin and translucent, cemented by a byssus only during early life, thereafter free-living, without byssal aperture; surface finely radially sculptured; inner side nacreous shiny, in the center with a roundish adductor muscle, only with a weak foot muscle; the ligament, similar to that in *Placunanomia*, borne by 2 diverging ridges of the right valve and corresponding furrows of the left valve.

Few species in the Indo-Pacific region.

Subgenus *Placenta* s. s. (synonym *Placuna* Bruguière, 1792). Shell flat, transparent; hinge ridges diverging at a sharp angle, the anterior shorter than the posterior. *P. (P.) orbicularis* (Retzius).

Subgenus *Ephippium* (Bolten) Röding, 1798 (synonym *Placunema* Stoliczka, 1870). Shell peculiarly curved saddle-shaped; hinge ridges diverging at a right angle, equally long. *P. (E.) sella* (Gmelin).

IV. STIRPS OSTREACEA

Shell inequivalve, cemented to solid substrata by the left valve, more or less irregularly formed; ligamental cartilage in a triangular pit; hinge margin toothless; mantle lobes completely separate; foot and byssus reduced; gill lamellae folded, with large inner marginal filaments; the outer ascending lamellae are fused with the mantle; the long ciliated funnels of the kidneys lie on the inner side of the outer sacks, which are posteriorly connected with one another and anteriorly receive the gonoducts.

1. Family OSTRÉIDAE

Characters of the stirps. The shell structure of the two valves in most cases appears to differ; the ostracum of the right valve shows a sometimes irregular prismatic structure; the left valve is in most cases

deeper than the right. Form and exterior sculpture are highly variable, not seldom are the margins more or less strongly folded.

Ostrea Linné, 1758

Synonyms *Peloris* + *Peloriderma* Poli, 1795.
Characters of the family.
Several species in warm and temperate seas.

814   Subgenus *Lopha* (Bolten) Röding, 1798. Animals of separate sex; shell with more or less strong folds. Section *Ostreola* Monterosato, 1884. Shell strongly inequivalve; folds of the left valve more distinct, inner margin with a row of tubercles. *O. (O.) stentina* Payraudeau.—Section *Lopha* s. s. (synonyms ? *Rastellum* (Lister) Schröter, 1782; *Alectryonia* Fischer von Waldheim, 1807; *Dendrostrea* Swainson, 1840). Valves not greatly differing, with strong folds; inner margin denticulate; left valve sometimes cemented by irregular processes. *O. (L.) cristagalli* Linné.

Subgenus *Pycnodonta* Fischer von Waldheim, 1834. Sexes separate; lower valve greatly deepended, without folds, the upper one flattened, with wrinkles anterior and posterior to the hinge margin. *O. (P.) vesicularis* Lamarck †; the living *O. cochlear* Poli.

Subgenus *Crassostrea* Sacco, 1897 (synonym *Dioeciostraea* Orton, 1928). Sexes separate; shell thick, not folded, with external lamellae; ligamental surface high; form often much higher than long. *O. (C.) virginica* Gmelin. According to Dall, *O. angulata* Lamarck, in most cases included in *Gryphaea*, belongs here.

Subgenus *Ostrea* s. s. (synonyms *Anodontostrea* Suter, 1917; *Monoeciostraea* Orten, 1928). Animals hermaphroditic; the embryos develop inside the gills of the mother; shell roundish or oval; valves not greatly differing. Surface with irregular lamellae; lower valve with folds; umbo straight and flattened. Section *Ostrea* s. s. Inner margin smooth. *O. (O.) edulis* Linné.—Section *Eostrea* Jhering, 1907. Inner margin folded. Genotype?, the living *O. puelchana* Orbigny.

3. Order EULAMELLIBRANCHIATA

Gill filaments as a rule fused on either side to form 2 perforated, often folded laminae. Mantle often with posterior siphons. Anterior adductor muscle seldom reduced. Hinge teeth in most cases few in number, alternating in the two valves, often with a right central tooth; lateral teeth, in addition, often present; however, all hinge teeth may disappear and very seldom be replaced by irregular tooth formations.

Suborder SCHIZODONTA

Shell variously formed; the ostracum consists of an inner nacreous layer and outer prismatic layer; the hinge is primitively schizodont; according to more recent opinion, a central tooth is present in the right valve, situated in front of the center, clasped on the left valve by an anterior simple tooth and a posterior tooth subdivided below by a sinus; in addition, the right valve has a posterior, more or less elongated, tooth and often an anterior, in most cases weak, tooth near the margin; in the left valve a posterior elongated tooth present below the margin. In most cases well-developed foot has no byssus; the mantle is in most cases completely open, although sometimes with a septum below the excurrent opening, and which can be separated from the supraanal opening by a bridge; the gill laminae consist of a descending and an ascending lamella, which in *Trigonia*, similar to that in *Arca*, consist of filaments which are joined only by ciliary tufts; in unionaceans, they are formed of filaments which are more or less fused with one another, forming continuous, lattice-like, perforated lamellae; the two lamellae of a lamina are more or less connected with one another by septa, and the outermost lamellae are in most cases fused to the mantle by their upper margin; the innermost ones often attached to the visceral sack and posterior to it they are fused with one another; the labial palps are well-developed; the heart chamber is nearly always traversed by the intestine.

I. STIRPS TRIGONIACEA

Shell fairly thick, rounded-triangular; ligament external, fairly short; hinge strong, especially the triangular, ventrally distinctly indented central tooth of the left valve; the main teeth with strong transverse ridges, only the anteriormost tooth of the right valve is a narrow, smooth lamella; the anterior adductor muscle lies close to the hinge teeth and its attachments to the shell are distinctly deepened, whereas the posterior ones are more shallow; foot large, anteriorly tongue-shaped, with an only slightly deep groove, into which open 2 rows of large glandular cells; a byssal gland is indicated by a narrow although fairly long tube; mantle completely open, at the posterior margin with small papillae; gills similar to that in *Arca* with a rachis and with filaments fused with one another only at the margin, without connection with the mantle and visceral sack; the kidneys are similar to those in *Arca*, with strongly branched sacks; the sexes are separate. Marine.

Family TRIGONIIDAE

Characters of the stirps. The genus *Trigonia* Bruguière, the species of which are variably sculptured, is extinct.

Neotrigonia Cossmann, 1912

Shell with strong, tuberculate radial folds; umbo only slightly projecting, not posteriorly inclined; tooth 2 high and ventrally divided. *N. pectinata* (Lamarck). Few species near Australia (Fig. 806).
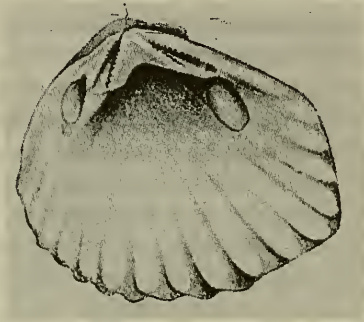
Fig. 806. Internal side of the left shell valve of *Neotrigonia margaritacea* (Lamarck).

II. STIRPS UNIONACEA

Shell of medium to considerable size; the schizodont hinge is sometimes completely reduced, and in *Iridina* replaced by a row of tubercle-shaped teeth; the mantle margins are sometimes completely separated from one another, sometimes variable fused with one another in the posterior part; foot in most cases hatchet-shaped, reduced in *Aetheria;* the leaf-shaped gills are fused with one another posterior to the foot, often the outer one is also fused with the mantle, the inner one with the visceral sack; in them the eggs develop in the female, sometimes in all four laminae, sometimes only in the inner or the outer ones; after they are freed, the embryos almost always live parasitic on fishes. In fresh waters, distributed over all continents.

For distinguishing the families, mainly the behavior of the gills and their relationship to brood care have been used.

1. Family MARGARITANIDAE

Shell strong, fairly elongated, anteriorly rounded; umbo low, with weak concentric sculpture; in the left valve with 2 more or less complete anterior teeth and with one in the right valve; posterior lamellae short, in most cases incomplete or totally absent; gills not fused posteriorly with the mantle, forming an incomplete diaphragm; the outer lamina is only anteriorly fixed to the mantle; the anterior end of the inner lamina is separated from the labial palps; the gills have scattered interlamellar junctions, which at places form irregular rows or oblique continuous septa; the posterior mantle margins are separate, so that a separate supraanal opening is absent; the larvae are small half-circle-shaped glochidia without hooks, in all 4 gill laminae.

Margaritana Schumacher, 1817

Characters of the family.

The genus includes few species in the northern hemisphere.

Subgenus *Potamida* Swainson, 1840 (*Potomida*) (synonym *Pseudunio* Haas, 1910). Posterior hinge teeth distinctly developed, 2 in the left, 1 in the right valve. *M. (P.) sinuata* (Lamarck) = *auricularia* (Spengler). *Margaritanopsis* Haas, 1912, proposed for "*Unio*" *laosensis* (Lea) from Indochina, is similar.

Subgenus *Margaritana* s. s. (synonyms *Baphia* (Meuschen) + *Damalis* (Leach) Gray, 1847). Posterior hinge teeth rudimentary or absent; gills without water tubes. *M. (M.) margaritifera* (Linné).

Subgenus *Cumberlandia* Ortmann, 1912. Shell as in *Margaritana* s. s.; gills with incomplete water tubes and continuous, obliquely descending septa. *M. (C.) monodonta* (Say).

2. Family UNIONIDAE

Shell of highly variable form and size; umbonal sculpture more or less reduced; hinge sometimes more or less strongly developed, sometimes completely reduced. The diaphragm formed by the gills is complete; outer gill lamina posteriorly fused with the mantle to the end; the incurrent and excurrent apertures are separated from one another by the diaphragm, the latter is closed above in most cases and separated from a supraanal opening; gill lamina with interlamellar septa, which extends parallel to the filaments and with water tubes; glochidial larvae in all or only the outer gill laminae.

A. Subfamily Unioninae

Umbonal sculpture variable, concentric or zig-zag-shaped or tuberculate, often indistinct; hinge teeth more or less strong; both sexes equal. A supraanal opening is sometimes not separated from the anal opening; brood space (marsupium) in all or only the outer laminae, which always have smooth margins; water tubes of gravid females undivided; glochidia semi-elliptical or half-circle-shaped, without hooks.

A separation of the groups, which harbor embryos in all gill laminae (Quadrulinae) from those which keep them only in the outer laminae (Unioninae s. s.), is not practical at present, because the animals are still unknown in many genera.

The Unioninae live in North and Central America, in Asia, Europe and Africa.

817   *Virgus* Simpson, 1900

Shell fairly solid-walled, compressed, anteriorly shortly rounded, posteriorly greatly produced, almost straight below, with or without wrinkled folds; main teeth small, solid, strongly cuspidate, anterior to that of the right valve with an accessory tooth; lamellae fairly short and low, thin. Gill diaphragm complete; anal opening of the mantle large, combined with the supraanal opening; foot small; inner gill attached to the visceral sack to the labial palps; the gill laminae has no complete septa, but only irregular connective tissue bridges of highly variable length, those in the anterior part of the inner laminae most densely situated and probably indicate that the embryos, which are not known, are received here.

Few species on New Guinea.

Section *Leiovirgus* Haas, 1912 (synonym *Nesonaia* Haas, 1913). Posterior beak truncated, without wrinkled folds. *V. (L.) misoolensis* (Schepman).—Section *Virgus* s. s. Posterior beak fairly pointed, with wrinkled folds. *V. (V.) beccarianus* (Tapparone Canefri). Judging from the structure of the gills, the genus is very primitive and perhaps needs to be included in a separate subfamily.

Haas considers it possible that the Australian "*Unio*" *novaehollandiae* Gray belongs in this genus; if this is confirmed, then the genus must receive the name *Cucumeria* Conrad, 1853. The named species is sculptured in the posterior, larger half with irregularly radiating tuberculate folds.

Parreysia Conrad, 1853

Shell fairly small and in most cases inflated, ovoid to rhomboid; umbo elevated, with radial or zig-zag-shaped, sometimes fairly extensive sculpture; left valve with 2 irregular, sometimes strong and striated, sometimes weak, anterior teeth and 2 posterior lamellae; right valve with an anterior tooth, above which there may be a second smaller and compressed one, and a posterior lamella, at the lower side of which a furrow is sometimes developed, corresponding to the lower lamella of the opposite side. All 4 gill laminae contain glochidia; the inner is anteriorly longer and broader than the outer, largely attached to the large foot.

Several species in India, China (?), and in tropical Africa.

Subgenus *Parreysia* s. s. Glochidia only slightly higher than broad, with somewhat incurved ventral margin. *P. (P.) multidentata* (Philippi) = *corrugata* (Müller) (Fig. 807).
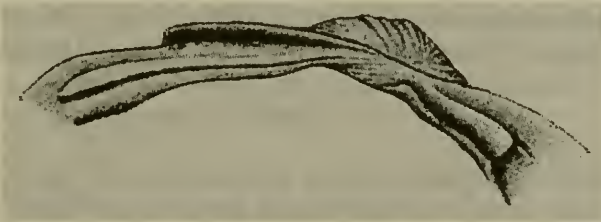
Fig. 807. Hinge margin of the left valve of *Parreysia corrugata* (Müller), enlarged.

Subgenus *Radiatula* Simpson, 1900 (synonym *Indonaia* Prashad, 1918). Innermost gill lamella completely fused; embryos distinctly higher than broad, with short hinge margin and stronger incurved ventral margin. *P. (R.) crispisulcata* (Lea). The group is erected for the named species, placed by Prashad in *Indonaia*, which accordingly must bear the older name.

? Subgenus *Diaurora* Cockerell, 1903 (synonym *Aurora* Simpson, 1900, non Ragonot, 1887, nec Sollas, 1888). Shell small, egg-shaped, sculptured with tubercles and angular folds; anterior teeth truncate cone-shaped. *P. (D.) aurorea* (Heude), in China.

Grandidieria Bourguignat, 1885

Synonym *Ruellania* Bourguignat, 1885.

Shell small, strong, inflated, ovoid to rhomboid; umbo elevated, ın most cases sculptured with fine zig-zag lines, which may form tuberculate

ribs mainly anteriorly and posteriorly; left valve with 1 or 2 anterior, often irregular teeth and right valve and 2 anterior teeth; 2 lamellae in the left and 1 in the right valve. Animal unknown.

G. burtoni (Woodward). A few species in Lake Tanganyika.

Caelatura Conrad, 1853

Synonyms *Pharaonia* Bourguignat, 1880 (nom. nud.); *Zairia* + *Reneus* Rochebrune, 1886; *Renatus* Rochebrune, 1904.

Shell more or less elongated egg-shaped, medium-sized; umbo in most cases with zig-zag ridges and tubercles; anterior hinge teeth thin or tuberculate; lamellae left 2, right 1; inner gill lamina broader anteriorly than the outer, all containing small, roundish embryos, the innermost lamella is fused to the foot only in the anterior part.

A few species in the Nile and tropical Africa.

Pallary, 1924, proposed as sections: *Horusia* for *C. rugifera* (Küster), *Nitia* (?) for *teretiuscula* (Philippi), and *Jaronia* and *nilotica* (Cailliaud).

? Subgenus *Laevirostris* Simpson, 1900. Umbo without distinct sculpture; anterior hinge teeth thin. *C.* (*L.*) *stagnorum* (Dautzenberg).

Psilunio Stefanescu, 1896

Synonyms *Rhombunio* Germain, 1911; *Migranaja* Hannibal, 1912.

Shell fairly strong, somewhat inflated, anteriorly fairly short, rounded, posteriorly angulate; umbo projecting, with fine, fairly parallel wrinkles; anterior hinge teeth somewhat compressed; lamellae straight or weakly curved. Supraanal opening separated from the anal opening; gill laminae with complete and incomplete septa, the outer ones narrower than the inner, all containing embryos; innermost lamella attached only very anteriorly.

P. littoralis (Lamarck). A few species in the Near East, central Europe, and the Mediterranean region.

Stefanescu based the groups *Psilunio*, *Rytia*, and *Iridea* (non Swainson, 1840) = *Cuneopsidea* Wenz, 1928, on fossil species.

According to Prashad, "*Unio*" *semirugatus* Lamarck (called by him *Rhombunio*) contains embryos only in the outer gill laminae.

Rhombuniopsis Haas, 1920

Shell thick, anteriorly short, egg-shaped; umbo more or less anterior in position, inflated, sculptured with wavy wrinkles; anterior teeth massive; lamellae short and strong. Animal unknown.

R. tauriformis (Fulton). A couple of species in China.

Schepmania Haas, 1912

Shell fairly solid-walled, elongated oval, with parallel wrinkled folds along the posterior edge; anterior hinge teeth low, bluntly cone-shaped; lamellae short and low. Animal unknown.

S. nieuwenhuisi (Schepman). 2 species in Borneo.

Inversidens Haas, 1911

Shell fairly strong, more or less elongated egg-shaped, anteriorly short, posteriorly obliquely truncated; right valve with one anterior tooth and 2 lamellae, left one with 2 main teeth, one of which is sometimes indistinct, and one lamella. Animal unknown.

I. brandti (Kobelt). A few mainly Japanese species.

Pseudobaphia Simpson, 1900

Shell strong, short egg-shaped, inflated, anteriorly rounded, posteriorly somewhat truncated; umbo elevated; anterior teeth strong, strongly cuspidate; lamellae very small and weak. Animal unknown.

P. biesiana (Heude), in China.

Lamprotula Simpson, 1900

Synonym *Gibbosula* Simpson, 1900.

Shell thick, roundish to egg-shaped; umbo anterior in position; surface sculptured with tubercles and ridges; anterior teeth strongly furrowed; 2 strong, transversely furrowed lamellae in both vales. Gills similar to those in *Psilunio*; all 4 laminae forming pillow-shaped marsupia not sharp at the margins; innermost lamella attached only very anteriorly.

L. plumbea (Chemnitz). A few species in China.

Discomya Simpson, 1900

Shell strong, compressed, roundish, anteriorly shortly rounded, posteriorly somewhat truncate; umbo low; surface with numerous tubercles, in the posterior part sculptured with bulging folds; right hinge tooth fairly broad, somewhat furrowed; anterior tooth of the left valve triangular, high, posterior one longish, low; lamellae short and fairly weak. Animal unknown.

D. radulosa (Drouet & Chaper). 2 species on Borneo.

Pseudodon Gould, 1844

Synonyms *Monocondylus* Morelet, 1886; *Pseudodus* Morgan, 1885.

Shell more or less elongated egg-shaped; umbo situated fairly far forward, only slightly projecting, with W-shaped wrinkles which are seldom retained; each valve with a tubercle-shaped anterior tooth; posterior lamellae rudimentary or absent. Mantle in most cases with a supraanal opening; inner and outer gill laminae containing embryos.

Several species in Indochina to Burma and south China and on the Greater Sunda Islands; one in Japan.

Section *Trigonodon* Conrad, 1865. Shell strong; right valve with a strong triangular tooth, posterior to it with a distinct pit and behind the latter with a weak tooth; left valve with a strong triangular tooth and indication of a tooth anterior to it. *P. (T.) crebristriatus* (Anthony). —Section *Indopseudodon* Prashad, 1922. A supraanal opening is not separated from the anal one; innermost gill lamella attached in the anterior third. *P. (I.) salwenianus* (Gould).—Section *Pseudodon* s. s. (synonyms *Monodontina* Conrad, 1853; *Suborbiculus* Simpson, 1900). Shell compressed, anteriorly lower than posteriorly; each valve with a smooth tooth parallel to the margin; inner lamella of the inner gill lamina not fused with the foot for 2/3 of its length. *P. (P.) inoscularis* (Gould) = *vondembuschianus* (Lea).—Section *Obovalis* Simpson, 1900. Shell elongated egg-shaped, fairly thin, on the edge of the area with V-shaped folds, the upper limbs of which cross the area, whereas the lower ones extend over the external surface; hinge teeth high, triangular. *P. (O.) loomisi* Simpson.—Section *Cosmopseudodon* Haas, 1920. Shell fairly elongated, solid-walled, umbo with 2 V-shaped folds, gradually becoming more wavy; posterior part of the shell with radial folds, which in most cases become indistinct in adult animals; hinge teeth thick and blunt. *P. (C.) resupinatus* Martens.—Section *Diplopseudodon* Haas, 1920. Shell elongated rhomboid, thick-walled; right valve with 2, left with one, hinge tooth. *P. (D.) crassus* Drouet.—Section *Nasus* Simpson, 1900. Shell strongly elongated, moderately thick; umbo not projecting; hinge teeth compressed, high. *P. (N.) nankingensis* (Heude).—Section *Chrysopseudodon* Haas, 1920. Shell small, rhomboid, solid-walled and inflated; umbo approaching the center, projecting, with wavy wrinkles; area broad; hinge tooth of the right valve triangular, parallel to the margin, that of the left valve obliquely directed. *P. (C.) aureus* Heude.—Section *Bineurus* Simpson, 1900. Shell longish rhomboid, posteriorly fairly high, compressed, thin-walled; edges of the area distinct; hinge teeth low. *P. (B.) mouhoti* (Lea).

820

Trapezoideus Simpson, 1900

Shell trapezoidal, anteriorly shortly rounded, posteriorly higher, broadly truncated; umbo only slightly projecting, with zig-zag-shaped sculpture; right valve with a lamella-shaped anterior tooth and a weaker one above it and a posterior lamella; left valve anteriorly with a lamella-shaped tooth and posterior to it a wart-shaped tooth and 2 posterior lamellae. Outer gill lamina anteriorly narrower than the inner, the innermost lamella fused with the visceral sack for 2/3 of its length; all 4 laminae containing embryos; supraanal opening separate.

T. foliaceus (Gould). A few species in Indochina and Sumatra.

Ensidens Frierson, 1911

Shell more or less long, fairly thin, posteriorly pointed; umbo elevated, smooth or with weak zig-zag lines; area without distinct edges; right valve with 2 sharp anterior teeth, left one with a very long and sharp anterior tooth, a rudimentary tooth below the umbo; lamellae very long and thin. Supraanal opening separated; innermost gill lamella not fused with visceral sack; all 4 laminae containing embryos.

A few species in Indochina.

Section *Uniandra* Haas, 1912. Shell egg-shaped, posteriorly scarcely pointed, inflated; umbo elevated, with zig-zag-shaped concentric ridges, *E. (U.) inaequalis* (Rouchebrune). —Section *Ensidens* s. s. Shell posteriorly pointed; umbo without sculpture. *E. (E.) ingallsianus* (Lea).

Rectidens Simpson, 1900

Shell elongated, posteriorly prolonged, fairly solid-walled; umbo only slightly elevated, with concentric sculpture only on the outermost tips; edges of the area distinct, keel-like; right valve with 2 anterior thin teeth and a posterior lamella, left one with 2 anterior and 2 posterior lamellae; the smaller anterior tooth lies below the umbo. Supraanal opening separated from the anal aperture by a narrow bridge; innermost gill lamella attached to visceral sack only very anteriorly; the laminae are narrow, the outer ones anteriorly considerably shorter and narrower than the inner ones, all containing embryos, the incurved ventral margin of which bearing regularly arranged small tubercles.

821

R. prolongatus (Drouet). A few species in Malacca, Sumatra, Java and Borneo.

Ctenodesma Simpson, 1900

Synonym *Christadens* Simpson, 1914.

Shell fairly thin, elongated egg-shaped, compressed; umbo scarcely projecting, with delicate zig-zag ridges which merge into small radial folds; anterior teeth longish or triangular, low, furrowed or deeply cleft; lamellae short and low. Animal unknown.

C. borneense (Issel), on Borneo.

A change of the generic name because of *Ctenodesmus* O. F. Cook, 1896, seems superfluous.

Balwantia Prashad, 1919

Shell greatly elongated, moderately long anterior to the umbones, rounded anteriorly, posteriorly greatly elongated, distinctly higher than anteriorly, obliquely truncated at the end; hinge teeth rudimentary. Supraanal opening separated; gills very long and narrow; innermost lamella fused to the visceral sack for a considerable length; all 4 gill laminae containing roundish embryos; foot very strong.

B. soleniformis (Benson), in Assam.

Lamellidens Simpson, 1900

Shell moderately elongated, posteriorly pointed with low posterior edge; umbo with curved radial ridges, which are sometimes somewhat zig-zag-shaped or nearly concentric; left valve with 2 compressed anterior teeth and 2 posterior lamellae, right one with 2 parallel anterior teeth and one lamella. Supraanal opening separate. Gill laminae in the posterior part broader than anteriorly; innermost lamella fused to the visceral sack over a fairly long distance; embryos contained either in all or only in the outer laminae.

L. marginalis (Lamarck). Few species in India.

Simpson designated *Spathopsis* Simpson, 1900, as a subgenus of *Lamellidens*; umbo fairly low, with concentric wrinkles and weak folds anterior and posterior to them; hinge teeth greatly elongated. Animal unknown; systematic position uncertain.

S. guillaini (Recluz), in Somaliland.

Contradens Haas, 1913

Synonym *Schizocleithrum* Haas, 1913.

Shell more or less elongated egg-shaped, posteriorly obliquely truncated; umbo only slightly projecting, with wavy concentric wrinkles, occasionally extending over the entire shell; left valve with 2 anterior teeth one behind the other, the posterior of which sometimes disappears, and 2 lamellae; right valve with 2 anterior teeth lying one over the other and one lamella; the teeth are lamellae-shaped, sometimes sharp, sometimes thickened. Supraanal opening separated from the anal one by a narrow bridge; gill laminae broadened in the centre; innermost lamella in anterior half fused with the visceral sack; embryos are contained in the outer laminae and part of the inner ones; the egg-shaped glochidia have several rows of small tubercles on the incurved ventral margin.

C. *contradens* (Lea). A few species on Sumatra.

822   *Caudiculatus* Simpson, 1900

Shell egg-shaped, inflated, anteriorly rounded, posteriorly oblique and below it truncated straight; right valve with an anterior tooth and a lamella, left one with 2 teeth and 2 lamellae. Animal unknown.

C. *caudiculatus* (Martens), on Borneo.

Pressidens Haas, 1910

Shell egg-shaped, thin; umbo low, sometimes with concentric wavy wrinkles; both valves with a long, compressed main tooth and a long low lamella; posterior tooth and upper lamella of the left valve rudimentary; above the right anterior tooth there may be a weak accessory tooth. Animal unknown.

P. *moellendorffi* Haas. Few closely related species on Borneo, Palawan and Banguey.

Acuticosta Simpson, 1900

Shell egg-shaped; umbo strongly projecting, with zig-zag-shaped concentric wrinkles; anterior hinge teeth strong, compressed, dorsally serrated or notched; lamellae short and strong. Supraanal opening separated from the anal one by a fairly narrow bridge; gill laminae broad; innermost lamella largely fused to the foot; the outer gills contain roundish glochidia, which on the ventral side have a rectangular plate with 2 rows of pointed small warts and a few rows of very small granulations.

A. *chinensis* (Lea). Few species in China.

Protunio Haas, 1913

Shell rounded rhomboid, solid-walled, posteriorly truncated; umbo with somewhat wavy wrinkles; anterior hinge tooth of the right valve low, rectangular to triangular; left valve with 2 teeth, the anterior one lamella-shaped the posterior one low, trigonal, furrowed above, and with 2 lamellae which become thicker posteriorly. Animal unknown.

P. messageri (Bavay & Dautzenberg), in Tonkin.

Elongaria Haas, 1913

Shell elongated, anteriorly rounded, posteriorly obliquely truncated; umbo not projecting, without sculpture; anterior hinge teeth fairly weak, on the right with one accessory tooth; lamellae long. Animal unknown.

Section *Elongaria* s. s. Shell medium-sized, moderately solid-walled, smooth; anterior teeth broadly lamellae-shaped *E. (E.) orientalis* (Lea), on Java.—Section *Nannonaia* Haas, 1913. Shell small, thin, sculptured with fine wrinkles in the posterior part; anterior teeth thin, sharp. *E. (N.) trompi* (Drouet & Chaper), on Borneo.

Simpsonella Cockerell, 1903

Synonym *Dalliella* Simpson, 1900, non Cossmann, 1895.

Shell more or less elongated, thin-walled, fairly inflated, anteriorly short and rounded, posteriorly truncated or somewhat pointed; umbo somewhat projecting, with concentric wavy wrinkles; hinge teeth rudimentary, on either side with a lamellae-shaped main tooth and a short, very low lamella, or completely absent. Mantle bridge between the anal and supraanal openings fairly short, deeply sunken; gills moderately broad, with complete septa; innermost lamellae largely fused with the visceral sack; the outer laminae contain triangular glochidia, which have pointed hooks beset with spinules on the outer side.

823

S. purpurea (Valenciennes). Few species on the Philippines (Luzon and Panay).

Pilsbryoconcha Simpson, 1900

Shell elongated, thin, anteriorly shortly rounded, posteriorly long and more or less pointed, compressed; umbo scarcely projecting, with concentric wavy wrinkles; hinge margin narrow, non-denticulate. Animal unknown.

P. exilis (Lea). A few species in Indochina and on the Sunda Islands.

Schistodesmus Simpson, 1900

Shell strong, roundly triangular, anteriorly steeply sloping, posteriorly oblique, pointed at the end, with concentric bulges; umbo nearly centrally positioned, high, inflated; anterior tooth of the right valve high and strong, triangular, with a furrow in the center; posterior lamella thick; left valve with a lamella-shaped anterior tooth and a thick tooth below the umbo; lower lamella stronger than the upper. Supraanal opening separate; gills broad, with complete septa; innermost lamella attached only very anteriorly; the outer laminae containing the embryos.

S. lampreyanus (Baird & Adams), in China.

Unionella Haas, 1913

Shell small and thick, short, anteriorly very steeply sloping, posteriorly obliquely truncated; umbo projecting, inflated, with concentric zig-zag wrinkles; anterior tooth of the right valve tri- or quadrangular, low, furrowed above; below the lamella with an accessory lamella; anterior main tooth of the left valve small, lamella-shaped, the posterior one blunt, triangular; lamellae short and strong. Animal unknown.

U. fabagina (Deshayes & Jullien). 2 species in Indochina.

Physunio Simpson, 1900

Synonym *Lens* Simpson, 1900.

Shell fairly thin, in most cases inflated, anteriorly short and low, posteriorly elongated and sometimes very high; umbo with zig-zag wrinkles on the tips; anterior tooth of the right valve lamella-shaped with a similar accessory tooth above it; anterior main tooth of the left valve long and lamella-shaped, the posterior one small, wart-shaped, sometimes lost; lamellae short, an accessory lamella is sometimes formed with age. Supraanal opening small; gills broad, with simple septa; innermost lamella largely fused with the visceral sack; embryos in the outer laminae.

Section *Physunio* s. s. Shell in most cases inflated. *P. (P.) gravidus* (Lea). A few species in Indochina and on the Sunda Islands.—Section *Velunio* Haas, 1920. Shell flat, very high. *P. (V.) velaris* (Sowerby), in Assam.

Prohyriopsis Haas, 1914

Shell elongated oval, thin, compressed, anteriorly very short, posteriorly elongated and beaked; umbo scarcely projecting, without

distinct sculpture; posterior to edge of the area with small longitudinal folds; right anterior tooth lamella-shaped; a similar anterior tooth in the left valve and below the umbo a higher, leaf-shaped tooth; lamellae long and straight. Animal unknown.

824

P. *stolata* (Martens), in Danau Baru Lake on Sumatra.

Hyriopsis Conrad, 1853

Shell large, compressed, posteriorly obliquely truncated and with a dorsal wing, sometimes also with a small wing at the anterior end; umbones low, with small concentric folds; left valve with 2 to 3, right with 1–3 anterior hinge teeth, which are compressed in young shells, in older shells frequently divided into irregular denticles; lamellae long, 2 left, 1 right. Animal unknown.

H. *delphinus* (Gruner). A few species in Indochina and China, one each in Borneo and Japan.

Prisodontopsis Tomlin, 1928

Synonym *Pseudavicula* Simpson, 1900, non Jack & Etheridge, 1892.

Shell similar to that in *Hyriopsis*, with a broad posterior and a small, pointed anterior wing; left valve with an elongated anterior tooth and 2 lamellae, right one with 2 teeth and one long, thin lamella. Animal unknown.

P. *johnstoni* (E. Smith) in Lake Meru (Africa).

Chamberlainia Simpson, 1900

Synonym *Simpsonia* Rochebrune, 1905.

Shell very large and thick, roundish, in the young with a posterior wing; anterior hinge teeth fairly small, blunt, 1 right, 2 left; lamellae short, separated from the teeth, 1 right, 2 left, the lower one larger. Animal unknown.

C. *hainesiana* (Lea). Few species in Siam.

Scabies Haas, 1911

Shell fairly solid-walled, moderately large, elongated elliptical, anteriorly rounded, posteriorly long and pointed; umbo with radiating ridges or rows of tubercles, the median of which continue V-shaped over most of the shell; anterior to the main tooth of the right valve there is a weak lamella-shaped accessory tooth and below the lamella there is an accessory lamella. Animal unknown.

S. *scobinata* (Lea). Few species in Indochina.

Arcidopsis Simpson, 1900

Shell fairly thick, longish, obliquely sloping anterior to the umbones, posteriorly elongated and obliquely truncated; surface radially striated; umbo only slightly projecting, somewhat inflated with fine radial wrinkles; right valve with an anterior and a posterior accessory tooth and one lamella, on the left with 2 teeth and 2 lamellae; the teeth are striated. Animal unknown.

A. footei (Theobald), in India.

Ptychorhynchus Simpson, 1900

Shell fairly long, anteriorly rounded, posteriorly pointed, strong; umbones low, in the posterior part with radiating wrinkled folds; left valve with 2 fairly blunt, rough anterior teeth and 1 or 2 lamellae; the right one with a blunt tooth and an irregular, sometimes cleft lamella. Animal unknown.

P. pfisteri (Heude). A few species in China.

825

Oxynaia Haas, 1913

Shell solid-walled, anteriorly short and roundish, posteriorly more or less elongated and pointed; umbones distinctly elevated, with concentric zig-zag lines; main tooth of the right valve rectangular, deeply furrowed; accessory tooth very small, lamella-shaped; anterior main tooth of the left valve narrowly rectangular, sharp and deeply furrowed above; posterior main tooth pyramidal, often thicker than the anterior one; lamellae long, those of the right valve often with a thin accessory lamella. Animal unknown.

O. jourdyi (Morlet). A few Indochinese species.

Unio Retzius, 1788

Synonyms *Lymnium* Oken, 1815; *Mysca* Turton, 1822; *Canthyria* Swainson, 1840; *Nodularia* Conrad, 1853.

Shell oval or more elongated, not inclined; umbones in most cases not very close to the anterior end and somewhat projecting, with zig-zag ridges or 2 rows of tubercles, which are in most cases not continued further; right valve with a moderately strong anterior tooth and one lamella, the left one with 2 teeth and 2 lamellae. Supraanal and anal mantle openings separated; innermost gill lamella fused only anteriorly; septa of the outer gill lamina, which contains the embryos, more dense than in the inner lamina; glochidia in most cases with pointed, externally spinulose hooks.

A few species in Asia, Europe, and Africa.

Prashad, 1919, erected the subgenus *Eolymnium* for *U. terminalis* Bourguignat living in Jordan; the shell has a very short anterior part, similar to that in *Psilunio*; the foot is weak; the outer gill lamina, which contains the embryos, is considerably narrower than the inner; glochidia not known.

Subgenus *Cafferia* Simpson, 1900. Hinge teeth fairly strong; glochidia triangular, but without hooks. *U. (C.) caffer* Krauss. A few South African species.

Lanceolaria Conrad, 1853

Shell solid-walled, greatly elongated, sword-shaped; anterior part short, the posterior pointed; umbones low, with radial rows of small tubercles, which seldom continue further downward; anterior hinge teeth plump, deeply furrowed above, smooth below; accessory teeth may be present anterior and posterior to them; lamellae long and thick. Animal unknown.

A few species in eastern Asia (Indochina to Japan).

Section *Lanceolaria* s. s. Shell laterally compressed. *L. (L.) grayana* (Lea).—Section *Pericylindrica* Tomlin, 1930 (synonym *Cylindrica* Simpson, 1900, non Clessin, 1882). Shell nearly cylindrical, anteriorly very short, posteriorly very long. *L. (P.) cylindrica* (Simpson).

Cuneopsis Simpson, 1900

Shell strong, anteriorly rounded, posteriorly more or less elongated and pointed; umbones situated fairly far forward, distinctly elevated, with few strong, nearly parallel, often tuberculate bulges; left valve below the umbo with 2 main teeth separated by a deep triangular pit; the right one with a strong triangular main tooth and often a small, low tooth posterior to the pit; lamellae granulose striated. Animal unknown.

C. celtiformis (Heude). Few species in China and one in Tonkin.

Arconaia Conrad, 1865

Shell strong, greatly elongated, twisted around the longitudinal axis and in most cases with posterior part curved to the right or left, posteriorly in most cases pointed and also beaked anteriorly; umbones low, situated far forward; right valve with an accessory tooth, which is separated from the cleft main tooth by a rectangular pit, and with a weak accessory lamella; left valve with 2 teeth and 2 strong lamellae.

A. contorta (Lea), in China.

Gonidea Conrad, 1857

Shell fairly strong, inflated, elongated triangular, posteriorly much higher than anteriorly, in most cases with a distinct edge to the lower corner; umbones fairly sharp, but not high, with a few strong concentric wrinkles; hinge with a rudimentary tooth and a lamella in each valve. The 4 gill laminae contain embryos; the septa are often interrupted, mainly at the upper and lower margins, and shorter septa may be interposed between them; glochidia roundish, without hooks.

G. angulata (Lea), in the western United States of North America.

Fusconaia Simpson, 1900

Synonym ? *Syntoxia* Rafinesque, 1820 (*Sintoxia*).

Shell short elliptical, roundish, rhomboid-shaped or triangular, with elevated umbones, which have few parallel wrinkles; the remaining surface smooth; hinge teeth strong. Bridge between anal and supraanal openings very short, often absent; all gill laminae are marsupial, with nearly cylindrical egg sacks; glochidia small, oval, without hooks.

F. trigona (Lea). A few species in the United States.

Quincuncina Ortmann, 1922

Shell medium-sized, anteriorly rounded, posteriorly obliquely truncated; umbones only slightly projecting, with nearly concentric ridges, which farther on become zig-zag-shaped and merge into alternately placed tubercles; both valves with 2 cardinal teeth, the posterior of which is larger; left valve with 2 lamellae, the right with one which however is sometimes cleft. The 4 gill laminae are marsupial; the egg sacks scarcely compressed; innermost lamella attached only at the anterior end.

Q. burkei Walker, in the United States.

Quadrula Rafinesque, 1820

Shell longish, quadratic or rounded or triangular, strong, inflated; posterior edge in most cases distinct; umbones projecting, in most cases with few irregular, parallel ridges; the remaining surface smooth or sculptured; hinge margin broad; main teeth strong, furrowed; one lamella in the right valve, 2 in the left. Bridge between the anal and supraanal openings short, sometimes absent; innermost gill lamella free; all 4 laminae contain embryos; the egg sacks compressed; glochidia somewhat oval, without hooks.

A few species in the United States.

According to Herrmannsen, the typical species is *Q. quadrula* (Rafinesque), and of *Theliderma* Swainson, 1840: *metaneura* (Rafinesque); the latter is considered as a section. *Amphinaias* Crosse & P. Fischer, 1894 [*couchiana* (Lea)] may also represent a section.

827   Frierson, 1927, recognized the following as subgroups of *Quadrula*: *Quadrula* s. s. for *quadrula* Rafinesque; *Tritogonia* L. Agassiz, 1852, for *verrucosa* (Rafinesque); *Pustulosa* (= *Bullata* non Jousseaume, 1875) for *pustulosa* (Lea); *Quincuncina* Ortmann, 1922, for *burkei* Walker; *Luteacarnea* (= *Striata* non O. Boettger, 1878) for *striata* (Rafinesque); *Orthonymus* L. Agassiz, 1852, for *cylindrica* (Say); *Cyclonaias* Pilsbry, 1922, for *tuberculata* (Rafinesque); *Obliquata* for *obliquata* (Rafinesque); *Fusconia* (err. pro *Fusconaia* Simpson, 1900) for *undata* (Barnes); and *Pleuronaia* for *barnesiana* (Lea).

Amblema Rafinesque, 1819

Synonyms *Bariosta* Rafinesque, 1831; *Crenodonta* Schlüter, 1838.

Shell large, roundly oval, with far forwardly situated umbones, which are sculptured with concentric wrinkles; posterior part of the shell in most cases with broad radial folds. Bridge between the anal and supraanal openings very short or absent; innermost gill lamella free; all 4 gills marsupial; egg sacks compressed; water tubes of the inner laminae somewhat wider than those of the outer laminae; glochidia small, oval, without hooks.

A few species in the United States and Mexico.

Section *Amblema* s. s. Umbonal sculpture not extending over the surface. *A. (A.) costata* Rainfesque.—Section *Megalonaias* Utterback, 1915. The zig-zag-shaped umbonal sculpture extends over the surface in the form of tuberculate folds. *A. (M.) heros* (Say).—Section *Psorula* Haas, 1930. Umbones projecting, with many densely placed, wavy, concentric wrinkles, which merge into the warty or granulose scaly sculpture of the external surface, which also in most cases shows strongly bulging growth lines. *A. (P.) rudis* (Simpson). In addition, Frierson mentions *Plectomerus* Conrad, 1853, for *A. dombeyana* (Valenciennes).

Walker recognizes *Cokeria* Marshall, 1916 (*southalli* Marshall), as an abnormal shell of *Amblema costata*.

Tritogonia L. Agassiz, 1852

? Synonym *Ellipsaria* Rafinesque, 1820.

Shell strong, in the female distinctly longer than in the male, with a posterior obliquely descending bulge, warty anterior to it; umbones

fairly low, with strong, irregular, nearly parallel bulges and with fine radial ridges anterior and posterior to these; hinge teeth strong, furrowed; lamellae long and straight. Supraanal opening long; in the female the mantle forms a thickened lobe in the posterior part, at the inner side of which hangs a smaller lobe; inner gill laminae much broader than the outer ones; innermost lamella largely free; all 4 laminae marsupial.

T. tuberculata (Barnes), in the United States.

Rotundaria Rafinesque, 1820

Shell roundish; umbones projecting, with numerous fine, irregular, discontinuous roughenings, the posterior 3 fifths of the surface warty; nacre purple-colored. Supraanal opening not separated from the anal opening; gill laminae broad; innermost lamella free; the outer lamina has much more densely-spaced septa than the inner lamina and alone contains embryos.

828 According to Herrmannsen, *Obliquaria subrotunda* Rafinesque is to be considered as the typical species, whereas Simpson considers *O. tuberculata* Rafinesque as such.

A few species in Central and North America.

Psoronaias Crosse & P. Fischer, 1893

Shell fairly variable, in most cases somewhat triangular, with projecting umbones; surface with small warts and sometimes posteriorly with a few folds; anterior hinge teeth of the right valve unequal, the upper one weak, compressed, the lower one thick and grooved. Animal?

P. psoricus (Morelet). A few species in Central America.

Plethobasus Simpson, 1900

Shell large and strong, irregularly oval, inflated. Umbones fairly high, with a few strong folds; outer surface with a row of broad and flat warts; main teeth triangular, rough. Supraanal opening separated from the anal opening by a very narrow bridge; only the outer gill laminae, which have much more densely-spaced septa, are marsupial.

P. aesopus (Green), in the United States.

Pleurobema Rafinesque, 1820

Synonyms ? *Scalenaria* + *Aximedia* Rafinesque, 1820.

Shell strong, triangular or rhomboid, in most cases with projecting umbones which are situated more or less far forward, and are sculptured

with few, often interrupted folds; a rounded posterior edge is present; hinge teeth double in both valves. Supraanal opening separated from anal opening by a fairly narrow bridge; outer gills marsupial.

P. mytiloides Rafinesque (= *Unio clava* Lamarck). Several species in the United States.

Lexingtonia Ortmann, 1914

Shell rounded quadrangular; umbo only slightly elevated, situated almost in the center, with fairly densely placed, parallel wrinkles which form an indistinct angle at the posterior edge and are somewhat wavy anterior to it; lateral surfaces smooth; hinge teeth well developed. The outer gill laminae have cylindrical, red egg sacks; supraanal opening distinctly separated from the anal opening; glochidia without hooks.

L. subplana (Conrad), in the United States.

Elliptio Rafinesque, 1819

Synonyms *Eurynia* Rafinesque, 1820; *Eurynaia* Frierson, 1927; *Cunicula* Swainson, 1840.

Shell more or less elongated, oval to rhomboid-shaped; umbo with few, fairly strong, parallel wrinkles; lateral surfaces smooth. Supraanal opening separated from the anal opening; innermost gill lamella free; the outer lamina marsupial; glochidia small, without hooks.

Several species in North and Central America.

Section *Elliptio* s. s. Shell only slightly elongated; posterior edge smooth. *E.* (*E.*) *crassidens* (Lamarcq[1]).—Section *Micronaias* Simpson, 1900. Shell small, distinctly concentrically striated. *E.* (*M.*) *arata* (Lea). —Section *Canthyria* Swainson, 1840. Shell with a row of spines on the posterior edge; hinge teeth fairly compressed; lamellae short. *E.* (*C.*) *spinosa* (Lea).—Section *Uniomerus* Conrad, 1853. Shell distinctly elongated; umbo scarcely projecting; hinge teeth in most cases compressed. *E.* (*U.*) *tetralasma* (Say).—Section *Nephronaias* Crosse & P. Fischer, 1893 (synonyms *Leptonaias* + *Simonaias* + *Caenonaias* + *Graphonaias* Crosse & P. Fischer, 1893). Shell elongate oval to kidney-shaped; hinge teeth short and strong. *E.* (*N.*) *plicatula* (Charpentier).—Section *Popenaias* Frierson, 1927. Shell long, anteriorly low; hinge teeth compressed, sharp. *E.* (*P.*) *popei* (Lea).—Section *Barynaias* Crosse & P. Fischer, 1893 (synonym *Sphenonaias* Crosse & P. Fischer, 1893). Shell strong, somewhat

829

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[1] This is a typographical error in the original; read Lamarck. —Editors.

trapeze-shaped; anterior hinge teeth thick. *E.* (*B.*) *pigerrima* (Crosse & P. Fischer).

Because Herrmannsen designated *Unio dilatatus* Rafinesque, which is = *Elliptio gibbosa* (Barnes) as the genotype of *Eurynia*, *Eurynia* has to be considered as a synonym of *Elliptio*. *Elliptoideus* Frierson, 1927 [*sloatianus* (Lea)], named as a subgenus of *Elliptio*, has eggs in all 4 gill laminae.

In addition, Frierson, 1927, has proposed the following groups: *Reticulatus* for *E. reticulata* (Simpson) with net-shaped sculptured surface, *Martensnaias* for *E. rubicunda* (Martens) with coarse concentric striae and strong hinge teeth, and *Nephritica* for *E. poeyana* (Lea).

Hemistena Rafinesque, 1820

Synonyms *Odatelia* Rafinesque, 1832; *Hemilastena* L. Agassiz, 1852; ? *Sayunio* Gregorio, 1914.

Shell fairly strong, considerably elongated, anteriorly rounded, posteriorly pointed; umbo low, with few irregular longitudinal folds; sides smooth; one rudimentary hinge tooth in each valve; lamellae scarcely indicated. Foot very large; only the median part of outer gill marsupial; glochidia half-circle-shaped, with unequal sides, without hooks.

H. lata (Rafinesque), in the United States.

B. Subfamily Anodontinae

Shell often thin, more or less elongated; umbonal sculpture concentric or biseriate; hinge teeth in most cases incomplete or absent. Supraanal opening of the mantle in most cases separated from the anal opening by a broad bridge; outer gill laminae marsupial, in gravid females with tripartite water tubes, of which only the middlemost serves as an egg sack; glochidia half-circle-shaped or triangular, with hooks on the ventral side; during winter they remain within the maternal gills.

Frierson distinguishes the subfamily Alasmidontinae from the Anodontinae.

Arkansia Ortmann & B. Walker, 1912

Shell moderately thick, inflated, only slightly elongated; umbo elevated, with 2 or 3 double rows of ridges which are not continuous with the sculpture of the lateral surfaces; hinge well developed, with strong main teeth and fairly short lamellae.

A. wheeleri Ortmann & Walker, in the United States.

Arcidens Simpson, 1900

Shell similarly formed to that in *Arkansia*; umbo with very strong, irregular wrinkles in 2 rows, with warts which continue onto the lateral surfaces; anterior and posterior to the umbones with fine small radial folds; left valve with 2 compressed, elongated main teeth, the posterior of which lying below the umbo is upwardly curved and bisects the right hinge margin, which has a compressed tooth; lamellae numerous, short, irregular.

830

A. confragosus (Say), in the United States.

Alasmodonta Say, 1818 (*Alasmidonta*)

Synonyms *Monodonta* Say, 1816 (non Lamarck, 1801); ? *Anadontina* Schlüter, 1838; *Uniopsis* Swainson, 1840; *Anelasmodonta* Herrmannsen, 1846.

Shell inflated, in most cases rhomboidal, usually with a distinct posterior edge to the lower corner; umbo elevated, with concentric or somewhat biseriate sculpture; left valve with 2, right with one main tooth; lamellae in most cases incomplete or absent.

A few species in the United States.

Section *Prolasmidonta* Ortmann, 1914. Umbonal sculpture moderately strong; ridges with an angle on the posterior edge; hinge lamellae present, 2 in the right, one in the left valve. *A. (P.) heterodon* (Lea). —Section *Alasmodonta* s. s. Shell strong, inflated, moderately elongated, with very strong, in most cases concentric umbonal sculpture; main teeth strong, blunt; lamellae short, very incomplete or absent. *A. (A.) undulata* (Say).—Section *Bullella* Simpson, 1900. Shell thin, greatly inflated, somewhat triangular, with sharp edge; umbo strongly projecting, with very strong concentric sculpture; main teeth compressed and recurved. *A. (B.) arcula* (Lea).—Section *Decurambis* Rafinesque, 1831 (synonym *Rugifera* Simpson, 1900). Shell elongated, inflated, posterior to the edge with radiating wrinkles; teeth very incomplete; lamellae absent. *A. (D.) atropurpurea* Rafinesque.—Section *Pressodonta* Simpson, 1900 (synonym *Calceola* Swainson, 1840, non Lamarck, 1801). Shell small, elongated; umbo with weak wrinkles; teeth compressed. *A. (P.) calceolus* (Lea). —Section *Pegias* Simpson, 1900. Shell small, with 2 posterior bulges; umbo with somewhat cone-shaped wrinkles; hinge teeth fairly strong; lamellae absent. *A. (P.) fabula* (Lea).

Lasmigona Rafinesque, 1831

Shell compressed; umbo low, with strong ridges; right valve with one, the left with 2 hinge teeth, the posterior of which bisects the right hinge margin; lamellae in most cases incomplete.

A few species in the United States.

Section *Platynaias* Walker, 1917. Shell moderately strong, smooth, longish; umbonal sculpture sharply biseriate; hinge teeth weak; lamellae compressed. *L. (P.) compressa* (Lea).—Section *Lasmigona* s. s. Shell with posterior folds; umbo with several coarse wrinkles, in most cases somewhat biseriate and often with radial wrinkles in front and behind; hinge lamellae consisting of irregular oblique ridges. *L. (L.) costata* (Rafinesque).—Section *Sulcularia* Rafinesque, 1831 (synonym *Alasminota* Ortmann, 1914). Shell fairly small, distinctly elongated, smooth; umbo with 4 or 5 fairly fine, sharp ridges, the median of which are sharply biseriate; hinge teeth weak; lamellae scarcely developed. *L. (S.) badium* (Rafinesque) = *holstonia* (Lea).—Section *Pterosyna* Rafinesque, 1831 (synonyms *Complanaria* Swainson, 1840; ? *Megadomus* Swainson, 1840). Shell large, high and inflated in the posterior part; umbo greatly compressed, with sharp biseriate sculpture; hinge teeth strong. *L. (P.) complanata* (Barnes).

Simpsoniconcha Frierson, 1914

Synonym *Simpsonaias* Frierson, 1914.

Shell small, elongated oval; umbo fairly sharp, but only slightly elevated, with fine parallel ridges which are upwardly curved in the center; an irregular compressed tooth in each valve; lamellae scarcely developed.

S. ambigua (Say), in the United States.

Anodontoides Simpson, 1898

Shell thin, inflated, longish, with weak posterior edge; umbo bulging, with few concentric, abruptly upwardly arched wrinkles, posterior to which are fine radial wrinkles; lateral surfaces smooth; hinge teeth scarcely indicated.

A. ferussaciana (Lea), in the United States.

Lepidodesma Simpson, 1896

Shell large, thin, inflated, with 2 posterior edges; umbo greatly elevated, with concentric folds, which continue over the entire shell, in

addition 2 rows of tubercles are developed; ligament very strong; left valve with 2 main teeth, the anterior of which is elongated, internally crossing the hinge margin and terminating abruptly, whereas the posterior one is shorter and narrower, and with 2 strong lamellae; right valve with a low anterior tooth, and an upwardly curved lamella. Animal unknown.

L. languilati (Heude). 2 species in China.

Cristaria Schumacher, 1817

Synonyms *Barbala* Mus. Calonn., 1797, *Dipsas* Leach, 1814, non Laurenti, 1768; *Appius* (Leach) Menke, 1830; *Dianisotis* Rafinesque, 1831; *Cleone* Gistel, 1848.

Shell in most cases thin, moderately elongated, sometimes with a wing-shaped process; umbo low, initially with biseriate wrinkles, thereafter with flat concentric ridges; lateral surfaces smooth; hinge teeth rudimentary—on either side with a compressed tooth—or absent; lamellae simple, often absent in adult shells.

A few species in eastern Asia.

Section *Crassitesta* Simpson, 1900. Shell fairly small and strong, without wings; umbo somewhat projecting; hinge teeth and lamellae very weak. *C. (C.) radiata* Simpson.—Section *Pletholophus* Simpson, 1900. Shell medium-sized, anteriorly scarcely thickened; umbo compressed, with flat concentric wrinkles, scarcely winged; hinge teeth very weak. *C. (P.) discoidea* (Lea).—Section *Cristaria* s. s. Shell large, anteriorly thickened, posteriorly winged, in the posterior part with weak radial bulges and a row of folds. *C. (C.) plicata* (Leach).

Leguminaia Conrad, 1865

Shell longish, with 2 weak posterior bulges; umbo situated more or less far forward, with fine concentric, somewhat biseriate wrinkles; sides fairly smooth, in each valve with one smooth tooth, the left one below the umbo, the right one anterior to it. Animal insufficiently known.

Section *Leguminaia* s. s. Shell fairly strong; umbo projecting; teeth strong, sometimes with an accessory tooth in the left valve. *L. (L.) mardinensis* (Lea). Few species in the Near East and Tripoli.—Section *Pseudoleguminaia* Germain, 1911. Shell fairly thin, somewhat inflated, elliptical; umbo close to the center, with irregular wrinkles; teeth very blunt, fairly high and thick. *L. (P.) chantrei* (Locard) = *locardi* Simpson, in Syria.—Section *Microcondylaea* Vest, 1866. Shell compressed, fairly thin, with low umbones; teeth rudimentary, greatly compressed. *L. (M.) uniopsis* (Lamarck), in the Po region and Illyria.

832

Anodonta Lamarck, 1799

Shell thin, inflated, more or less elongated, often posteriorly angulate; umbo with several parallel, often somewhat biseriate wrinkles; lateral surfaces in most cases smooth; hinge margin weak, toothless.

Several species in North and Central America, in Asia, and Europe.

A few subgroups, which were proposed by various zoologists, seem to have little justification. Simpson considers *Colletopterum* Bourguignat, 1881 (*letourneuxi* Bourguignat) in the Danube, identical with *Anodonta* s. s.; Pallary, 1933, erected a section *Euphrata* for *A. bahlikiana*, and Bédé, 1932, a group *Liouvillea* for the Moroccan *A. pallaryi*. *Gabillotia* Servain, 1890 [*pseudodopsis* (Locard)], in Syria to Asia Minor, and *Pteranodon* P. Fischer, 1886 [*magnifica* (Lea) = *woodiana* (Lea)], in China, may perhaps have the rank of section, but the latter must perhaps be called *Patularia* Swainson, 1840; *Haasiella* Lindholm, 1925 (*arcaeformis* Heude, in China) is said to differ by the hook-less glochidia. A few groups have been erected for American species, such as *Brachyanodon* Crosse & P. Fischer, 1893, for *chapalensis* Crosse & P. Fischer, *Mesanodon* Crosse & P. Fischer for *lurulenta* Morelet, and *Pyganodon* Crosse & P. Fischer, 1893, for *globosa* Lea; *Arnoldina* Hannibal, 1912 (*dejecta* Lewis), has non-elevated umbones with tubercles and few biseriate wrinkles, alternating with punctures on the posterior bulge and *Nayadina* Gregorio, 1914 (*venusta* Gregorio), has a small process on the posterior part of the hinge margin in the left (only known) valve. *Lastena* Rafinesque, 1820 (*ohiensis* Rafinesque) = *Utterbackia* F.C. Baker, 1927, is said to be hermaphroditic; *Utterbackiana* Frierson, 1927 (*orbiculata* Say), is said to be non-hermaphroditic. *Pseudanodonta* Bourguignat, 1877, considered as a genus by Haas, has not been recognized even as a section by Ortmann.

Strophitus Rafinesque, 1820

Synonym *Hemiodon* = *Hemidonta* Swainson, 1840.

Shell fairly strong, inflated, posteriorly with 1 or 2 corners and a flat edge; umbo elevated, with few strong, posteriorly sharply upcurved concentric wrinkles; in each valve with a rudimentary compressed tooth and sometimes an accessory tooth; lamellae seldom present. The marsupium, which occupies the entire outer gills, consists of short, horizontal, transversely oriented egg pouches.

S. undulatus (Say). Few species in the United States.

Frierson recognizes *Jugosus* Simpson (*wrightianus* Walker) and *Pseudodontideus* Frierson, 1927 [*alabamensis* (Lea)], as subgroups.

? Solenaia Conrad, 1868

Shell fairly thin, greatly elongated, anterior part shorter and lower than the posterior, an edge runs to the posterior corner; both ends gaping; umbo low, with concentric, indistinctly biseriate wrinkles; hinge with indications of one or more lamellae; mantle line with a posterior sinus. Foot very strong; all gills with egg sacks.

S. emarginata (Lea). Few species in China and Indochina.

833

C. Subfamily Lampsilinae

Shell roundish or longish; umbonal sculpture in most cases biseriate, often indistinct, seldom concentric; hinge teeth as a rule well developed, occasionally the sexes are different. Supraanal mantle opening separate, seldom completely closed; mantle margin anterior to the gill opening smooth or folded or with peculiar papillae or a lobe; marsupium in most cases formed of the posterior part of the outer gill lamina, which is usually folded during the gravid state; water tubes simple; glochidia without hooks or with 2 thorns. Frierson placed the first 4 genera in the Unioninae.

In North and Central America.

Ptychobranchus Simpson, 1900

Shell strong, longish triangular; umbo elevated, with weak, somewhat biseriate wrinkles; posterior edge rounded; hinge margin fairly broad; anterior teeth small, low, triangular, rough; lamellae club-shaped. Supraanal opening long, separated from the anal opening by a narrow bridge; marsupium formed by greater part of the outer gill lamina, with 6–20 folds; egg sacks continuing below into a roundish swelling, which has a colored patch in the center.

P. phaseolus (Hildreth) [= *fasciolaris* (Rafinesque) ?]. Few species in the United States.

Frierson, 1927, proposed a group *Subtentus* for *P. subtentus* (Say).

Obliquaria Rafinesque, 1820

Shell especially anteriorly strong, inflated, only slightly elongated, with a bulge at the posterior corner and a straight descending row of large warts alternating on the two valves; umbo projecting, with 4 or 5 coarse wrinkles, which are posteriorly upwardly curved; anterior teeth strong; lamellae short. Marsupium consisting of 4–7 distinctly different

egg sacks, which lie somewhat behind the center of the outer gill lamina, and are elongated; their ends are rounded.

O. reflexa Rafinesque, in the United States.

Conchodromus Haas, 1930

Synonym *Dromus* Simpson, 1900, non Selby, 1840.

Shell especially strong anteriorly, rounded triangular; umbo fairly high, with fine concentric wrinkles, a row of tubercles runs down over the center of the sides; hinge margin broad and flat; main teeth triangular, small and low; lamellae short, club-shaped. The marsupium occupies the greater part of the outer gill lamina and forms numerous narrow, elongated egg sacks.

C. dromas (Lea), in the United States.

Cyprogenia L. Agassiz, 1852

Shell strong, inflated, rounded triangular; umbo elevated, with very weak, somewhat biseriate wrinkles; lateral surfaces tuberculate; hinge margin broad and flat; main teeth strong, blunt, triangular; lamellae short, transversely striated. The marsupiums formed of 7–23 very long, red egg tubes, which are together spirally inrolled; supraanal opening long, separated from the anal opening by a narrow bridge.

C. irrorata (Lea) [= *stegaria* (Rafinesque) ?] in the United States.

834   ### *Plagiolopsis* nom. nov.

Shell strong, longish triangular, posteriorly more inflated in the female, with posterior edge, concentrically striated; umbo high, with fine parallel, somewhat biseriate wrinkles; hinge teeth rough; lamellae club-shaped. The marsupium is formed of a part of the posterior half of outer gill lamina, and consists of distinctly different, ventrally rounded egg sacks.

P. securis (Lea), in the United States.

Whereas Herrmannsen, 1847, named *Unio interruptus* Rafinesque as the genotype of *Plagiola*, Simpson accepted *U. lineolata* Say = *securis* Lea as such. On the other hand, according to Herrmannsen, the genotype of *Truncilla* is *U. truncatus* Rafinesque, a species considered synonymous with *U. elegans* Lea and placed by Simpson and Ortmann in *Amygdalonaias*, while Agassiz also considers it as a *Plagiola* species. Therefore, these generic names have to be changed, but unfortunately, opinions vary with respect to *Unio interruptus*; otherwise considered

identical with *U. brevidens* Lea, Frierson considers it synonymous with *U. menkianus* Lea, which according to him belongs to *Lampsilis*; if this is correct, then would *Plagiola* = *Lampsilis*.

Truncilla Rafinesque, 1820

Synonym *Amygdalonaias* Crosse & P. Fischer, 1893.
Shell inflated, posteriorly obliquely truncate, with distinct edge to the posterior corner; umbo somewhat projecting, with fine, somewhat biseriate sculpture; hinge margin narrow; main teeth fairly compressed, high and rough. Marsupium consisting of numerous egg sacks, with a distinct furrow some distance above their base.
T. truncata Rafinesque. A couple of species in Mexico and the United States.

Medionidus Simpson, 1900

Shell fairly inflated, longish, wrinkled in the upper and sometimes the posterior part; umbo only slightly projecting, with fairly fine, often interrupted, biseriate wrinkles; anterior hinge teeth small, blunt, somewhat rough; lamellae fairly short; females posteriorly somewhat swollen. The marsupium occupies a more or less large part of the outer gill lamina and consists of fairly large, irregular egg sacks which are rounded at the ends.
M. conradicus (Lea). A few species in the United States.

Glebula Conrad, 1853

Shell strong, short, posteriorly obliquely truncated, with a low posterior edge, posteriorly more inflated in the female than in the male; umbo compressed; anterior hinge teeth divided into several irregular parts, forming a granulose lamella; hinge margin very weak; lamellae short; egg sacks distinctly separated from one another by a furrow.
G. rotundata (Lamarck), in the United States.

Proptera Rafinesque, 1819

Synonyms *Metaptera* Rafinesque, 1820; *Symphynota* Lea, 1829; *Naidea* Swainson, 1840.
Shell in most cases large, differently formed in the two sexes, anteriorly somewhat gaping, with a dorsal wing; umbo with weak sculpture, with a posterior and sometimes also an anterior row; hinge teeth often rudimentary. The marsupium consists of several egg sacks which occupy the posterior part of the outer gill lamina; supraanal

opening long; posterior part of the lower mantle margin somewhat folded in the female; glochidia on either side with 2 thorns on the ventral margin.

P. alata (Say), in the United States.

Leptodea Rafinesque, 1820

Synonyms *Lasmonos* Rafinesque, 1831; *Paraptera* Ortmann, 1911.

Shell large and thin, more or less compressed, dorsally winged; umbo low; hinge teeth compressed, weak and often incomplete; sexes scarcely differing. Mantle and marsupium similar to those in *Proptera*. Glochidia very small, oval.

L. fragilis Rafinesque, in the United States.

Obovaria Rafinesque, 1819

Shell strong, roundish to oval, inflated, anteriorly thickened, differently formed in the two sexes; umbo high, with fine, irregular, somewhat tuberculate wrinkles; anterior hinge teeth strong, blunt; lamellae short, club-shaped. Marsupium consisting of several elongated egg sacks in the posterior part of the outer gill lamina; supraanal opening fairly long, separated from the anal opening by a very short bridge.

Few species, in the United States.

Subgenus *Obovaria* s. s. Shell roundish, with high umbones situated in the center *O. (O.) retusa* (Lamarck).

Subgenus *Pseudoon* Simpson, 1900. Shell oval; umbo close to the anterior end; marsupium situated somewhat farther forward. *O. (P.) ellipsis* (Lea).

Actinonaias Crosse & P. Fischer, 1893

Shell longish, fairly compressed; umbo closer to the anterior end, with few weak wrinkles; sexes only slightly different. Marsupium formed of several, somewhat elongated egg sacks in the posterior part of the outer gill lamina.

A. sapotalensis (Lea). A few species, in Mexico and the United States.

Graphonaias Crosse & P. Fischer, 1893 [*medellina* (Lea)], is probably not separable.

Toxelasma Rafinesque, 1831 (*Toxolasma*)

Synonym *Carunculina* Simpson, 1898.

Shell small, fairly strong, inflated, longish; umbo situated anterior to the center, with fairly strong concentric wrinkles which are strongly upwardly curved posteriorly; anterior hinge teeth compressed, in most cases upwardly curved; sexes somewhat different. Marsupium consisting of few fairly large, somewhat elongated egg sacks; the mantle in the female has a lobe anterior to the incurrent opening.

T. lividum (Rafinesque). A few species, in the United States.

Ligumia Swainson, 1840

Shell more or less elongated, smooth; umbonal sculpture fine, biseriate; the posterior part of the shell in the female somewhat widened or swollen. Marsupium occupying the posterior part of the outer gill lamina; posterior half of the ventral mantle margin in the female with distinct papillae; supraanal opening fairly long.

A few species in the United States.

Subgenus *Ligumia* s. s. Shell long, posteriorly more or less pointed; papillae at the mantle margin identical, extending to the center. *L.* (*L.*) *recta* (Lamarck).

Subgenus *Micromya* L. Agassiz, 1852. Shell oval, posteriorly only slightly pointed; mantle papillae dissimilar, not extending to the center of the margin *L.* (*M.*) *fabalis* (Lea).

Friersonia Ortmann, 1912

Shell fairly small, longish; umbonal sculpture biseriate, with 6–8 fine wrinkles; sides smooth; sexes scarcely different. The marsupium occupies the greater part of the outer gill lamina; it consists of numerous elongated egg sacks with their ends posteriorly curved; the margin is sharp; posterior part of the ventral mantle margin finely folded.

P. iridella (Pilsbry & Frierson), in Mexico.

Lampsilis Rafinesque, 1820

Synonym *Aeglia* Swainson, 1840.

Shell more or less longish, smooth or concentrically striated; umbo close to the center, with parallel wrinkles; right valve with 1 or 2 anterior teeth and a lamella, the left one with 2 teeth and 2 lamellae; the shell is posteriorly distinctly truncated in the female. The marsupium occupies the posterior part of the outer gill lamina and consists of numerous egg sacks; in the female the posterior part of the ventral mantle margin forms a rib-shaped lobe (Fig. 808).
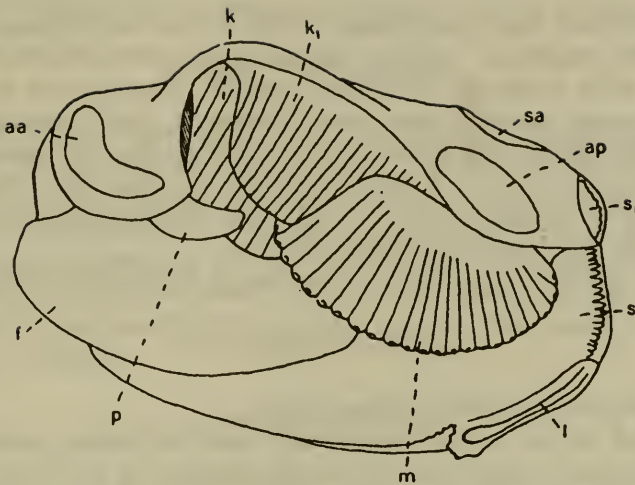
836

Fig. 808. Female of *Lampsilis ovata* (Say).
aa, ap, anterior and posterior adductor muscle; f, foot; k, k₁, inner and outer gill lamina; l, posterior ventral lobe of the mantle margin; m, marsupium; p, oral lobes; s, s₁, incurrent and excurrent opening; sa, supraanal opening of the mantle (after Ortmann).

L. ovata (Say). Several species, in Central America and the United States.

The following groups proposed by Crosse & P. Fischer, 1893, are considered as sections: *Cyrtonaias* for *Unio berlandieri* Lea (shell thick, oval or somewhat quadrangular, smooth or concentrically striated; umbo inflated in most cases), *Mesonaias* for *U. explicatus* Morelet (shell elongated oval, smooth or concentrically striated; umbo only slightly elevated; anterior hinge teeth oblique, compressed), *Disconaias* for *U. discus* Lea (shell large, oval or somewhat triangular, greatly flattened, concentrically striated; anterior hinge teeth strong), *Phyllonaias* for *U. paludosus* Morelet (shell flattened, posteriorly with a weak dorsal wing; anterior hinge teeth in most cases compressed), and *Delphinonaias* for *U. delphinulus* Morelet (shell greatly flattened, posterior to the umbones with a large wing; hinge teeth compressed). Moreover, Frierson, 1927, named *Ortmanniana* for *L. carinata* (Barnes), *Villosa* for *L. villosa* (Wright), *Venustaconcha* (= *Venusta* Frierson non O. Boettger, 1877) for *L. venusta* (Lea).

837

Pachynaias Crosse & P. Fischer, 1893

Synonyms *Arotonaias* Martens, 1900; *Ptychoderma* Simpson, 1900.

Shell rounded or triangular, strong, strongly concentrically striated; umbo fairly projecting, with fine, irregular, discontinuous wrinkles; hinge margin narrow; anterior teeth compressed, rough; lamellae short, obliquely striated. Gills small; the marsupium occupies the posterior part of the outer lamina and forms 11–20 separate egg sacks which are rounded at the ends, with a furrow near the base; mantle margin thickened and doubled, sometimes folded.

P. spheniopsis (Morelet). A few species, in Central America.

Lemiox Rafinesque, 1831

Synonym *Conradilla* Ortmann, 1921.

Shell strong, more or less inflated, somewhat longish; umbo high, with biseriate sculpture, on the posterior part of the shell with strong radial wrinkles; hinge teeth low, rough, 2 in the left 1–3 in the right valve; lamellae double on the left, some of them double on the right; sexes different; females smaller than males; mantle margin exteriorly denticulate anterior to the incurrent opening; interiorly with a few small papillae and then elevated, thin, probably extensible.

L. caelatus (Conrad), in the United States.

Epioblasma Rafinesque, 1831

Shell strong, inflated, roundish, oval or triangular, differing in the two sexes, in most cases smooth; umbo projecting, weakly sculptured. In the posterior part of the mantle margin, the inner and outer margins in the female are more or less separated from one another and the inner margin is beset with papillae; marsupium consisting of many egg sacks and occupying the posterior part of the outer gill lamina.

A few species, in the United States.

Section *Truncillopsis* Ortmann & Walker, 1922. Shell longish, smooth; male without posterior furrow; female inflated at the posterior edge. *E. (T.) triquetrum* (Rafinesque).—Section *Pilea* Simpson, 1900. Shell oval; female with a rounded radial bulge. *E. (P.) personatum* (Say). —Section *Epioblasma* s. s. (synonym *Dysnòmia* L. Agassiz, 1852). Shell oval, in the male with a broad, shallow radial furrow behind the center, in the female with a bulge passing into a large lobe. *E. (E.) bilobum* (Rafinesque) = *foliatum* (Hildreth). In addition, Frierson, 1927, also names: *Penita* for *E. penitum* (Conrad), *Torulosa* for *E. torulosum*

(Rafinesque), and *Capsaeformis* for *E. capsaeforme* (Lea). Ortmann and Walker, 1922, erected a subgenus *Scalenilla* for "*Unio*" *sulcatus* Lea.

3. Family MUTELIDAE

Shell variably formed; umbo with radial sculpture or without sculpture. Incurrent and excurrent openings separated by a mantle bridge, the latter is sometimes short, sometimes long, but a supraanal opening is not separated, the attachment of the inner gill lamina extends to the oral lobes; the gills sometimes have no water tubes; interlamellar junctions scattered or forming perforated or solid septa; marsupium only in the inner lamina; occasionally the mantle margins are fused anterior to the incurrent opening.

A. Subfamily Hyriinae

Shell with hinge teeth and radial umbonal sculpture; the upper part of the anal mantle opening is closed; interlamellar junctions weakly developed in the outer gills of the female and in all those of the male, in the marsupium in most cases forming a discontinuous network, often arranged in rows, so that incomplete septa, rarely solid septa and separate water tubes, are formed; often the marsupium occupies only a part of the inner gill lamina; the innermost lamella is completely attached; the larvae are glochidia, in most cases with a ventral corner, on which a simple, long and thin, curved thorn is often attached.

In South America and Australia.

Hyridella Swainson, 1840

Synonym *Microdontia* Tapparone Canefri, 1883.

Shell oval; umbo low, with curved, in most cases tuberculate wrinkles, which below approach one another; sides in most cases furrowed; hinge teeth fairly weak, compressed, sometimes somewhat rudimentary. Anal opening small, roundish, with expanded margin; a small opening is present between the posterior end of the gill and the mantle bridge.

A few species, in Australia, New Guinea, and New Zealand.

Section *Protohyridella* Cotton & Gabriel, 1932. Shell strong, somewhat rhomboidal, with an edge from the umbones to the posterior corner, dividing the surface into an anterior wrinkled and a posterior smooth part; umbo not projecting; hinge teeth well developed. *H. (P.) glenelgensis* (Dennant). —Section *Propehyridella* Cotton & Gabriel,

1932. Shell similar to *Hyridella australis*, strong, irregularly wrinkled on the umbones, thereafter smooth; hinge teeth well developed. *H. (P.) nepeanensis* (Conrad).—Section *Hyridella* s. s. Umbo without sculpture. *H. (H.) australis* (Lamarck).

Diplodon Spix, 1827

Shell roundish to elongated oval; umbo closer to the anterior end, only slightly elevated, with more or less distinct radial sculpture; a posterior edge not or weakly developed; hinge teeth smooth or rough, but not transversely furrowed. The interlamellar junctions in the gills variable, sometimes scattered in small numbers, sometimes joined to form a network or solid septa.

Several species in South America.

Subgenus *Diplodon* s. s. (synonyms *Iridea* Swainson, 1840; *Niaea* (Swainson) Mörch, 1853). Shell longish; umbo with continuous ridges. *D. (D.) ellipticus* (J. A. Wagner) = *wagnerianus* Simpson.

Subgenus *Rhipidodonta* Mörch, 1853 (synonym *Cyclomya* Simpson, 1900). Shell roundly oval; umbo anteriorly inclined, with irregular radial sculpture; hinge margin arched, lower main tooth of the right valve often divided into small denticles; the teeth of the left valve are also denticulate. *D. (R.) paranensis* (Lea).

839 Subgenus *Bulloideus* Simpson, 1900. Shell inflated, roundish, thin, with posterior edge; umbo with regular radial ridges; hinge teeth elongated, compressed, somewhat divided, 2 on the right, 1 on the left; 1 lamella on the right, 2 on the left. *D. (B.) bulloides* (Lea) = *variabilis* (Maton).

Castalina Jhering, 1891

Shell somewhat triangular, laterally flattened, with moderate posterior edge and a weak wing; umbo elevated, with radial sculpture; hinge teeth smooth, pleated, or with parallel furrows. Interlamellar junctions of the gills scattered.

C. martensi Jhering. A few species, in Brazil.

Castalia Lamarck, 1819

Synonym *Tetraplodon* Spix, 1827.

Shell strong, triangular, with distinct posterior edge; umbo high, with distinct sculpture extending over a large part of the shell; hinge margin curved, on the left with a very strong, compressed tooth, and on the right with 2 teeth anterior to the umbones, posterior to these with a few small denticles; on the right with 1, on the left with 2 transversely

grooved lamellae; mantle margins below the incurrent opening in most cases fused with one another.

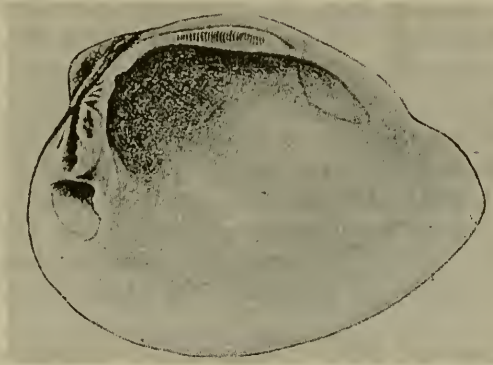C. *ambigua* Lamarck (Fig. 809). A few species, in South America.

Fig. 809. Inner side of the right shell valve of *Castalia undosa* Martens.

Castaliella Simpson, 1900

Shell fairly strong, triangular, with sharp posterior edge and strong concentric sculpture; umbo high, with regular radial sculpture; hinge margin narrow, curved; right valve with 2 furrowed main teeth, the lower of which is larger and cleft; left valve with 3 main teeth, the median of which is the largest; posterior to the teeth with a few minute warts; a granulose lamella in the right valve, 2 indistinctly transversely striated ones in the left valve; nacre purplish. Animal unknown.

C. *sulcata* (Krauss), in Surinam.

Callonaia Simpson, 1900

Shell thin, inflated, triangular, with sharp posterior edge and high umbones, without sculpture; hinge margin strongly curved, on either side with 2 high and compressed main teeth; on the left with 2, on the right with 1 lamella, which are somewhat granulose transversely striated. Animal unknown.

C. *duprei* (Recluz), in Brazil.

Prisodon Schumacher, 1817

Shell somewhat triangular or rhomboidal, in most cases with small anterior and larger posterior wing. Interlamellar junctions of the gills

scattered, more densely-spaced and forming net-like interrupted septa in the marsupium, which occupies the median part of the inner lamina; mantle open below.

840 A few species, in Guyana and the Amazon River.

Subgenus *Triplodon* Spix, 1827 (synonyms *Naia* Swainson, 1840; *Harmandia* Rochebrune, 1881). Umbo with strong radial sculpture; posterior edge moderate. Section *Triquetrana* Simpson, 1900. Wings scarcely developed; sculpture very extensive; each valve with 3 main teeth; 2 lamellae on the left, one on the right. *P. (T.) stevensi* (Lea). —Section *Triplodon* s. s. Wings distinctly developed, on either side with 2 or more short, compressed and cleft main teeth. *P. (T.) rugosus* Spix.

Subgenus *Prisodon* s. s. (synonyms *Triquetra* Klein, 1753;? *Paxyodon* Schumacher, 1817; *Hyria* Lamarck, 1819, *Hyriana* Simpson, 1900). Umbo without sculpture; posterior edge sharp. *P. (P.) obliquus* Schumacher.

The genotype of *Hyria* designated by Herrmannsen is *Mya syrmatophora* Meuschen, which has also been considered as the genotype of *Prisodon* by Simpson; therefore the two names are synonymous.

B. Subfamily Mutelinae

Shell variably formed, without distinct umbonal sculpture; hinge teeth incomplete, always without lamellae, or completely absent, or replaced by a series of tubercles. Anal opening of the mantle in most cases widened above; gills with septa and water tubes; in the marsupium the septa are more strongly developed and have a longitudinal ridge on the outer lamella; in the gravid condition only the inner part of the water tubes is somewhat widened and filled with eggs, its outer part forms secondary water tubes; larvae of most genera unknown, in *Anodontites* they are very different from glochidia, the anterior pear-shaped part is ciliated, the median bears a thin small shell, and the posterior is cleft, with a few stiff bristles; they produce a broad thin secretory band; they are known as lasidia.

In Africa, South and Central America.

Haasica Strand, 1932

Synonym *Marshalliella* Haas, 1931, non Kieffer, 1913, nec Poppius, 1914.

Shell fairly small, roundly oval, inflated, on a well-developed hinge plate on the right is a high, narrow, oblique tooth, behind which is a pit bordered posteriorly by a narrow denticle; on the left with a callous

thickening and posterior to a deep, narrow groove is a high, slender, somewhat hooklike, curved tooth.

H. balzani (Jhering), in southern Brazil.

Diplodontites Marshall, 1922

Shell elongated oval; umbo moderately elevated; sides sculptured with radial furrows and microscopic granulose striae; right valve with 3 teeth, the anteriormost of which is the strongest, high, and triangular; left valve also with 3 teeth, the anteriormost of which is weak, whereas the median is very strong and triangular.

D. cookei Marshall, from the Rio Colorado, tributary of the Magdalena River, in Colombia and from the Rio Huancabamba in Peru.

Tamsiella Haas, 1931

Shell elongated oval; right valve with a low, blunt tooth, which does not lie on a hinge ridge, but represents a receded part of the dorsal margin, and behind it a shallow pit; left valve with a weak dentiform tubercle below the umbo, anterior and posterior to it with a shallow pit.

841   *T. tamsiana* (Dunker), from a tributary of the Orinoko.

Jheringella Pilsbry, 1893

Synonym *Plagiodon* Lea, 1856, non Dumeril, 1853.

Shell small and thick, inflated, anteriorly and posteriorly truncated; umbo high; left valve with an irregular tooth below the umbo; right valve with 2 teeth.

J. isocardioides (Lea). A couple of species, in Rio la Plata and in Peru.

Monocondylaea Orbigny, 1835

Synonyms *Aplodon* Spix, 1827, non Rafinesque, 1818; *Spixoconcha* Pilsbry, 1893.

Shell fairly strong, roundish to oval, with weak posterior edge, on either side with one hinge tooth, which in most cases is compressed, the left one situated anterior to the right, sometimes with indications of accessory teeth; surface in most cases with somewhat lamellose concentric striae. Anal mantle opening wide; gills with well-developed septa, which are alternately stronger and weaker; in the marsupium they are more regular and stronger.

M. paraguayana Orbigny. A few species, in the eastern parts of South America.

Fossula Lea, 1870

Shell strong, inflated, oval, with weak edge and fairly high umbones; right valve with 2 teeth, which clasp the single one of the left valve, sometimes with indications of accessory teeth; hinge margin narrow. Animal similar to that in *Monocondylaea*.

F. fossiculifera (Orbigny), in Brazil.

Anodontites Bruguière, 1792

Synonyms ? *Patularia* Swainson, 1840; *Glabaris* Gray, 1847; *Styganodon* Martens, 1900.

Shell oval or somewhat trapezoidal, sometimes somewhat gaping; lunule anteriorly prolonged; hinge teeth absent. Anal mantle opening wide; mantle completely open below; foot moderately large; gill septa well developed. The larva is a lasidium.

Several species, in South America east of Cordillera and in Central America to Mexico.

Section *Anodontites* s. s. Shell more or less longish, but not greatly elongated or posteriorly pointed, without sharp posterior edge. *A. (A.) crispata* Bruguière. *Euryanodon* and *Pseudoleila* Crosse & P. Fischer, 1893, are also to be placed here.—Section *Lamproscapha* Swainson, 1840 (synonym *Virgula* Simpson, 1900). Shell greatly elongated and posteriorly pointed, with sharp posterior edge. *A. (L.) ensiformis* (Spix). —Section *Ruganodontites* Marshall, 1931. Shell moderately long, often somewhat indented ventrally; surface with fine, irregular radial wrinkles. *A. (R.) colombiensis* Marshall.

Leila Gray, 1840

Synonym *Columba* Lea, 1833, non Linné, 1758.

Shell large, inflated, somewhat oval; hinge margin straight, toothless, anteriorly and posteriorly somewhat produced wing-shaped, gaping. The mantle line forms a sinus posteriorly; mantle margins fused anterior to the incurrent opening.

L. esula (Orbigny). Few species, in South America.

842

Mycetopoda Orbigny, 1835

Synonym *Mycetopus* Orbigny, 1847.

Shell thin, elongated, anteriorly gaping, posteriorly obliquely truncated, with low posterior edge and low umbones; hinge margin long,

straight, toothless. Foot very long, swollen at the end; anal mantle opening closed in the upper part; gills very long; innermost lamella completely attached.

M. siliquosa (Spix). A few species, in South America.

Mycetopodella Marshall, 1927

Shell greatly elongated, anteriorly very low; umbones close to the anterior end; a broad constriction running from them to the lower margin, posterior to which the shell gradually broadens to the obliquely truncated posterior end; posterior edge sharp; hinge margin behind the umbones straight, toothless, obliquely descending anterior to the umbones.

M. falcata (Higgins), in South America (Amazon River).

Aspatharia Bourguignat, 1885

Shell more or less elongated oval; hinge margin toothless, posteriorly abruptly or obliquely delimited by a deep triangular sinus, sometimes with a low blunt, tooth-like projection below the umbo of the left valve. Mantle completely open below or with a short fusion anterior to the incurrent opening; anal opening short; innermost gill lamella not attached.

A few species, in tropical Africa to Egypt.

Subgenus *Aspatharia* s. s. Umbo with obtusely angled wrinkles; shell longish, moderately bulging, smooth or with warty wrinkles; mantle completely open below. *A. (A.) vignouana* (Bernardi).

Subgenus *Spathopsis* Simpson, 1900 (synonyms *Spathella* Bourguignat, 1885 (non J. Hall, 1885); *Leptospatha* Rochebrune & Germain, 1904; *Mitriodon* Rochebrune, 1904). Umbo with short concentric wrinkles; shell oval or longish, moderately bulging, smooth or with a few wrinkles in the posterior part; lunule very narrow; mantle margins with a very short fusion anterior to the incurrent opening. *A. (S.) guillaini* (Recluz). *Arthropteron* Rochebrune, 1905 (*ouassouloui* Rochebrune), is said to differ by the broader lunule, and *Moncetia* Bourguignat, 1885 (*anceyi = lavigeriana* Bourguignat), by its strongly compressed form.

Subgenus *Brazzaea* Bourguignat, 1885. Shell thin, oval, greatly inflated; the dorsal margin of the left valve anterior to the umbones slightly surpassing that of the right valve. *A. (B.) anceyi* (Bourguignat).

Pseudospatha Simpson, 1900

Synonym *Burtonia* Bourguignat, 1883, non Bonaparte, 1850.

Shell thin, smooth, strongly compressed, somewhat winged; umbo low, in about the anterior quarter, nearly smooth or wavy and warty; hinge margin straight, toothless, with an angular or narrowly elevated, anteriorly and posteriorly diverging edge.

P. tanganyicensis (Edg. Smith). Few species, in Lake Tanganyika.

Mutela Scopoli, 1777

Synonyms *Spatha* Lea, 1838; *Calliscapha* Swainson, 1840; *Mutelina* Bourguignat, 1885; *Pseudomutela* Simpson, 1900.

843   Shell more or less elongated; hinge margin posteriorly not delimited by a sinus, narrow, toothless or with weak, short denticles, especially anterior to the umbones; mantle closed below to a greater extent.

A few species, in tropical Africa and in the Nile.

Section *Mutela* s. s. Shell without keels or wings on the posterior edge. *M.* (*M.*) *dubia* (Gmelin).—Section *Chelidonopsis* Ancey, 1887 (synonym *Chelidonura* Rochebrune, 1886, non A. Adams, 1850). Shell with keels or wings on the posterior edges. *M.* (*C.*) *hirundo* (Martens).

Iridina Lamarck, 1819

Synonyms *Platiris* Lea, 1838; *Eufira* Gistel, 1848.

Shell oval or longish; hinge margin with a row of tubercle-shaped teeth; mantle fairly widely closed below; gill laminae fairly equally broad.

A few species, in tropical Africa.

Section *Iridina* s. s. Shell longish; hinge margin with many small denticles and a low projection below the umbo of the left valve. *I.* (*I.*) *exotica* Lamarck.—Section *Cameronia* Bourguignat, 1879. Shell longish; hinge margin narrowed below the umbones, with strong, irregular teeth which are weaker anterior to the umbones *I.* (*C.*) *spekii* S.P. Woodward. —Section *Pliodon* Conrad, 1834 (*Pleiodon*). Shell oval; hinge with strong teeth anterior and posterior to the umbones. *I.* (*P.*) *ovata* Swainson (Fig. 810).

4. Family AETHERIIDAE

Shell irregularly formed, often with one valve cemented to the substratum, without hinge teeth. The very wide anal opening separated from the incurrent opening by a mantle bridge; the innermost gill lamellae anteriorly fused with the visceral sack, posteriorly fused with one another; the gill laminae smooth in *Acostaea*, in *Aetheria* they have

Fig. 810. Inner side of the right shell valve of *Iridina* (*Pliodon*) *ovata* Swainson. Length 10.5 cm.

numerous small folds; the two lamellae of each lamina are joined with one another by some complete, some incomplete, septa running parallel to the filaments; those in the inner laminae are considerably stronger than in the outer ones, between them very small eggs were found (only in the inner lamina ?); embryos unknown; a foot absent; the ventricle is not traversed by the intestine, but lies below it; the anterior adductor muscle is sometimes reduced.

Bartlettia H. Adams, 1866

Shell solid-walled, more or less elongated, often with a ventral sinus, anteriorly narrowed; umbo scarcely projecting; outer side with irregular, rough growth lines; posterior to the strong ligament with a triangular sinus; adductor muscle scars far removed from one another, the anterior one narrow. One of the valves appears to be only slightly or not at all attached. Animal unknown.

844

B. stefanensis (Moricand), in the Amazon River.

Aetheria Lamarck, 1807 (*Etheria*)

Shell irregularly formed, inequivalve, cemented by one valve, which is sometimes greatly thickened and has a lighter structure; posterior to the ligament with a deep, narrow sinus; both adductor muscles present. Mantle margins with papillae all around.

A. elliptica Lamarck, in tropical Africa, in the Nile, and the northwestern part of Madagascar.

Acostaea Orbigny, 1851

Synonym *Mulleria* Férussac, 1823, non Leach, 1814.

Shell inequivalve, cemented by one valve, solid-walled; umbo lying far forward; posterior to the ligament with a sinus; anterior adductor muscle reduced. Along the posterior part of the mantle margin with a row of papillae.

Subgenus *Acostaea* s. s. (synonym *Eumulleria* Anthony, 1907). Shell with a thin anterior process, which encloses the embryonic shell. *A. (A.)* *rivolii* (Deshayes), in the Magdalena River (South America).

Subgenus *Pseudomulleria* Anthony, 1907. Shell without conspicuous anterior process. *A. (P.) dalyi* (Edg. Smith), in India.

Suborder HETERODONTA

In most cases well-developed hinge plate bears few alternating and interlocking main teeth, of which the right central tooth is occasionally reduced, and often anterior and posterior lateral teeth; ligament in most cases external, more seldom sunken between the hinge teeth. Siphons more or less developed.

I. STIRPS ASTARTACEA

Shell small or of medium size, in most cases strong and roundish triangular or somewhat elongated, often with concentric sculpture; hinge margin broad, in most cases on the right with one central tooth, which is clasped by 2 teeth of the left valve; in addition there may be fairly distinct indications of outer main teeth or lateral teeth; adductor muscle scars distinct; mantle line without sinus. Mantle open except for a short anal siphon; gill laminae of unequal breadth, without fusions with the visceral sack and the mantle, as a rule smooth, with regular interfilamentar junctions in the lamellae and scattered interlamellar junctions; proximal limb of the kidney short and fairly wide; distal limb sack-shaped, with a few rather strong lobes, united with one another above the ciliated funnels. Marine.

1. Family ASTARTIDAE

Shell angulate above, rounded below, fairly strong, externally smooth or in most cases concentric sculpture; ligament external; central tooth of the right valve strong, occasionally with a weak anterior or posterior main tooth; left valve with 2 strong main teeth and sometimes with a

845 posterior tooth below the ligament; lateral teeth variable, situated at the margin, in most cases rudimentary; sometimes the dentition of the two sides is reversed.

Astarte J. Sowerby, 1816

Synonym *Crassina* Lamarck, 1818.
Characters of the family.
Several species, mainly in the cold Nordic seas.

Section *Astarte* s. s. Inner margin of the shell denticulate, externally concentrically sculptured. *A. (A.) sulcata* (da Costa). —Section *Tridonta* Schumacher, 1817. Inner margin smooth. *A. (T.) borealis* [(Chemnitz) Schumacher] (Fig. 811). *Nicania* Leach, 1819, is separated only by smaller size. *A. (A.) banksi* Leach. —Section *Gonilia* Stoliczka, 1871. Shell small, externally with furrows, which form angles in the center; inner margin denticulate. *A. (G.) calliglypta* Dall = *bipartita* (Philippi) non J. Sowerby. —Section *Rictocyma* Dall, 1872 (synonym *Rhectocyma* Martens, 1874). Shell externally with concentric, discontinuous and sometimes bifurcated wrinkles; inner margin smooth. *A. (R.) esquimalti* Baird. —Section *Digitaria* S. Wood, 1853 (synonym *Woodia* Deshayes, 1860). Shell with curved furrows, which obliquely cut the growth lines; inner margin denticlulate. *A. (D.) digitaria* (Linné) (Fig. 812). —Section
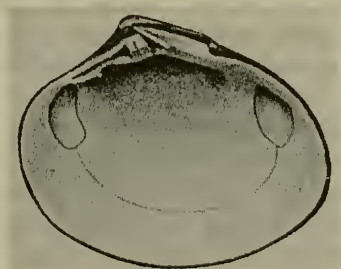

Fig. 811. Inner side of the right shell valve of *Astarte arctica* Gray.

Fig. 812. Shell of *Astarte* (*Digitaria*) *digitaria* Linné, enlarged.

Goodallia Turton, 1822 (synonym *Mactrina* T. Brown, 1827). Shell very small, smooth, interiorly denticulate, central tooth of the right valve interiorly indented; an anterior main tooth absent. *A. (G.) triangularis* (Montagu).

Grant and Gale have referred to the fossil *A. lurida* J. Sowerby as the typical species of the genus, whereas Lamy and most other malacologists consider *A. sulcata = danmoniensis* (Lamarck) as such.

2. Family CRASSATELLIDAE

Shell variable in size, in most cases strong, oval or posteriorly somewhat beak-like, often concentrically furrowed; umbo angular; ligament internal, situated posterior to the main teeth on the broad hinge margin; left valve with 2 teeth, which clasp the central tooth of the right valve, anterior to which a weaker tooth is also present, whereas a posterior one is more or less rudimentary; these teeth are often transversely grooved; lateral teeth are scarcely developed. The animals are in part similar to those in *Astarte* in part strikingly different in the structure of the gills of the foot.

Crassatella Lamarck, (1799) 1801

Shell of small or medium size, in most cases longer than broad, oval or posteriorly truncated or beaked, besides the main teeth more or less distinctly developed lateral teeth are formed, 1 anterior and 2 posterior in the left valve, 2 anterior and 1 posterior in the right valve.

Several species, mainly in warm seas.

846   Subgenus *Crassinella* Guppy, 1874 (synonyms *Thetis* C. B. Adams, 1845, non J. Sowerby, 1826; *Pseuderiphyla* P. Fischer, 1887). Shell small, greatly compressed, triangular; umbo pointed, situated almost in the center, 2 main teeth on either side; lateral teeth distinctly developed. Animal unknown. *C. (C.) martinicensis* Orbigny.

Subgenus *Crassatina* Weinkauff, 1881. Shell more or less large; umbo angular, posterior part rounded or truncate or beaked; gill laminae smooth as in *Astarte*, but the margins of the ascending lamellae are fused outwardly with the mantle, interiorly in the posterior part with one another; the gill in female contains eggs; foot moderately large, with byssus. Section *Crassatina* s. s. Shell oval, fairly small, inner margin denticulate. *C. (C.) divaricata* (Chemnitz) = *contraria* (Gmelin) (according to P. Fischer, 1887). *Talabrica* Iredale, 1924 (*C. aurora* A. Adams & Angas) is identical to it; *Salaputium* Iredale, 1924 (*C. fulvida* Angas), has

on either side in the ligamental pit a small spoon-shaped process; arising from the main tooth and catching below that of the opposite valve; inner margin smooth.—Section *Eucrassatella* Iredale, 1924. Shell large and strong. *C. (E.) kingicola* (Lamarck).

Subgenus *Scambula* Conrad, 1869. Shell posteriorly beaked; inner margin smooth; gill laminae distinctly folded, with well-developed main filaments; the interlamellar junctions are alternating high and low septa; foot very strong, suited for springing. *C. (S.) supplana* Conrad, fossil; the animal of *C. floridana* Dall was studied.

Although Lamarck, 1799, mentioned only an uncertain fossil species, according to Lamy there is no doubt that he meant *Crassatella* in the modern sense, probably corresponding with *Crassatellites* Krüger, 1823; it seems doubtful whether it is really identical with *Eucrassatella* but the latter is probably to be considered only as a subgroup.

Bernardina Dall, 1910

Shell very small, oval, with fine concentric furrows; embryonic shell hat-shaped; hinge margin with 2 right and 3 left main teeth, posterior to which the ligamental cartilage is sunken; posterior dorsal margin of the right valve sunken into a shallow furrow of the left valve, and anterior left lateral tooth clasped between 2 right lamellae; lower margin smooth.

B. bakeri Dall, near the Coronado Islands (California).

? *Cuna* Hedley, 1902

Shell very small, triangular or roundish; umbo angular, situated nearly in the center, externally concentrically or radially sculptured; ligament internal; right valve with a strong triangular, below more or less cleft, central tooth and an often rudimentary anterior and posterior tooth; left valve with 2 main teeth; lateral teeth weak. Animal unknown.

A few species, in Australia, New Zealand and South Africa.

Section *Cuna* s. s. Shell triangular, in most cases concentrically, sometimes radially sculptured. *C. (C.) concentrica* Hedley (Fig. 813). —Section *Hamacuna* Cotton, 1931. Umbo hook-shaped downwardly 847 curved; hinge margin strong, compressed. *C. (H.) hamata* Hedley & May.—Section *Propecuna* Cotton, 1931. Surface with furrows, which obliquely cut the growth lines, and with radial furrows. *C. (P.) obliquissima* Tate.
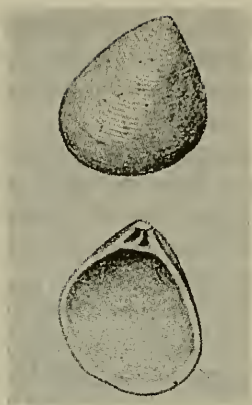
Fig. 813. Exterior and interior sides of a shell valve of *Cuna concentrica* Hedley, enlarged.

II. STIRPS CARDITACEA

Shell in most cases with radial ribs; umbo more or less shifted anteriorly, correspondingly the posterior main teeth are elongated; lateral teeth in most cases reduced; ligament as a rule external; mantle line nearly always without sinus. Foot in most cases with byssus. Marine.

1. Family CARDITIDAE

Shell in most cases of medium size and strong, transversely oval or elongated, sometimes with greatly projecting umbones and therefore more triangular; the umbones in most cases lie anterior to the center and often shifted far forward, then the posterior adductor muscle becomes larger than the anterior; the ligament is as a rule external; the ventral margin denticulate; the main teeth of the hinge margin are almost always transversely grooved, 2 in the left, 3 in the right, but the anteriormost of which is often reduced; lateral teeth in most cases rudimentary. Byssal gland present; gill laminae smooth, the inner ones posteriorly fused with one another; mantle open except for the excurrent opening; the ventricle lies below the intestine; kidney similar to that in *Astarte*; development with brood care.

Cardita Bruguière, 1792

Shell strong, bulging, in most cases roundish or oval, with elevated umbones which are close to the center; anterior main teeth more or less

reduced, as a rule without posterior lateral teeth; adductor muscle scars not greatly different.

Several species in various seas.

Section *Venericardia* Lamarck, 1801. Shell oval, with projecting, umbones situated only slightly anterior to the center; hinge teeth not greatly diverging; the right central tooth surrounded by 2 teeth of the left valve, in addition a small anterior and posterior tooth on the right; anterior lateral teeth may be represented by small tubercles; mantle line without sinus. *C. (V.) imbricata* Lamarck, fossil; also a couple of living species. *Vimentum* Iredale, 1925, was erected for a small Australian species, *C. dilecta* Edg. Smith.—Section *Pleuromeris* Conrad, 1867. Shell small; umbo situated nearly in the center, projecting; anterior and posterior main tooth of the right valve weak; a small anterior and posterior lateral tooth in the left valve. *C. (P.) tridentata* (Say). —Section *Cardiocardita* (Blainville) Anton, 1839 (synonyms *Agaria* Gray, 1847; *Actinobolus* (Klein) Mörch, 1853; *Azaria* Tryon, 1872). Shell form similar to that in *Venericardia*; mantle line with a shallow posterior sinus; 2 left, 3 right main teeth; lateral teeth reduced. *C. (C.) ajar* (Adanson).—Section *Cardita* s. s. (synonyms *Cardites* Link, 1807; *Arcinella* Oken, 1815). Shell in most cases oval, with elevated umbones; anterior main tooth of the left valve small, triangular; the posterior one large, elongated; anterior main tooth of the right valve fused with the margin, the posterior one large and elongated; lateral teeth rudimentary. *C. (C.) sulcata* Bruguière = *antiquata* (Linné) (according to Children).

848 —Section *Cyclocardia* Conrad, 1867 (synonyms *Arcturus* Gray, 1847, non Cuvier, 1829; *Scalaricardita* Sacco, 1899). Shell roundish or oval, colorless, with strong periostracum; umbo more or less high; hinge teeth similar to those in *Cardita* s. s. *C. (C.) borealis* Conrad. In cold seas. —Section *Pteromeris* Conrad, 1862 (synonyms *Coripia* Gregorio, 1885; *Triodonta* Könen, 1893). Shell small, triangular; umbo pointed, anteriorly inclined; posterior side very short; right valve with a triangular, strong central tooth; anterior teeth rudimentary; left valve with 2 main teeth; lateral teeth absent. *C. (P.) perplana* Conrad, fossil; few living species, mainly *corbis* Philippi; *Miodontiscus* Dall, 1903 (synonym *Miodon* Carpenter, 1864, non Dumeril, 1859) seems to be scarcely different. *C. (M.) prolongata* (Carpenter).—Section *Bathycardita* Iredale, 1924. Shell oval; umbo only slightly elevated, close to the anterior end; the broad ribs bear short thorns. *C. (B.) raouli* Angas, near Australia.—Section *Megacardita* Sacco, 1899. Shell fairly elongated oval; umbo situated far forward; posterior main teeth elongated; lateral teeth rudimentary. *C. (M.) jouanneti* Basterot fossil; *C. turgida* Lamarck belongs here.

Beguina (Bolten) Röding, 1798

Synonym *Trapezium* Mus. Calonn., 1797.

Shell more or less elongated, ribbed; umbo close to the anterior end; posterior main teeth of the hinge margin long; lateral teeth sometimes reduced in adult shells; posterior adductor muscle scar larger than the anterior one.

A few species in warm seas.

Section *Glans* Megerle von Mühlfeld, 1811. Shell fairly small, quadrangular, with tuberculate or spiny ribs; anterior main tooth situated close to the shell margin; the posterior one moderately elongated; lateral teeth well developed. *B. (G.) trapezia* (Linné).—Section *Mytilicardita* (Blainville) L. Agassiz, 1847; *Jesonia* Gray, 1847]. Shell elongated, posteriorly broadened; umbo nearly terminal; ribs often scaly; anterior main teeth small, the posterior ones elongated; often a parallel tooth above that of the right valve. *B. (M.) calyculata* (Linné).—Section *Carditamera* Conrad, 1838 (synonyms *Lazaria* Gray, 1854; *Lazariella* Sacco, 1899). Shell long, anteriorly lower than posteriorly; umbo not terminal; a few strong folds, mainly in the posterior part; posterior main teeth distinctly elongated, the anterior one of the right valve sometimes reduced; lateral teeth well developed. *B. (C.) arata* (Conrad), fossil; few living species.—Section *Beguina* s. s. (synonym *Azarella* Gray, 1854). Shell large and strong, compressed, finely ribbed, umbo terminal, similar to *Modiolus*; left valve with 1, right with 2 elongated posterior main teeth, lateral teeth absent. *B. (B.) semiorbiculata* (Linné).

Calyptogena Dall, 1891

Shell longish, weakly concentrically striated; umbo situated anterior to the center; posterior part gradually narrowed; periostracum strong; inner margin smooth; each valve has 2 main teeth and one anterior lateral tooth, which become reduced in old shells. Mantle margin finely fringed; siphonal openings warty; foot ovate cylinder-shaped.

C. pacifica Dall, on the western coast of North America.

849   ## *Thecalia* H. & A. Adams, 1857

Shell similar to *Mytilicardita*, but in the female with a strong ventral infolding, which with the opposite one forms a space in which the embryos develop.

T. concamerata (Chemnitz) (Fig. 814), near South Africa.

Fig. 814. Inner side of the right shell valve of *Thecalia concamerata* (Chemnitz). ♀. Length about 15 mm.

Milneria Dall, 1881

Synonym *Ceropsis* Dall, 1871 (non Solier, 1839).

Shell small, with anteriorly situated umbones, from which a strong edge runs to the posterior corner, delimiting the flattened lower side, thereupon with a few unequal radial ridges which are rough because of the growth lines; right valve with an elongated triangular tooth and a very small anterior and posterior denticle; left valve with 2 diverging main teeth and a posterior lateral tooth; in the female the ventral shell margin forms a hemispherical depression, which is closed by the mantle margin and receives the eggs, which develop within it.

M. minima (Dall), near California.

2. Family CONDYLOCARDIIDAE

Shell small, ribbed or more seldom smooth; ligament partly or completely internal; main teeth weak, sometimes scarcely separated from the lateral teeth. Animal unknown.

Carditella Edg. Smith, 1881

Shell small, ribbed, in most cases oval; umbo angulate; ligament fairly weak, partly internal; left valve with 2, the right with 3 main teeth, but of which only the median is well developed; 1 anterior and 1 posterior lateral tooth on either side.

C. pallida Edg. Smith. A few species in various, mainly southern, seas.

Carditopsis Edg. Smith, 1881

Shell very small, ribbed or smooth; ligament completely internal, one tooth anterior to the ligament on either side and 2 posterior to it, which are joined above; lateral teeth weak.

C. flabellum (Reeve). Few species in various seas.

Condylocardia Bernard, 1896

Shell very small, roundish or triangular, ribbed or concentrically striated; umbo projecting, with distinctly delimited embryonic shell; ligament internal; the main teeth of the hinge are indistinctly separated from the lateral teeth and somewhat different; on the left 1 anterior and 1 posterior main tooth; on the right 2 connected anterior, and 1 rudimentary triangular posterior main tooth; 1 lateral tooth on either side.

C. sanctipauli Bernard. A few species, mainly near Australia and in southern seas.

850

Benthocardiella Powell, 1930

Shell similar to *Condylocardia*, roundish to triangular, smooth, with delimited embryonic shell; on the right with 2, on the left with 3 or 4 elongated main teeth; without lateral teeth.

B. pusilla Powell (Fig. 815). A few species near New Zealand and the neighboring islands.
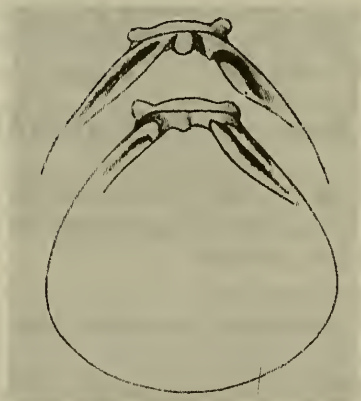
Fig. 815. Hinge margins of the shell of *Benthocardiella pusilla* Powell, enlarged (after Powell).

III. STIRPS SPHAERIACEA

Shell porcellan-like, rounded triangular to oval; main teeth situated below the umbones, sometimes strong, sometimes incompletely developed, in most cases lateral lamellae are also developed; mantle line without or with a weak sinus below the scar of the posterior adductor muscle; ligament external. The mantle, which is open below, forms posteriorly

closed incurrent and excurrent openings, which are sometimes produced into short siphons; gills lamella-shaped, sometimes folded, with variably developed interlamellar septa, posteriorly fused with one another; foot without byssus. In fresh and brackish water.

1. Family CORBICULIDAE

Shell more or less large and strong, triangular to oval, externally concentrically striated; with yellow, green, or brown peristracum; hinge margin well developed, in most cases with 3 diverging main teeth below the umbones and in most cases with anterior and posterior lateral teeth. Posterior mantle opening not or shortly produced; foot large, hatchet-shaped; both limbs of the kidney arch-shaped, the proximal one lateral to the distal, which communicates with that of the opposite side by a small aperture. In most cases without brood care.

A. Subfamily Corbiculinae

Ligament external.

Polymesoda Rafinesque, 1820

Shell large and strong, with projecting umbones, rounded below, only slightly longer than high, on either side with 3 main teeth, on the left with one anterior and one longer, smooth posterior lateral tooth, corresponding to each of which there are 2 teeth in the right valve.

Numerous species in America, Asia, and Oceania.

Section *Geloina* Gray, 1842. Shell roundish to short oval, sometimes with a shallow mantle sinus. *P. (G.) ceylanica* (Lamarck).—Section *Pseudocyrena* Bourguignat, 1854 (synonyms *Anomala* Deshayes, 1854, non Block, 1799, nec Samouelle, 1819; *Egeta* H. & A. Adams, 1858; *Cyrenocapsa* P. Fischer, 1872). Umbo high; shell anteriorly and posteriorly rounded, without mantle sinus. *P. (P.) maritima* (Orbigny). In brackish water of Central America.—Section *Polymesoda* s. s. (synonyms *Cyprinella* Gabb, 1864, non Girard, 1856; *Diodus* Gabb, 1868; *Leptosiphon* P. Fischer, 1872). Shell rounded triangular, with rather deep and very narrow mantle sinus. *P. (P.) caroliniana* (Bosc), in America.—Section *Egetaria* Mörch, 1861. Shell anteriorly shortly rounded, posteriorly elongated and pointed; mantle sinus narrow. *P. (E.) pullastra* (Mörch), in South America.

851

Villorita Griffith & Pidgeon, 1834

Synonym *Velorita* Gray, 1847.

Shell medium-sized, thick, obliquely triangular, posteriorly flattened and angulate below; umbo high; hinge margin very broad, on either side with 3 main teeth, of which the anteriormost right and the posteriormost left are weakly developed; the right anterior lateral tooth is very short, situated on the broad hinge margin, whereas the corresponding left one forms an angle enclosing it; the posterior lateral teeth are long, situated on the posterior margin, the right one anterior to the left; the anterior adductor muscle scar lies closely below the hinge margin, the posterior one at the end of the posterior lateral tooth; anterior to it the mantle line forms a small sinus. The siphons are short, the lower one larger than the upper, at the ends with papillae; foot triangular, anteriorly pointed; inner gill lamina broader than the outer; labial palps narrowly triangular.

V. cyprinoides (Gray), in brackish water in India.

Batissa Gray, 1852

Shell oval or triangular, large and strong; umbo only slightly projecting; hinge margin broad, on either side with 3 main teeth; lateral teeth transversely striated, the anterior ones short, left single, right double; ligament strongly projecting; mantle line without distinct sinus. Mantle fairly thick, but the marginal part not sharply delimited; foot large, with sharp margin; outer gill lamina broad; labial palps very broad and thin.

B. tenebrosa Hinds. A few species on the islands in the Indo-Pacific region.

Corbicula Megerle von Mühlfeld, 1811

Shell in most cases fairly small, roundish or oval; umbo more or less projecting; hinge margin moderately broad, on either side with 3 main teeth; anterior and posterior lateral teeth long, lamella-shaped, transversely striated, double in the right valve; anterior and posterior adductor muscle scars nearly equally sized. Siphons only slightly different, without papillae; inner gill lamina broader than the outer; foot triangular; labial palps pointed.

Subgenus *Corbicula* s. s. Without mantle sinus and brood care. Section *Corbicula* s. s. (synonym *Cyrena* Lamarck, 1818). Shell in most cases fairly strong and concentrically sculptured. *C.* *(C.)* *fluminalis*

(Müller) (Fig. 816). Several species in Asia, Africa, and Australia. —Section *Cyrenodonax* Dall, 1903. Shell small, thin, smooth, umbo situated at the beginning of the posterior third, somewhat inflated. *C. (C.) formosana* Dall, on Formosa.

Fig. 816. Inner side of the left shell valve of *Corbicula fluminalis* (Müller). Length 3 cm.

Subgenus *Cyanocyclas* Férussac, 1818. With brood care. ? Section *Corbiculina* Dall, 1903. Small and thin; without mantle sinus. *C. (C.) angasi* Prime, in Australia. —Section *Cyanocyclas* s. s. (synonym *Neocorbicula* P. Fischer, 1887). With a small mantle sinus. *C. (C.) limosa* Maton. A few species in South America.

852

The manner of brood care is not known.

? *Soleilletia* Bourguignat, 1885

Shell small and thin, with sharp umbones; right valve with a central tooth and 2 elongated swellings; left with 2 teeth, without distinct lateral teeth; without mantle sinus. Animal unknown.

S. abbadiana Bourguignat. 2 species in Abyssinia.

? 2. Family CYRENOIDIDAE

Shell thin, fairly small, roundish, with somewhat projecting umbones situated anterior to the center; hinge margin narrow; left valve with 2 thin teeth meeting at an angle, that situated below the umbo short, the anterior one elongated and curved; the teeth of the right valve clasp the left ones, the upper ones are similar to these, below this lies an angular lamella; lateral teeth absent; muscle scars and the nonsinuate mantle line

very shallow. Siphons fairly long, fused; gill laminae dissimilar; foot club-shaped; labial palps triangular; proximal limb of the kidneys partly lateral to the outer sack, it forms 2 sacks and 3 lobes, the median of which passes into the tube-shaped distal limb.

Cyrenoida Joannis, 1835

Synonyms *Cyrenella* Deshayes, 1836; *Cyrenodonta* H. & A. Adams, 1858.

Characters of the family.

C. dupontia Joannis. Few species in Australia, the Philippines, West Africa, and Central America; in rivers.

Pilsbry wants to place this group in the Lucinacea; its systematic position is uncertain.

3. Family SPHAERIIDAE

Shell thin and small, permeated by fine pores, into which thread-shaped processes of the mantle epithelium extend; hinge margin very narrow; main teeth differing in the two valves, at most 2 on either side, the right ones are fused to form an obtusely angled or elongated lamella, separate in the left valve; lateral teeth elongated. Mantle margin smooth, it forms 1 or 2 smooth-margined siphons. Foot tongue-shaped; the gill laminae are fused exteriorly with the mantle, interiorly with the visceral sack, and posteriorly with one another; the outer lamella of the inner lamina forms few brood pouches, in which the small number of young ones produced attain a fairly considerable size; the kidneys form repeatedly coiled ducts; gonads hermaphroditic.

The sphaeriids inhabit the fresh waters of all continents.

? *Pseudocorbicula* Dautzenberg, 1908

Shell fairly solid-walled, oval, with projecting umbones situated in the center; right valve with a rudimentary main tooth, left one with 2 of these; anteriorly and posteriorly on the left a smooth, fairly short lateral tooth, 2 of these on the right. Animal unknown.

P. alluaudi Dautzenberg, in Lake Victoria (Africa).

853   ## *Pisidium* C. Pfeiffer, 1821

Synonyms *Pisum* Megerle von Mühlfeld, 1811 (non *Pison* Spinola, 1808); *Galileia* O. G. Costa, 1840; *Euglesa* + *Pera* + *Cordula* Leach, 1852.

Shell in most cases very small; umbo closer to the posterior end; ligament internal; main teeth of the right valve fused to form a curved lamella, in the left valve angular or arcuate; lateral teeth 1 on the left, 2 on the right.

The genus is distributed over all continents.

Several subgroups have found little acceptance; Clessin, 1873, has named: *Fluminina* for *P. amnicum* (Müller) = *Pisidium* s. s., *Rivulina* for *P. supinum* A. Schmidt, and *Fossarina* for *P. obtusale* C. Pfeiffer (non *Fossarina* A. Adams & Angas, 1863) (= *Cycladina* Clessing, 1871, non Latreille, 1825, nec Cantraine, 1835); Dall, 1903, named: *Phymesoda* Rafinesque, 1820, for *P. virginicum* (Gmelin); *Cyclocalyx* Dall for *P. scholtzii* Clessin = *obtusale* C. Pfeiffer; *Tropidocyclas* Dall for *P. henslowianum* Sheppard, recognized as a synonym of *Fossarina* (Clessin, and *Cymatocyclas* Dall for *P. compressum* Prime; besides *Rivulina* and *Fossarina*, Sterki, 1916, named: *Lacustrina* for *P. idahoense* Roper; *Fontinalina* for *P. fontinale* C. Pfeiffer; Germain, 1913, proposed a subgenus *Pseudeupera* for the African *P. landeroini* Germain; *Clessinia* Piaget, 1912 (non Döring, 1877), as a section of *Fossarina*, has been named as *Cletella* by Strand, 1928. Odhner, 1921, divided the genus into 2 subgenera: *Eupisidium* (= *Pisidum* s. s.) for *P. (P.) amnicum* (Müller), with 2 gills on either side and with 2 siphons, and *Neopisidium* with one gill on either side and with only one (the anal) siphon. *P. (N.) torquatum* Stelfox.

Sphaerium Scopoli, 1777

Synonyms *Nux* Mus. Calonn., 1797; *Cyclas* Lamarck, 1798; *Cornea* Megerle von Mühlfeld, 1811; *Corneocyclas* Férussac, 1818; *Corneola* Clessin, 1890, non Held, 1837.

Shell in most cases fairly small, oval; umbo close to the center; right valve with a sometimes cleft main tooth, which is clasped by 2 oblique teeth of the left valve; lateral teeth lamella-shaped, 2 on the right, 1 on the left. Siphons unequally long, fused at the base.

Several species in America, Europe, Africa and northern Asia.

Section *Sphaeriastrum* Bourguignat, 1854. Shell fairly strong; hinge margin distinctly developed; ligament external, projecting. *S. (S.) rivicola* (Leach). *Amesoda* Rafinesque, 1820 (= *Amesodon* L. Agassiz, 1847; *Sulcastrum* Sterki, 1930) for *S. simile* (Say) = *sulcatum* (Lamarck) is similar, only with flat ligament and with rough, finely wrinkled surface. —Section *Cyrenastrum* Bourguignat, 1854. Shell strong, distinctly ribbed; ligament internal. *S. (C.) solidum* (Normand). *Serratisphaerium* Germain, 1909, for *S. courteti* Germain, has denticulate lateral teeth. —Section *Sphaerium* s. s. Shell fairly weak, with rounded umbones; ligament internal.

S. (S.) corneum (Linné).—Section *Musculium* Link, 1807 (synonyms *Calyculina* Clessin, 1871; *Primella* Cooper, 1891). Shell very thin; hinge plate weak; embryonic shell projecting, often delimited by a groove. *S. (M.) lacustre* (Müller).

Byssanodonta Orbigny, 1846

Synonyms *Eupera* Bourguignat, 1854; *Limosina* Clessin, 1872; *Clessinella* Waagen 1905.

854   Shell small, very thin, rhomboidal; umbo somewhat projecting, situated anterior to the center; hinge margin narrow, on either side with small main tooth parallel to the margin, sometimes reduced on the right; in the left 1, in the right 2 lateral teeth anteriorly and posteriorly. Siphons fused at base.

B. paranensis Orbigny. A few species, in South and Central America and in Africa.

The typical species is stated to possess a byssus, whereas the African species in most cases live in the cavities of *Aetheria* shells.

IV. STIRPS ISOCARDIACEA

Shell smooth or concentrically sculptured; ligament external; main teeth more or less parallel to the margin.

1. Family KELLYELLIDAE

Shell variable in size, roundish, oval or angulate, smooth or concentrically striated; umbo more or less close to the anterior margin and anteriorly directed, in most cases fairly projecting, often a lunule is delimited by a furrow; ligament external, weak; hinge variably strong; right valve with a central tooth situated anterior to the umbones and a main tooth, which is sometimes posteriorly triangular, and with its anterior end in most cases above the central tooth, occasionally upon this with a weak tooth-shaped thickening; the anterior main tooth of the left valve is elongated or angular, posterior to it is a shorter or longer tooth which is not always distinct; the mantle line is in most cases not indented. The mantle is variable, sometimes it is completely open, without siphons, sometimes with distinct siphons, at the margin with tentacle-like processes; the gill is thick, with fine filaments which are inwardly greatly broadened, in *Vesicomya stearnsi* with a narrow outer lamina; the ascending lamellae have free margins; foot ventrally flattened, without byssus; labial palps narrow. Inhabitants of the deep sea.

Kellyella M. Sars, 1870 (*Kelliella*)

Characters of the family.

Several species in the depths of various seas.

Subgenus *Kellyella* s. s. Shell very small and thin, roundish; lunule distinctly delimited. Mantle open, posteriorly with marginal tentacles; anal siphon short; gill laminae unequal. *K.* (*K.*) *miliaris* (Philippi) (Fig. 817).
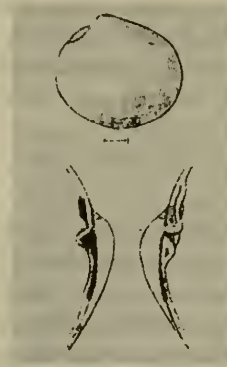

Fig. 817. Shell of *Kellyella miliaris* (Philippi) and the more highly enlarged hinge margins (after Sars).

Subgenus *Vesicomya* Dall, 1886. Shell fairly small, roundish; lunule delimited. *K.* (*V.*) *atlantica* (E. Smith).

Subgenus *Archivesica* Dall, 1908. Shell large, longish, without delimited lunule, without distinct mantle sinus. *K.* (*A.*) *gigas* (Dall).

Subgenus *Callogonia* Dall, 1889. Shell similar to *Archivesica*, but with distinct mantle sinus; animal unknown. *K.* (*C.*) *leeana* (Gall).

? *Veneriglossa* Dall, 1886 (synonym *Atopodonta* Cossmann, 1887).

Shell roundish; umbo anteriorly inclined; lunule delimited; the hinge appears to be similiar to that of *Vesicomya*, hence *Veneriglossa* may be identical with *Vesicomya*; Dall had doubts about this after he first placed it in the venerids. *V. vesica* (Dall).

855   ? *Pauliella* Munier-Chalmas, 1895

Shell small, roundish, angulate above; umbo only slightly projecting; lunule distinct; ligament external; hinge margin with main teeth similar to those in *Kellyella* and in each valve with 3 anterior lateral teeth

parallel to the margin; externally with fine concentric rings; mantle line posteriorly weakly indented.

P. bernardi Munier-Chalmas, near St. Paul Island.

2. Family ISOCARDIIDAE

Shell medium-sized, fairly weak, with very strong, anteriorly inrolled umbones; surface smooth or with concentric sculpture; ligament external; each valve with 2 main teeth which are parallel to one another and partly bilobed and a long posterior lateral tooth, sometimes with rudimentary anterior lateral teeth; mantle line not indented. Mantle with 2 posterior openings, papillose at the margin, without siphons; gill laminae broad, folded; foot hatchet-shaped, with byssus; labial palps narrow.

Isocardia (Klein) Lamarck, 1799

Synonyms *Glossus* + *Glossoderma* Poli, 1795; *Bucardium* Megerle von Mühlfeld, 1811; *Bucardia* Schumacher, 1817.

Characters of the family.

Subgenus *Isocardia* s. s. (synonym *Tychocardia* E. Römer, 1869). Shell with brown periostracum, smooth, without posterior edge. *I. (I.) humana* (Linné) (Fig. 818), in the Mediterranean Sea and the neighboring Atlantic Ocean.

Fig. 818. Inner side of the right shell valve of *Isocardia humana* (Linné).
Length 6 cm.

Subgenus *Miocardia* H. & A. Adams, 1857 (*Meiocardia*). Shell without distinct periostracum, with strong edge to a posterior corner, anterior to it with concentric folds. *I. (M.) moltkiana* (Spengler). Few species, in warm seas.

V. STIRPS CYPRINACEA

Shell oval to elongated; umbo more or less anteriorly shifted, ligament external; in addition to the right central tooth, posterior main teeth and a posterior lateral tooth are present; mantle line in most cases without sinus. Incurrent and excurrent openings with papillae, without siphons; gill laminae folded; foot with groove. Marine inhabitants.

1. Family CYPRINIDAE

Shell roundly oval, bulging, with strong periostracum, finely concentrically striated; umbo situated anterior to the center; hinge margin broad; posterior to the central tooth of the right valve, a deeply furrowed triangular main tooth; a pair of short anterior lateral teeth and a long posterior one; left valve with a high, often cleft tooth situated posterior to the central tooth, and one posterior main tooth, which is 856 separated from it by a triangular field, in addition with a short anterior lateral tooth. Mantle anteriorly open; foot thick, with ventral groove; gill laminae unequally broad, the outer one half-moon-shaped; the proximal part of the kidney is long and narrow, the distal part wide, sack-shaped.

Cyprina Lamarck, 1818

Synonyms *Arctica* Schumacher, 1817 (non Moehring, 1758); *Armida* Gistel, 1848; *Asmidia* Moerch, 1853; *Cypriniadea* Rovereto, 1900.
Characters of the family.
C. islandica (Linné) (Fig. 819), in the northern Atlantic Ocean.

2. Family LIBITINIDAE

Shell more or less elongated, with umbones situated far forward; hinge margin moderately broad or narrow, on either side with 2 main teeth and a posterior, more or less elongated lateral tooth, on the left also with a short anterior lateral tooth. Anterior mantle opening and foot small; labial palps short. The animals live in caverns of rocky and coral reefs.
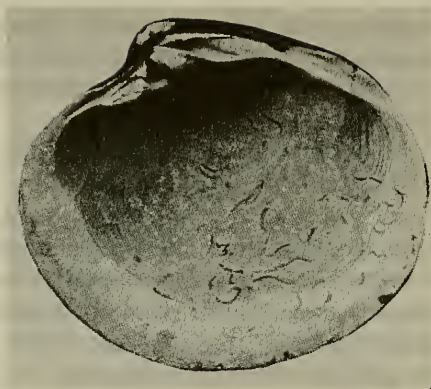
Fig. 819. Inner side of the right shell valve of *Cyprina islandica* (Linné).
Length about 8 cm.

Libitina Schumacher, 1817

Synonyms *Trapezium* Megerle von Mühlfeld, 1811 (non Mus. Calonn., 1797); *Cypricardia* Lamarck, 1819.

Shell strong, trapeze-shaped, with posterior edge and nearly terminal umbones; the central tooth of the right valve is sometimes more ventrally, sometimes more posteriorly directed, sometimes anterior to it a small lateral tooth is developed; the posterior main tooth is clasped by the two main teeth of the left valve; the left anterior lateral tooth situated anterior to the central tooth is in most cases well developed.

Few species, in warm seas.

Subgenus *Glossocardia* Stoliczka, 1870. Shell fairly large and inflated, exteriorly concentrically striated; central tooth of the right valve strong, the main tooth lying above it more or less bipartite; the main tooth of the left valve catching between the two is triangular, the upper one weak. *L.* (*G.*) *obesa* (Reeve).

Subgenus *Libitina* s. s. Shell not or only slightly inflated, concentrically and sometimes radially striated; umbo depressed; the upper main tooth of the right valve simple or cleft; the two main teeth of the left valve simple; right valve with 2 posterior lateral teeth. *L.* (*L.*) *bicarinata* Schumacher.

Coralliophaga Blainville, 1824

Synonym *Lithophagella* (Gray) H. & A. Adams, 1857.

Shell longish, fairly thin, colorless, radially striated; umbo low, much closer to the anterior margin; right valve with 2, in most cases

parallel, main teeth and one posterior lateral tooth; left valve with 2 parallel main teeth, a small anterior one and an elongated posterior lateral tooth; mantle line with a sinus below the posterior adductor muscle scar.

857

C. coralliophaga (Chemnitz). Few species, in warm seas.

Isorropodon Sturany, 1896

Shell small, elongated oval, concentrically striated; umbo closer to the anterior end; hinge margin narrow; on the right with 2 main teeth parallel to one another, the lower of which lies anterior to the umbo, and a thin posterior lateral tooth; on the left with a bipartite anterior and a thin posterior main tooth, as well as a ridge-shaped posterior lateral tooth; mantle sinus weak.

I. perplexum Sturany, in the eastern Mediterranean Sea (deep sea).

VI. STIRPS CYAMIACEA

A group of small bivalves, which live mainly in the southern seas and have been so far mostly classified with the Erycinacea, from which they differ by the presence of 2 posterior mantle openings; they have 2 gill laminae on either side and a byssal gland in the foot; an internal ligament is in most cases present, but sometimes does not seem to be separated from the external one.

1. Family CYAMIIDAE

Shell small and thin, in most cases colorless, sometimes with fine radial sculpture, more or less strongly bulging; hinge margin weak, with internal, short cartilage, anterior to which on the right is a more or less distinct bipartite tooth; correspondingly on the left are 2 teeth clasping it. Mantle ventrally open, posteriorly with 2 fairly large openings, the lower of which bears marginal papillae; gill laminae folded, the inner one very broad; labial palps small, triangular; foot fairly long, anteriorly pointed, with small byssal pit; anterior adductor muscle somewhat smaller than the posterior; sexes separate, in the inner gill lamina there is sometimes brood care.

Cyamiomactra Bernard, 1897

Shell very small, in most cases longer than broad, smooth or with radial striae; ligamental cartilage elongated; slanting; right valve with 2

main teeth which are continuous above and 2 anterior and posterior lateral teeth; left valve with a ventrally cleft main tooth and posterior to it a thin main tooth; anterior lateral tooth at the beginning greatly elevated, posterior one elongated; inner shell margin smooth or denticulate. Animal unknown.

C. problematica Bernard (Fig. 820). Few species, near Australia, New Zealand, and in the Antarctic Ocean.
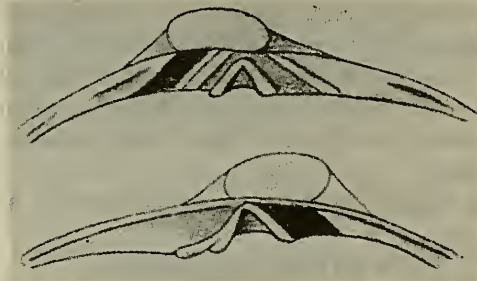

Fig. 820. Hinge margins of *Cyamiomactra problematica* Bernard, enlarged (after Bernard).

Perrierina Bernard, 1897

Shell very small, irregularly roundish, thin, smooth; ligamental cartilage internal, short; hinge margin fairly narrow; on the right with a angle-shaped main tooth, on the left with a forked one and posterior to it a thin main tooth, as well as with a short anterior and posterior lateral tooth; anterior and posterior to the hinge teeth are a few marginal denticles as indications of radial ribs.

P. taxodonta Bernard, near the Steward Islands and one species [*fragillima* (Thiele)] from Kerguelen.

858

Cyamium Philippi, 1845

Shell elongated oval; umbo more or less anteriorly shifted; ligament partly external, partly internal, the latter part sometimes triangular, sometimes more elongated; hinge teeth variable, when fully developed similar to those in *Perrierina*: on the right with an angle-shaped tooth, corresponding to which on the left is a forked one and anterior and posterior to it one short tooth each, sometimes the teeth are weak, 2 on either side; mantle line unindented. The mantle forms an opening for the byssus-bearing foot; a wide opening at the posterior end without siphons,

and above it an excurrent opening; on either side 2 gill laminae, the outer one fairly narrow.

C. antarcticum Philippi. A few species, in the Antarctic Ocean.

Legrandina Tate & May, 1901

Shell very small, oval, angulate above, with indications of a fine radial sculpture; ligamental cartilage oblique, anterior to it on the right a main tooth, corresponding to which on the left are 2 diverging teeth; anterior and posterior to the hinge teeth is a small number of marginal denticles. Animal unknown.

L. bernardi Tate & May, near Tasmania.

Pseudokellya Pelseneer, 1903

Shell roundish or somewhat angular, uniformly bulging, with weak radial sculpture; umbo moderately elevated, situated in the center; hinge margin posterior to the ligament prolonged somewhat ridge-shaped; anterior hinge teeth of the left valve fairly long, diverging in an acute angle.

P. cardiformis (Edg. Smith). Few species, in the Antarctic Ocean.

Ptychocardia Thiele, 1912

Shell somewhat higher than long, with high, anteriorly directed umbones, peculiarly angular, with a strong median fold and with numerous small radial folds; ligamental cartilage small; hinge teeth of the left valve short, the posterior one angle-shaped; right valve with a distinct bipartite tooth, anterior part angle-shaped. Animal unknown.

P. vanhöffeni Thiele (Fig. 821). 2 Antarctic species.

859

? *Turtonia* Alder, 1848

Shell small, smooth, brown, not gaping; umbo situated anterior to the center; ligament only external; hinge margin on either side with 2 anterior teeth and with a more or less distinct posterior lateral tooth, corresponding to which is a furrow in the other valve. Mantle open below; incurrent opening not separated from the anterior one; excurrent opening only slightly projecting; gill laminae unequal; foot fairly long, with byssus.

T. minuta (Fabricius), in the northern seas.

The systematic position of *Turtonia* is uncertain; the shell has little similarity with *Kellyella*; the hinge is similar to that of certain *Cyamium*
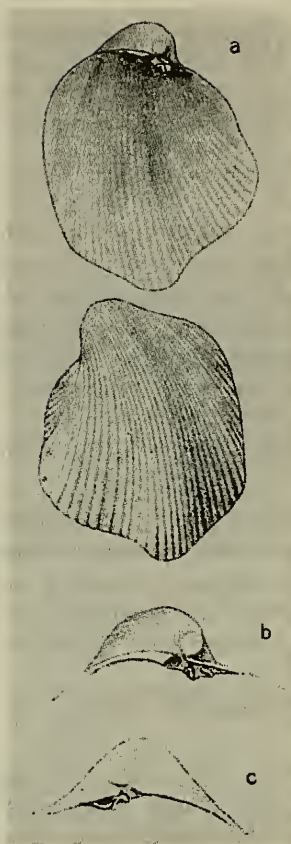
Fig. 821. *Ptychocardia vanhöffeni* Thiele.
a, inner and outer side of the left shell valve; b, c, the hinge margins, more strongly enlarged.

species, but it lacks the internal ligament and the animal differs by the wide open mantle.

2. Family SPORTELLIDAE

Dall established the family Sportellidae without sufficient diagnosis; he included the genera *Sportella* Deshayes, *Anisodonta* Deshayes, and *Hindsiella* Stoliczka, which are mainly Tertiary species; P. Fischer included some of them in the Galeommatidae, and some near *Libitina*. From the former it is distinguishable, according to Dall, by the absence of the mantle cover on the shell surface; the animal, known only in the case of *Anisodonta* (*Basterotia*) *quadrata* (Hinds), has a fairly small

opening for the foot and posteriorly 2 openings. In this respect it agrees with *Cyamium*, and it is possible that they are related with that genus, but the ligament is in most cases only external.

<h3 style="text-align:center">*Sportella* Deshayes, 1858</h3>

Synonym *Fabella* Conrad, 1863.
Shell transversely oval, smooth; umbo in most cases closer to the posterior end; ligament on a more or less distinct ridge; cartilage resting in a pit or on a thickening; hinge margin on either side with 2 teeth.
S. dubia (Deshayes) †. Dall has described a few recent Californian species and 2 from North Carolina.

<h3 style="text-align:center">*Anisodonta* Deshayes, 1858</h3>

Umbo more or less close to the anterior margin; ligament short; hinge margin on either side with one tooth.
Section *Fulcrella* Cossmann, 1886. Shell rounded rectangular, only slightly gaping, without posterior edge; ligament elongated, without larger intervening space along the slightly projecting teeth. *A. (F.) paradoxa* (Deshayes) †; Dall included a couple of species from North Carolina and the West Indies.—Section *Anisodonta* s. s. Shell longish, with more or less strong posterior edge, only slightly gaping; umbo only slightly projecting; surface rough; ligament support fairly long, not projecting; teeth moderately strong. *A. (A.) complanata* Deshayes †. —Section *Basterotia* C. Mayer, 1859 (synonym *Eucharis* Récluz, 1850, non Latreille, 1804). Shell inflated, posteriorly and ventrally more or less gaping, posteriorly angular; support of the ligament short, separated from the projecting teeth by an intervening space. Mantle margin beset with papillae; foot small, tongue-shaped, with a furrow; labial palps short; gill laminae unequally broad, posteriorly fused. *A. (B.) corbuloides* (Hörnes) †; a few living species in warmer seas.

<h2 style="text-align:center">3. Family NEOLEPTONIDAE</h2>

860

Shell very small, with internal ligamental cartilage; left valve with an angle-shaped, elongated anterior tooth, which is clasped by 2 teeth of the right valve, and a posterior lamella on either side. Mantle without tentacles, anteriorly and ventrally open, posteriorly with 2 slightly elongated openings with marginal papillae; foot anteriorly and posteriorly somewhat prolonged, without byssal pit; outer gill lamina very narrow, mainly formed of the ascending lamella; both laminae smooth.

Neolepton Monterosato, 1875

Shell oval, angulate above, concentrically striated; umbo situated close to the center; hinge margin on the right with one main tooth, on the left with 2 of these; the posterior lamella of the right valve corresponds to a pit of the left.

Lutetina Vélain, 1876 (*antarctica* Vélain, from St. Paul Island), according to Bernard, is not substantially different; *Notolepton* Finlay, 1927 (*antipodum* (Filhol), from New Zealand) is also scarcely separable.

N. sulcatulum (Jeffreys), in European seas.

Epilepton Dall, 1899, is similar to *Neolepton*; cartilage in a slanting posterior furrow; hinge on either side with a simple posterior and a hook-shaped anterior lamella. *E. clarkiae* (Jeffreys). Monterosato, 1909, proposed a group *Arculus* for *Lepton sykesii* Chaster.

Davisia J. E. Cooper & Preston, 1910 (non Del Guercio, 1909), likewise does not appear to differ significantly from *Neolepton*. *D. cobbi* Cooper & Preston, from the Falkland Islands.

Pachykellya Bernard, 1898

Shell very small, thick, higher than long, angulate above, posteriorly shorter than anteriorly, smooth; ligament internal; hinge margin inwardly delimited by ridges, since the umbones are not hollowed; hinge teeth similar to those of *Neolepton*. Animal unknown.

P. edwardsi Bernard (Fig. 822). Few species, near Stewart Island and in Foveaux Strait.

Fig. 822. Hinge margins of *Pachykellya edwardsi* Bernard, enlarged (after Bernard).

Puysegeria Powell, 1927

Shell obliquely oval; right valve with a long anterior lamella, which is hook-shaped anterior to the cartilage, and a more or less short posterior lamella; left valve with a strong, hook-shaped anterior lamella, a triangular main tooth, and a posterior tubercle.

P. cuneata Powell. 2 species, near New Zealand.

VII. STIRPS GAIMARDIACEA

Shell with umbones more or less close to the anterior end; hinge weak. Mantle with 3 openings; foot small, with a byssal gland; the eggs developed (always ?) in the gills. Marine.

1. Family GAIMARDIIDAE

Shell thin, smooth, in most cases small, brown; umbo more or less close to the anterior end, which is often somewhat pointed; ligament external or sunken; hinge margin weak, in most cases on either side with one main tooth, but which may however be completely absent; mantle line without sinus. Mantle with an anterior opening for the foot and 2 posterior openings; gill laminae smooth or folded; foot with byssus; pericardial limb of the kidney long and narrow, distal part sack-shaped, largely situated below the pericardium, posteriorly with lobes, which surround the foot retractor; interconnection of the two kidneys sometimes long and wide, sometimes not present.

Eugaimardia Cotton, 1931

Synonym *Neogaimardia* Cotton, 1931, non N. Odhner, 1924.
Shell small, umbo situated close to the roundly-angled anterior end, directed anteriorly; ligament external; right valve with a central tooth, which is surrounded by two dorsally continuous teeth, and one posterior tooth; left valve? Animal unknown.
E. perplexa (Cotton), near South Australia.

Gaimardia Gould, 1852

Shell in most cases small, thin, oval or trapeze-shaped; umbo close to the anterior end, sometimes nearly terminal; ligament external or somewhat sunken; hinge margin weak, on the right with an angular tooth, which surrounds a denticle of the left valve, often toothless; 2 gill laminae on either side.
A few species, in southern seas.
Subgenus *Gaimardia* s. s. (synonyms *Modiolarca* Gray, 1847 (non 1843); *Phaseolicama* Valenciennes, 1854). Shell trapeze-shaped; ligament external or somewhat sunken; gill laminae folded, with interlamellar septa; ventral mantle fusion shorter than the incurrent opening; anterior foot gland separated from the byssal groove; anterior part of the foot flattened sole-like. *G. (G.) trapezina* (Lamarck) (Fig. 823).
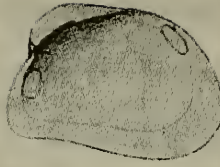
Fig. 823. Inner side of the right shell valve of *Gaimardia trapezina* (Lamarck).

Subgenus *Kidderia* Dall, 1876. Shell longish; ligament somewhat sunken; gill laminae smooth; interlamellar septa only in the marginal part; ventral mantle fusion longer than the two posterior openings together; anterior foot gland opening into the end of the byssal groove. Section *Kidderia* s. s. Shell smooth. *G.* (*K.*) *minuta* (Dall).—Section *Costokidderia* Finlay, 1927. Shell with radial folds. *G.* (*C.*) *costata* (N. Odhner).

? *Neogaimardia* N. Odhner, 1924

Shell small, oval, with nearly centrally placed umbones; anterior part somewhat beak-shaped because of a ventral sinus; ligament internal; right valve with central tooth and one tooth above it; left valve with a hook-shaped tooth. Outer gill lamina reduced; anterior mantle opening small; incurrent opening ventral, long; anterior foot gland separated from the byssal groove.

N. rostellata (Tate). Few species, near Australia and New Zealand.

862 ### ? 2. Family JULIIDAE

Shell small, oval; umbo more or less anteriorly positioned; ligament external, marginal; nearly in the center of the inner side lies the roundish scar of an adductor muscle. Animal unknown. The systematic position of the two genera is uncertain.

Julia Gould, 1862

Synonym *Prasina* Deshayes, 1863.

Shell fairly strong, green, covered; umbo close to the anterior end and forwardly inclined, on the right side with a small spiral process; the lunule is deeply sunken and in both valves has a tooth-like thickening of the margin, corresponding to a pit of the other valve; the thickening in the right valve lies above the pit, in the left valve below it.

J. exquisita Gould. Few species, in the Pacific and Indian Oceans.

? *Edenttellina* Gatliff & Gabriel, 1911

Synonym *Ludovicia* Cossmann, 1888, non Marschall, 1873 = *Ludovicius* Rondani, 1843.

Shell thin, yellow, smooth, flattened, oval, anteriorly pointed, umbo situated more or less anterior to the center; on the right with a spiral process; in the right valve with a tooth-shaped thickening of the anterior hinge margin, corresponding to a pit of the left valve; lunule not deepened.

N. typica Gatliff & Gabriel. 2 species, on the Australian coasts.

VIII. STIRPS DREISSENACEA

Shell anteriorly pointed, with completely or nearly terminal umbones, ventrally flattened; periostracum strong; inner side not nacreous; ligament marginal, somewhat sunken; hinge margin toothless; a septum in the anterior corner on either side, to which the anterior adductor muscle attaches; scar of byssal muscle long and narrow. The mantle below has an opening for the foot and posteriorly 2 short siphons, the lower one of which is larger; with papillae on the margin; foot with byssus; the gill laminae are nearly equally broad, smooth, with a few interlamellar septa, posteriorly fused with one another; pericardial limb of the kidney long and narrow; distal limb anteriorly low, interconnected, posteriorly bilobed, surrounding the byssal muscle. Development with free ciliated larvae. In fresh-water.

Dreissena P. van Beneden, 1835 (*Driessena*)

Characters of the family.

Several species, in Europe, Asia, Africa, and America.

Subgenus *Dreissena* s. s. (synonyms *Tichogonia* Rossmaessler, 1835; *Mytilina* Cantraine, 1837; *Mytilomya* (Cantraine) Bronn, 1838). Shell without process for the attachment of the anterior foot muscle. *D. (D.) polymorpha* (Pallas).

Subgenus *Congeria* Partsch, 1836 (synonym *Enocephalus* Münster, 1831, nom. nud.). Shell with a process for the attachment of the anterior foot muscle on the septum. Typical species, *D. (C.) subglobosa* (Partsch), 863 fossil, quadrangular, thick.—Section *Mytilopsis* Conrad, 1857 (synonyms *Praxis* H. & A. Adams, 1857; *Mytiloides* Conrad, 1874, non Brongniart, 1822). Shell elongated, thin. *D. (M.) leucophaeata* (Conrad).

IX. STIRPS LUCINACEA

Shell in most cases roundish; the right central tooth absent, and not seldom are all hinge teeth reduced. The mantle as a rule has 2 posterior openings, seldom the upper one is elongated somewhat funnel-shaped and invaginable, without retractor; foot in most cases long and worm-shaped, seldom short; gill laminae smooth or weakly folded; sexes separate.

1. Family UNGULINIDAE

Shell small or moderately large, in most cases without distinct sculpture, roundish; umbo only slightly elevated; hinge margin as a rule on either side with 2 teeth or toothless; ligament more or less sunken; mantle line unindented; adductor muscle scars narrow, the anterior one continuous with the mantle line; shell margin smooth. The mantle posteriorly has a small incurrent aperture and a larger excurrent aperture; the foot is long, often swollen at the end; labial palps different; gills on either side with 2 laminae.

A. Subfamily Ungulininae

Hinge teeth present.

Diplodonta Bronn, 1831

Synonyms *Mysia* T. Bronn, 1833 (non (Leach) Lamarck, 1818); *Gloconome* Leach, 1852; *Cycladicama* Valenciennes, 1854; *Mittrea* Gray, 1854.

Shell roundish, equivalve, completely covered, without distinct lunule; ligament and cartilage external, on a more or less projecting ridge; each valve with 2 teeth, of which the anterior of the left and the posterior of the right valve is divided by a furrow. Excurrent opening without siphon; labial palps fairly large.

Several species, mainly in warmer seas.

Section *Diplodonta* s. s. Shell moderately bulging, without lunule; umbo somewhat elevated; surface only with growth lines; hinge margin anteriorly prolonged ridge-shaped. *D.* (*D.*) *lupinus* Brocchi. Finlay, 1927, proposed a "genus" *Zemysia* for *D. zelandica* (Gray) and a subgenus *Zemysina* for *D. globus* Finlay, related to the Australian *D. globularis* (Lamarck).—Section *Felania* Recluz, 1851. Shell lens-shaped, with a small lunule; surface with growth lines; hinge margin anteriorly and

posteriorly prolonged ridge-shaped. *D.* (*F.*) *diaphana* (Gmelin).—Section *Sphaerella* Conrad, 1838. Shell large, concentrically striated; lunule indicated by a furrow; posterior right hinge tooth much larger and more oblique than that in *Diplodonta* s. s. *D.* (*S.*) *subvexa* Conrad †; living *D.* (*S.*) *verrilli* Dall = *turgida* Verrill & Smith.—Section *Felaniella* Dall, 1899. Shell compressed, smooth, with distinct periostracum; external ligament longer than the cartilage. *D.* (*F.*) *usta* (Gould). *Numella* Iredale, 1924, proposed for *D. adamsi* (Angas), appears to be related to *Felaniella*. —Section *Phlyctiderma* Dall, 1899. Shell fairly small, strongly bulging; surface sculptured with small warts or dots or crossed lines. *D.* (*P.*) *semiaspera* Philippi.

864   *Joannisiella* Dall, 1895

Synonym *Joannisia* Dall, 1895, non Monterosato, 1884, nec Kieffer, 1894.

Shell thin, with distinct periostracum and growth lines; hinge teeth as in *Diplodonta*; ligamental cartilage fairly deeply sunken. Animal unknown.

J. oblonga (Hanley). Few species, in brackish water of the Philippines and Australia.

Ungulina Daudin, 1802

Synonym *Clotho* Basterot, 1825, non Faujas de S.-Fond, 1808.

Shell somewhat irregularly roundish, smooth or concentrically striated, with more or less strong periostracum; umbo anteriorly directed; the ligament and the cartilage situated in 2 deep pits lying one behind the other; the smaller hinge tooth of both valves is in most cases weakly developed. Excurrent aperture with short tube; oral lobes small and pointed.

U. rubra Daudin. A couple of species on the African west coast, in holes of reefs.

B. Subfamily Thyasirinae

Shell in most cases small and thin, roundish or angulate, often with a posterior radial fold; hinge toothless or with indications of teeth. Mantle with a posterior opening; foot very long; liver and gonads situated in lateral bulges of the visceral sack; the kidneys are longish sacks anterior to the foot retractors and posterior to the pericardium, interconnected; proximal limbs long and narrow.

Thyasira (Leach) Lamarck, 1818

Synonyms *Axinus* J. Sowerby, 1818; *Cryptodon* Turton, 1822; *Bequania* (Leach) T. Brown, 1827; *Ptychina* Philippi, 1836; *Clausina* Jeffreys, 1837 (non T. Brown, 1827); *Thyatira* (Leach) Gray, 1847 (non Hübner, 1816); *Conchocele* Gabb, 1866.

Shell roundish or angulate, colorless, smooth, often with 1 or 2 posterior radial folds; umbo anteriorly directed; a small broad and short lunule is sometimes indistinct, but often deeply sunken and on the right forming a tooth-shaped projection; ligament and cartilage fused, the latter situated in a furrow; hinge margin toothless.

Several species, in various seas.

Section *Thysira* s. s. Shell with dorsal, more or less distinct fields; posterior field furrowed or folded. *T. (T.) flexuosa* (Montagu) (Fig. 824). —Section *Philis* P. Fischer, 1861. Lunule greatly sunken, forming a hemispherical pit. *T. (P.) cumingi* (P. Fischer).—Section *Axinulus* Verrill & Bush, 1898. Shell small, roundish or transversely oval, without distinct dorsal fields. *T. (A.) brevis* (Verrill & Bush). According to Dall, *Axinodon* Verrill & Bush, 1898 [*elliptica* (Verrill & Bush)] is not substantially different, likewise *Genaxinus* Iredale, 1930 (*albigena* Hedley).

Fig. 824. Shell of *Thyasira flexuosa* (Montagu), enlarged
(after Sars).

It is not clear as to how the "genera" *Parathyasira* and *Prothyasira* Iredale, 1930, are separable.

865   *Leptaxinus* Verrill & Bush, 1898

Shell with a weak posterior fold; ligament largely internal; hinge margin somewhat thickened, on the left forming a blunt denticle and a posterior lateral tooth, on the right a weak anterior and posterior lateral tooth.

L. minutus Verrill & Bush, in the northern Atlantic Ocean.

Axinopsis G. O. Sars, 1878

Shell small, roundish, bulging, without posterior depression of the dorsum; ligament narrow, internal; hinge margin of the right valve with a more or less strong tooth-shaped projection.

A. orbiculata G. O. Sars. Few species, mainly in cold seas.

2. Family LUCINIDAE

Shell of variable size, equivalve, roundish or transversely oval, smooth or with distinct concentric, sometimes also radial sculpture; not seldom an anterior and a posterior field are delimited by furrows or folds; umbones small, closely approximated, anteriorly directed; lunule in most cases small, depressed, asymmetrical; ligament in most cases fused with the cartilage, long, marginal, seldom completely internal; hinge margin as a rule on either side with 2 main teeth and with an anterior and posterior lateral tooth of the right valve, to which 2 teeth of the left valve correspond; some or all of these teeth may disappear; the anterior muscle scar is long and narrow, situated within the mantle line; the posterior one more roundish and situated higher; inner margin smooth, occasionally denticulate. The mantle has 2 posterior openings, the upper of which may be more or less elongated, but this tube has no retractors; the foot is in most cases long and worm-shaped but occasionally short; labial palps very small; the outer gill lamina absent, the inner is large and thick; sometimes the liver and the gonads lie in lateral bulges of the visceral sack; the kidneys, situated between the pericardium and the posterior adductor muscle, traversed by the median foot retractors; they are higher than long, joined with one another, proximal part short; sexes separate.

Phacoides Blainville, 1825

Synonym *Egraca* Leach, 1852.

Shell strong, roundish, colorless, with more or less distinct, concentric, sometimes also radial sculpture; ligament external; hinge margin with 2 main teeth on either side and with anterior and posterior lateral teeth.

Several species, mainly in warm seas.

Subgenus *Parvilucina* Dall, 1901. Shell small, strongly bulging, more or less strongly sculptured; hinge teeth complete; lower margin denticulate. Section *Parvilucina* s. s. Sculpture weak; anterior and posterior field only slightly or not delimited. *P. (P.) tenuisculptus* (Carpenter).—Section *Bellucina* Dall, 1901. Sculpture strong; anterior and posterior field distinctly demarcated. *P. (B.) eucosmia* Dall.

Subgenus *Linga* Gregorio, 1885. Shell nearly spherical, with concentric sculpture; anterior and posterior field more or less distinct. Section *Cavilucina* P. Fischer, 1887. Shell small, moderately bulging, concentrically striated; fields and teeth often weak; lunule small, often deep. *P.* (*C.*) *sulcata* (Lamarck) †; few living species.—Section *Pleurolucina* Dall, 1901. Shell with fine concentric sculpture and few strong radial folds. *P.* (*P.*). *leucocyma* (Dall).—Section *Linga* s. s. Shell very strong, spherical, with concentric lamellae and distinct dorsal fields. *P.* (*L.*) *columbella* (Lamarck) (Fig. 825).

866

Fig. 825. Inner side of the right shell valve of *Phacoides* (*Linga*) *columbella* (Lamarck).

Subgenus *Lucinoma* Dall, 1901. Shell in most cases large, lens-shaped, with concentric striae or lamellae and distinct periostracum; main teeth well developed; lateral teeth rudimentary; lower margin smooth. *P.* (*L.*) *filosus* (Stimpson). A few species, mainly in cold and deep water.

Subgenus *Callucina* Dall, 1901. Shell oval; dorsal fields indistinct; lunule small. Section *Epilucina* Dall, 1901. Sculpture weak; hinge teeth complete; lower margin smooth. *P.* (*E.*) *californicus* (Conrad).—Section *Callucina* s. s. Shell with concentric threads, sometimes with weak radial sculpture; each valve with only one main tooth; lower margin folded. *P.* (*C.*) *radians* (Conrad).—Section *Lucinisca* Dall, 1901. Shell with regular rough concentric and radial reticulate sculpture; dorsal fields distinct; right anterior main tooth rudimentary. *P.* (*L.*) *nassula* (Conrad).

Subgenus *Phacoides* s. s. (synonym *Dentilucina* P. Fischer, 1887). Shell fairly large, lens-shaped, with distinct dorsal fields and concentric sculpture; main teeth of full-grown shell weakly developed. *P.* (*P.*) *pectinatus* (Gmelin).

Miltha H. & A. Adams, 1857

Shell large, somewhat inequivalve; one valve often more bulging than the other, concentrically sculptured; dorsal fields indistinct, with a more or less deep posterior radial furrow; lunule very small; ligament deeply sunken, but not internal; main teeth well developed; lateral teeth rudimentary.

M. childreni (Gray). Few species, in warm seas.

Myrtea Turton, 1822

Synonym *Cyrachaea* Leach, 1852.

Shell fairly small, compressed, oval or somewhat angulate, with concentric sculpture, without delimited dorsal fields; lunule depressed; ligament sunken but not internal; right valve in most cases with 1, left with 2 main teeth; the lateral teeth of the left valve often indistinct.

Few species, in various seas.

Section *Myrtea* s. s. Shell without radial sculpture. *M. (M.) spinifera* (Montagu). Iredale, 1924, erected the genus *Notomyrtea* for *M. botanica* Hedley.—Section *Eulopia* Dall, 1901. Surface with fine radial sculpture between concentric lamellae. *M. (E.) sagrinata* (Dall).

Divaricella Martens, 1880

Shell colorless, roundish, more or less strongly bulging, sculptured with arch-shaped ridges, which meet angularly in a radial line, without distinct dorsal fields; lunule small, deply depressed; hinge margin on either side with 2 main teeth and somewhat variable lateral teeth, the anterior ones in most cases ·weak and close to the main teeth; posterior ones sometimes rudimentary.

867

A few species, in various seas.

Section *Divaricella* s. s. Ligament and cartilage fused, sunken in a groove, but not internal; dorsal fields not recognizable. *D. (D.) angulifera* Martens = *quadrisulcata* (Orbigny).—Section *Pompholigina* Dall, 1901. Shell greatly bulging; dorsal fields weakly marked; ligament external. *D. (P.) gibba* (Gray).—Section *Lucinella* Monterosato, 1883. External ligament reduced; cartilage internal, in an oblique pit. *D. (L.) divaricata* (Linné).

Loripes Poli, 1791

Synonyms *Ligula* Menke, 1830; *Lucinida* Orbigny, 1846.

Shell roundish, fairly thin, concentrically striated; dorsal fields scarcely indicated; lunule narrow and deep; cartilage separated from the ligament, completely internal; right valve with only one main tooth, the left with 2 of these; anterior lateral teeth often rudimentary, the posterior ones in most cases absent.

L. lacteus Poli. A few species, in various seas.

Iredale, 1930, proposed the following "genera": *Monitilora* for *Lucina ramsayi* Edg. Smith, *Wallucina* for *L. jacksoniensis* Edg. Smith, and *Nevenulora* for *Lucinida hilaira* Hedley. *Elathia* Issel, 1869, has only one main tooth on either side. *E. arconatii* Issel, in the Red Sea.

Megaxinus Brugnone, 1880

Shell roundish, concentrically striated; umbo anteriorly inclined; ligament externally visible, with projecting ridges; hinge margin toothless.

Few species, in warm seas.

Section *Pseudomiltha* P. Fischer, 1887. Shell more or less large; dorsal fields in most cases delimited. *M. (P.) giganteus* (Deshayes) †. —Section *Megaxinus* s. s. Shell fairly small and thin, anteriorly angulate, without dorsal fields. *M. (M.) transversus* (Bronn).

Lucina Lamarck, 1799

Synonym *Anodontia* Link, 1807.

Shell more or less large, fairly thin, roundish, bulging, concentrically striated, without dorsal fields; umbo only slightly projecting; ligament sunken in an oblique furrow, with few elevated ridges; hinge margin toothless.

Section *Lucina* s. s. Shell in most cases large; lunule fairly long and narrow; ligament distinctly external; anterior muscle scar long. *L. (L.) edentula* (Linné) (Fig. 826). Few species, in warm seas. Iredale, 1930, erected a genus *Prophetilora* for the Australian *arizela* Iredale, and a genus *Cavatidens* for his *omissa*.—Section *Loripinus* Monterosato, 1883. Shell small, inflated, thin; lunule broad and short; ligament almost completely internal; anterior muscle scar broad and short; foot short. *L. (L.) fragilis* Philippi, in the Mediterranean Sea.

? *Vaticinaria* Dall, 1901

Shell fairly small, very thin, without distinct sculpture, irregularly roundish; ligament more or less sunken; hinge margin toothless. Mantle with a posterior opening; foot short, with byssal groove; gills on either
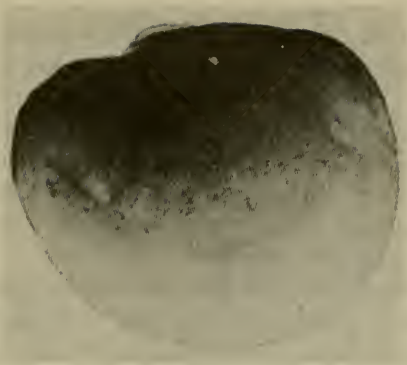
Fig. 826. Inner side of the right shell valve of *Lucina edentula* (Linné).
Length 8 cm.

side with only one lamina, posteriorly fused with one another; muscle scar oval; oral lobes small; anterior mantle margin thickened.

V. moseleyi (Edg. Smith). A couple of deep-sea species.

For a very small Australian species: *Lucina induta* Hedley (non Stoliczka), which in Hedley's opinion perhaps belongs to *Vaticinaria*, Iredale, 1924, has erected a genus *Mendicula* and named the species *M. memorata*; the animal is unknown.

Codokia Scopoli, 1777 *(Codakia)*

Synonyms *Lentillaria* Schumacher, 1817 (= *Lenticularia* Gray, 1847 = *Lintellaria* Bucquoy, Dautzenberg & Dollfus, 1898); *Orbiculus* Megerle von Mühlfeld, 1811; *Anfilla* Gregorio, 1884 (= *Antilla* P. Fischer, 1887).

Shell of variable size, roundish, lens-shaped, exteriorly with radial and concentric sculpture, interiorly often colored, without dorsal fields; umbo forwardly directed; hinge margin in most cases with 2 undivided main teeth on either side; lateral teeth may be absent.

Several species, in various seas.

Subgenus *Jagonia* Recluz, 1869. Shell fairly small and thin, radial sculpture stronger; lunule fairly large; ligament and cartilage external; anterior and posterior lateral teeth distinct; foot very short, anteriorly pointed. *C. (J.) orbiculata* (Montagu).

Subgenus *Codokia* s. s. Shell fairly large and strong, latticed; lunule very small; ligament and cartilage large, deeply sunken, exteriorly covered by a calcareous layer. Foot short; at the anterior part of the mantle is an accessory gill consisting of a few thin lamellae; siphon short or absent; anterior to the mouth opening is a glandular tube. *C. (C.) orbicularis*

(Linné). Iredale, 1930, erected a group *Pexocodakia* for *C. rugifera* (Reeve); main teeth more oblique; muscle scars longer; sculpture stronger.

Subgenus *Pillucina* Pilsbry, 1920. Shell small, strongly bulging, with radial sculpture; umbo fairly high; lunule small; ligament short, internal; hinge margin on either side with one main tooth; lateral teeth weak or absent; anterior adductor muscle scar only slightly elongated. Animal unknown. *C. (P.) spaldingi* (Pilsbry).

For a similar Australian species, which Iredale named *symbolica*, he in 1930 proposed a genus *Sydlorina*, and a genus *Epicodakia* for *consettiana* Iredale = *Lucina minima* Tenison-Woods, with strong radial sculpture and strong main and lateral teeth.

Corbis Cuvier, 1817

Synonyms *Fimbria* Megerle von Mühlfeld, 1811 (non Bohadsch, 1761); *Idothea* Schumacher, 1817 (non Fabricius, 1793).

Shell very strong, transversely oval, inflated, sculptured with concentric and intervening radial ridges; umbo almost median in position; lunule depressed; ligament partly external, partly sunken; hinge margin on either side with 2 main teeth and anterior and posterior lateral teeth, the latter of which are placed far from the main teeth; anterior muscle scar downwardly broadened, large, the posterior one smaller, oval; mantle line unindented, deepened; ventral margin denticulate. Mantle margin doubly fringed; excurrent opening with long, retractile process; foot long and pointed; oral lobes rudimentary; gills thick, folded.

869

C. fimbriata (Linné). Few species, in the Indo-Australian region.

? *Bathycorbis* Iredale, 1930

Shell very small, triangular-oval, sculptured with concentric lamellae; lunule weakly depressed, narrow and short, umbo elevated; left valve with 2, right with one main tooth; mantle line with a small indentation. Animal unknown.

B. despecta (Hedley), near Australia.

This small species was first included in *Chione*, subsequently in *Corbis*; Iredale appears to place this species with the lucinids, which however is less probable.

X. STIRPS ERYCINACEA

Shell as a rule small and thin, with internal ligament, sometimes partially or completely covered by the mantle margin; posteriorly the mantle has only one opening; foot as a rule with a posterior byssal gland.

1. Family ERYCINIDAE

Animal on either side with 2 gill laminae, the outer of which is narrower than the inner.

A. Subfamily Erycininae

Mantle margin in most cases with short papillae, but without tentacles, anteriorly often groove-shaped prolonged and in *Tellimya* forming a closed tube serving as an incurrent canal. Gonad hermaphroditic.

Scacchia Philippi, 1844

Shell transversely oval, thin, colorless, smooth; umbo situated somewhat posterior to the center; external ligament small; cartilage in a longish pit; right valve with one main tooth, left with 1 or 2 of these; lateral teeth weak. Mantle lobes largely separate, posteriorly with one opening; 2 gill laminae on either side; foot large, tongue-shaped; labial palps medium-sized.

S. elliptica (Scacchi), in the Mediterranean Sea.

Dall considered *Scacchia* as a subgenus of *Erycina* Lamarck, 1805 (synonyms *Eryx* Swainson, 1840; *Neaeromya* Gabb, 1873), the typical species of which, *pellucida* Lamarck, is fossil; also in the case of a few West Indian and Californian species only the shells are known, so that their relationship with *Scacchia* is uncertain. The external ligament is indistinct; cartilage situated in an oblique pit; hinge margin on either side with 1 or 2 small main teeth and 2 fairly long lateral teeth.

Iredale, 1924, proposed a genus *Melliteryx* for the Australian *E. acupuncta* Hedley; the shell is very small, exteriorly punctate, on either side with one main tooth and anterior and posterior lateral tooth. *Semierycina* (Monterosato) Cossmann, 1911, also has on either side one main tooth and an anterior and posterior lateral tooth. *E. (S.) prismaticum* Monterosato, in the Mediterranean Sea. Similar hinge teeth are also found in *E. bifurca* (Webster) from New Zealand, for which Finlay, 1927, has proposed a group *Arthritica*.

Bornia Philippi, 1836

Shell transversely oval or more triangular, in most cases shiny, sometimes somewhat folded; external ligament weak; cartilage short, a little posterior to the umbo; left valve with a moderately long posterior tooth and 2 shorter anterior ones; right valve with one anterior and 2 longer posterior teeth. Mantle margin anteriorly broadened, with a posterior opening; outer gill lamina smaller than the inner one; foot long; labial palps small.

A few species, in warmer seas.

Subgenus *Bornia* s. s. Mantle margin with short papillae, without long tentacles; byssal gland? *B. (B.) corbuloides* Philippi. Iredale, 1924, has proposed a genus *Borniola* for the Australian *B. lepida* Hedley.

Subgenus *Ceratobornia* Dall, 1899. Mantle with 2 anterior and 1 posterior long tentacles, in the greatly extensible posterior end of the foot with a byssal gland. *B. (C.) longipes* (Stimpson).

Kellya Turton, 1822 (*Kellia*)

Synonyms *Lasaea* (Leach) T. Brown, 1827; *Cycladina* Cantraine, 1835; *Poronia* Recluz, 1843; *Anapa* Gray, 1847; *Autonoe* Leach, 1852.

Shell small, transversely oval, inflated; umbo roundish, situated posterior to the center; ligament with large cartilage attached on the underside of the hinge margin; hinge teeth fairly variable, as a rule on either side with one small tooth below the umbones and on the left one anterior and one posterior lamella, corresponding to which on the right are 2 anterior and posterior lamellae each. Mantle margin anteriorly produced into a groove, which is continuous with the opening for the foot, posteriorly with a very short siphon; foot long, with byssus; outer gill lamina narrow, without ascending lamella; labial palps narrow; viviparous.

K. rubra (Montagu). Few species, in various seas.

Tellimya T. Brown, 1827

Synonyms *Chironia* Deshayes, 1839; *Oronthea* Leach, 1852; Goodalliopsis Raincourt & Munier-Chalmas, 1863; *Zoe* Monterosato, 1878 (non Philippi, 1840).

Shell roundish or transversely oval, smooth; umbo only slightly elevated; ligamental cartilage internal; hinge teeth somewhat variable, on either side 1 or 2 main teeth and 1 or 2 posterior teeth. Mantle margins beset with papillae, largely fused with one another and anteriorly

forming a tube serving as the incurrent canal, posteriorly with a short siphon; foot long, with byssus labial palps triangular; gill laminae not folded; viviparous.

A few species, in various seas.

Section *Tellimya* s. s. Shell roundish, inflated; external ligament rudimentary; cartilage strong; hinge in full development with 2 anterior and 2 posterior teeth on either side, the anterior of which are shorter and are sometimes fused above. *T. (T.) suborbicularis* (Montagu).— Section *Mancikellia* Dall, 1899. Shell small, roundish; right valve with a small main tooth; anterior and posterior lateral tooth elongated; left valve with a weak or rudimentary anterior and posterior lamella. *T. (M.) pumila* (S. Wood).—Section *Kelliola* Dall, 1899. Shell small, longish, posteriorly shortened, posterior to the umbones with a strong cartilage and a strong anterior tooth on either side. *T. (K.) symmetros* (Jeffreys).

Diplodontina Stempell, 1899 (*tumbesiana* Stempell, from Chile) is scarcely different from *Tellimya*. This genus has been known in most 871 cases as *Kellia* Turton; however, the typical species, the latter designated by Herrmannsen, is *Cardium rubrum* Montagu, so that it becomes a synonym of *Lasaea* Leach.

? *Sphaerumbonella* Coen, 1933

Shell thick, bulging, oval trapeze-shaped, greenish; umbo situated somewhat anterior to the center, with a hemispherical, smooth embryonic shell; ligament internal; hinge margin without main teeth, on either side with one anterior and posterior lateral tooth. Animal unknown.

S. brunellii Coen, in the Indian Ocean, near Massaua.

? *Thecodonta* A. Adams, 1864

Shell longish oval; umbo close to the anterior end; ligamental cartilage with a triangular ridge, anterior to which on the left is a short lamella, posterior to it with a long, narrow lamella, in the continuation of which another lamella is present; right valve and animal unknown.

T. sieboldi A. Adams, near Japan.

? Subgenus *Serridens* Dall, 1899 (synonyms *Pristes* Carpenter, 1864 (non Latham, 1794) = *Pristiphora* Carpenter, 1866, non Blanchard, 1835). Shell similar to *Thecodonta*, but cartilage without ridge; posterior lamella simple and teeth finely transversely striated. *S. oblongus* (Carpenter), near California.

B. Subfamily Leptoninae

Shell covered; ligamental cartilage short and thick; left valve with anterior and posterior lamella and a small anterior denticle, which is sometimes continuous with the lamella; right valve anteriorly and posteriorly with a couple of lamellae. Mantle anteriorly and posteriorly open, at the margins with more or less numerous tactile threads and at the anterior and posterior junction of the two lobes, each bearing a longer tentacle; on either side 2 smooth gill laminae; foot with a creeping sole and a posterior byssal gland; sexes separate (Fig. 827).
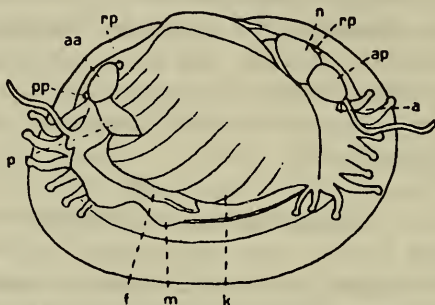
Fig. 827. *Lepton* sp., seen from the left, after removal of the left mantle lobe. a, anus; aa, ap, anterior and posterior adductor muscle; f, foot; k, gill; m, mantle margin (partly fused ventrally with that of the opposite side); n, kidney; p, labial palps; pp, attachment of the protractor of the foot; rp, rp, retractor of the foot (after Pelseneer).

Lepton Turton, 1822

Synonym *Eupoleme* Leach, 1852.
Shell colorless, roundish or oval or somewhat triangular, in most cases thin and only slightly bulging, smooth or rough; umbo small, close to the center.
    L. squamosum (Montagu). A few species, in various seas.

C. Subfamily Galeommatinae

Shell in most cases ventrally gaping and often more or less covered by the reflected mantle margin, which is beset with a few small warts; the shell in most cases is elongated, with internal ligamental cartilage;

hinge teeth variable. The mantle anteriorly and posteriorly has a tentacle; anteriorly it is open and posteriorly has a fairly small opening; 2 smooth gill laminae on either side; foot with small byssal gland situated in the posterior part; sexes separate.

Pythina Hinds, 1844

Shell not gaping and not covered by the mantle margin, but by a distinct periostracum, in most cases with fine radial sculpture, trapezoidal or triangular, with straight or somewhat concave lower margin; hinge margin with 2 main teeth (?) and weak lateral teeth. The interpretation of the main teeth is not clear, probably only an anterior tooth is to be considered as such. The not reflected mantle margin is beset with papillae; anterior opening wide; foot with short posterior furrow and small byssal gland.

Section *Pseudophythina* P. Fischer, 1878. Periostracum with scaly rays; shell only with growth lines; both valves with 2 main teeth and a weak posterior tooth. *P. (P.) macandrewi* (P. Fischer), in the Atlantic Ocean, near Portugal. The animal is similar to that of *Pythina*, therefore this group belongs neither to *Bornia* nor to *Tellimya*, but it also has similarity with a *Lepton*-species studied by Pelseneer.—Section *Phythina* s. s. Both valves have a strong first anterior main tooth, anterior to which on the left are present a small, short lamella and posteriorly on the right 2, on the left one lamella. *P. (P.) deshayesiana* Hinds. Few species, in the Indo-Pacific region.—Section *Rochefortula* Finlay, 1927. Shell latticed; hinge margin on one side with an anterior and posterior tooth, on the other side with longer lamellae. *P. (R.) reniformis* (Suter), near New Zealand.

Also belonging here are perhaps *"Rochefortia" excellens* and *viastellata* Hedley, for which Iredale, 1929, proposed the genera *Barrimysia* and *Fastimysia*.

Myllita Orbigny & Recluz, 1850

Shell colorless, transversely oval, only slightly bulging, with strong folds diverging in the center; ligamental cartilage in an oblique pit; right valve with a small main tooth and the left with 2 of these; an anterior and a posterior lamella on the right and 2 each of these on the left.

M. deshayesii (Orbigny & Recluz) (Fig. 828). Few species, near Australia and New Zealand. Finlay, 1927, proposed a "genus" *Zemyllita* for the more elongated New Zealand *M. stowei* (Hutton); further for roundish, small species, the sculpture of which has greater similarity with *Divaricella*, a genus *Myllitella*; genotype *M. vivens* Finlay.

Fig. 828. Interior and exterior sides of a shell valve of *Myllita deshayesii* (Orbigny & Recluz).

Solecardia Conrad, 1849

Shell thin, in most cases smooth and shiny, more or less elongated oval; umbo only slightly projecting, close to the center; ligament external and with an oblique internal cartilage; hinge often only weakly developed. Shell more or less extensively covered by the mantle margin, which is sometimes smooth, sometimes beset with small warts, sometimes also with longer threads, anteriorly and posteriorly with an unpaired tentacle; foot large, with small posterior byssal gland.

Several species, in warm seas.

Subgenus *Solecardia* s. s. Shell not gaping; left valve with an anterior and posterior lamella, corresponding to which are 2 each in the right valve; surface more or less punctate. *S. (S.) eburnea* Conrad. *Barclayia* H. Adams, 1874, is scarcely different.

Subgenus *Scintilla* Deshayes, 1855. Shell more or less gaping; hinge teeth weak, in most cases on the left with 2 anterior and 1 posterior lamella, on the right with 1 or 2 short anterior and 1, seldom 2, weak posterior lamellae. *S. (S.) philippinensis* (Deshayes). *Scintillula* and *Lionelita* Jousseaume, 1888, may be synonymous; Iredale, 1931, proposed a genus *Lactemiles* for *S. strangei* (Deshayes); the animal is said to possess siphonal processes at both ends and a smooth mantle, whereas in *Varotoga* Iredale, 1931 (*S. cryptozoica* Hedley), has a few small warts on the reflected mantle and longer threads at the margin.

Subgenus *Scintillona* Finlay, 1927. Hinge on either side with one tooth, the right one hook-shaped, the left one broadly triangular; reflected mantle margin very narrow. *S. (S.) zelandica* (N. Odhner), near New Zealand.

873

Subgenus *Scintillorbis* Dall, 1899. Shell small, roundish, very thin, transparent, with concentric rings and regular fine radial striae; external ligament rudimentary; hinge margin on the right with 1, on the left with 2 denticles. *S. (S.) crispata* (P. Fischer), near France.

Subgenus *Divariscintilla* Powell, 1932. Shell small, very thin, transparent; umbo situated anterior to the center; ventral margin with an angular indentation in the center; right valve with a denticle anterior to the ligament; left valve toothless. *S. (D.) maoria* (Powell), near New Zealand.

Vasconiella Dall, 1899

Shell small; umbo close to the center; ventral margin with deep indentation, to which a fold descends; hinge margin with a sharp tooth; ligamental cartilage small and short, without external ligament.

V. jeffreysiana (P. Fischer), near Portugal.

Galeomma Turton, 1825

Synonyms *Parthenope* Scacchi, 1833; *Thyreopsis* H. Adams, 1868.

Shell longish, ventrally gaping; umbo scarcely projecting; ligamental cartilage in a median pit; hinge weak, often toothless. The mantle below forms a fold surrounding the foot and a covering on the surface of the shell; foot with small posterior byssal gland.

A few species, in various seas.

Subgenus *Galeomma* s. s. Shell bulging, laterally enclosing the body. Section *Amphilepida* Dall, 1899. Shell moderately gaping, without radial scultpure; hinge margin on either side of the cartilage with a small tooth-shaped process. *G. (A.) politum* Deshayes.—Section *Galeomma* s. s. Shell with radial sculpture, moderately gaping; hinge margin toothless. *G. (G.) turtoni* Broderip.—Section *Paralepida* Dall, 1899 (synonym *Lepirodes* P. Fischer, 1887, non *Lepyrodes* Guénée, 1854). Shell widely gaping, with fine radial sculpture; hinge margin anterior and posterior to the cartilage with a tooth-shaped process. *G. (P.) formosum* Deshayes.

Subgenus *Libratula* Pease, 1865. Shell flat and smooth; both valves horizontal; hinge margin finely denticulate *G. (L.) planum* (Pease).

874   ### *Levanderia* Sturany, 1905

Both valves flatly broadened, long and narrow, exteriorly with zig-zag-shaped lines; hinge toothless.

L. erythraeensis Sturany, in the Red Sea.

Ephippodonta Tate, 1889

Both valves lying in one plane, together circular, in the typical species with marginal teeth, which continue ray-shaped toward the center, and on the dorsal side with small cone-shaped elevations; in another species (*lunata* Tate) without marginal teeth and papillae; the very straight hinge margin on one side has an anterior and a posterior denticle; corresponding sockets on the other side. With the exception of a small anterior and median part, the shell is enclosed by the mantle margin beset with small warts; below the mantle has an opening for the foot and posteriorly an excurrent opening; foot with byssal gland; sexes separate.

E. macdougalli Tate (Fig. 829). A couple of Australian species.
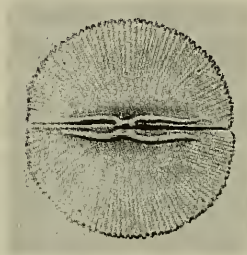
Fig. 829. Inner side of the shell of *Ephippodonta macdougalli* Tate. Length 9 mm.

D. Subfamily Chlamydoconchinae

Shell completely enclosed by mantle, long and narrow, anteriorly pointed, posteriorly blunt; umbo roundish, close to the posterior end; ligamental cartilage weak; no hinge. The mantle covering the shell and animal is thick, with a small anterior and posterior opening; anterior mantle margin broadened similar to that in *Bornia*; adductor muscles completely absent; 2 gill laminae on either side; labial palps triangular; sexes separate.

Chlamydoconcha Dall, 1884

Characters of the subfamily.
C. orcutti Dall, near California.

2. Family MONTACUTIDAE

Shell anteriorly longer than posteriorly, external or covered by the mantle margin; mantle with an anterior and a posterior opening, on either side with only one gill lamina. Foot with byssal gland; gonad hermaphroditic; development often with brood care. Living in most cases commensally with sipunculids or echinoderms.

Litigiella Monterosato, 1909

Shell oval, anteriorly longer than posteriorly; external ligament very weak, internal one strong; hinge margin on either side with a small main tooth and 2 elongated lamellae.

L. glabra (P. Fischer), near France, on *Sipunculus*, and *L. buryi* Lamy, near Brazil.

Mysella Angas, 1877

Synonym *Rochefortia* Vélain, 1878.

Shell external, transversely oval or somewhat angulate, in most cases smooth; umbo more or less close to the posterior margin; external ligament weak; cartilage short, situated below the umbones, anterior and posterior to it one valve has an oblique tooth, above which the more or less distinct expansions of the other valve are connecting.

M. anomala Angas. Several species, in various seas.

Sometimes only the anterior tooth is well developed, as also in *Malvinasia* J. E. Cooper & Preston, 1910 (*arthuri* J. E. Cooper & Preston, near the Falkland Islands), which is scarcely different from *Mysella*.

? Subgenus *Rochefortina* Dall, 1924. Shell very small, oval; umbo situated nearly in the center, with small embryonic shell; sculpture radial and concentric; both valves with 2 denticles. *R. semele* Dall, from Oahu.

? Subgenus *Sphenalia* S. Wood, 1874. Shell somewhat angular; umbo nearly terminal; left valve with 2 very small teeth; right valve with 2 small expansions of the hinge margin. *S. donacina* S. Wood, near England.

? Subgenus *Pythinella* Dall, 1899. Shell elongated triangular; lower margin straight; right valve with 2 teeth. *P. cuneata* (Verrill & Bush), near North Carolina; commensal with crustaceans.

Montacuta Turton, 1822

Shell external, smooth or with a few narrow radial ribs, transversely oval, anteriorly in most cases longer than posteriorly; external ligament

weak, the internal one in most cases on ridges posterior to the umbones, anterior to it on either side with a narrow lamella, which at the posterior end bears a more or less distinct tooth.

Several species, in various seas.

Section *Montacuta* s. s. (synonym *Coriareus* Hedley, 1907). Shell very small and thin, with a few thread-shaped radial ribs. *M. (M.) substriata* (Montagu) (Fig. 830).—Section *Decipula* (Jeffreys) Friele, 1875. Ligamental ridges absent; left valve without tooth. *M. (D.) ovata* (Jeffreys). —Section *Orobitella* Dall, 1900. Attachment of the ligament elevated; teeth without lamellae. *M. (O.) floridana* Dall.

Fig. 830. *Montacuta substriata* (Montagu), (after Sars).

? Subgenus *Aligena* H.C. Lea, 1845 (synonyms *Spaniodon* Reuss, 1867; *Laubriereia* Cossmann, 1887; *Kelliopsis* Verrill & Bush, 1898) is not distinctly different from *Montacuta*; ligament with a calcareous part; the anterior teeth may become rudimentary *A. striata* Lea †; few living species described from the American coasts; *Montacuta salamensis* Jaeckel & Thiele, from East Africa, probably also belongs here.

Asbjörnsenia Friele, 1886 (*striata* Friele) is presumably related or identical with *Montacuta ferruginosa* (Montagu). According to Lamy, *Issina* Jousseaume, 1898 (*issina* Jousseaume, from the Red Sea), is probably = *Montacuta*.

Benthoquetia Iredale, 1930

Synonyms *Austroturquetia* Cotton, 1930; *Isoconcha* (Pelseneer) Prashad, 1932.

Shell external, transversely oval, somewhat compressed in the center; umbo close to the center, only slightly projecting; ligament only external; hinge margin on either side with one tooth. Mantle with a posterior opening, which is separated by a long suture from the anterior opening, which forms an incomplete incurrent tube by means of folds; foot with strong byssus; the single gill lamina is smooth; the eggs are stored within it.

876

B. integra (Hedley), near Australia.

Pelseneer, 1911, described the animal of *Isoconcha sibogai*, but not the shell, which was first described by Prashad in 1932, in whose opinion this Australian species belongs to the same genus as Hedley's species. This genus differs from other montacutids by the completely external ligament.

? *Turqetia* Vélain, 1876

Shell small, posteriorly truncated; ligament external, situated posterior to the umbones; hinge margin on either side with a tubercle-shaped tooth. Animal unknown.

T. fragilis Vélain, near the islands of St. Paul and Amsterdam.

Jousseaumiella Bourne, 1907

Synonym *Jousseaumia* Bourne, 1906, non Sacco, 1894.

Shell small, triangular, anteriorly somewhat longer than posteriorly; internal ligament moderately long; right valve with one tooth, which is clasped by 2 lamellae of the left valve; on the left with an elongated anterior and posterior lateral tooth. Mantle widely open, with smooth margins; foot with small byssus.

J. heterocyathi (Bourne). 2 species in the Indian Ocean, on *Heterocyathus* and *Heteropsammia*.

Devonia Winckworth, 1930

Synonym *Synapticola* Malard, 1903, non Voigt, 1892.

Shell external, thin, oval or somewhat angulate, gaping; umbo close to posterior end; hinge ?; mantle margin with large papillae, with an anterior and a posterior opening; it forms a narrow covering over the shell margin; the posterior part of the mantle cavity forms a bell-shaped brood chamber; foot large, with a sucker-shaped depression; labial palps absent.

D. perrieri (Malard), on *Leptosynapta inhaerens*, near France; another species, *D. semperi* (Ohshima), on *Protankyra bidentata*, near Japan.

Entovalva Völtzkow, 1890

Shell oval, smooth; umbo close to the posterior end; mantle larger than the shell, completely enclosing it; its posterior bell-shaped part

forms a large brood chamber, otherwise the animal is similar to that in *Devonia*.

E. mirabilis Völtzkow, in the esophagus of *Patinapta crosslandi* Heding, near Zanzibar.

Cycladoconcha Spärck, 1932, may be considered as a subgenus; the shell is lost except for ring-shaped parts of the valves, with small hinge teeth; foot and siphon large; gills small. *C. amboinensis* Spärck, in the esophagus of *Patinapta laevis* (Bedford).

Scioberetia Bernard, 1895

Shell oval, radially ribbed; umbo close to the posterior end; ligament internal; hinge margin toothless. Adductor and foot musculature weak; foot small, with groove-shaped sole; mouth surrounded by narrow lips; the mantle completely encloses the shell; its margin is anteriorly broadened; its posterior part serves as a brood space; the excurrent opening is small.

S. australis Bernard, on spatangids, near Tierra del Fuego.

XI. STIRPS CHAMACEA

877

Shell with one valve cemented, more or less inequivalve; ligament variable; hinge margin fairly thick, with few teeth; mantle line unindented.

The bivalves belonging here are largely extinct; the rudists have evolved very peculiarly, so that they have little similarity with normal bivalves; their two valves are very different and are not joined with one another by a ligament.

1. Family CHAMIDAE

Shell irregularly formed, thick, exteriorly with divided, sometimes distinctly elongated lamellae or spines, often vividly colored; the cemented, in most cases left, valve larger and deeper than the other one, both distinctly spiral; ligament external, on short, thick ridges, anteriorly cleft; hinge margin thick, on the right with a lower, sometimes disappearing tooth and an arch-shaped main tooth, between which on the left catches a somewhat arch-shaped tooth, whereas an upper tooth is only weakly developed in the posterior part; a posterior lateral tooth is indicated on both sides; muscle scars large, elongated oval. Mantle margin with numerous tentacles; the incurrent opening ventral between that for the foot and the excurrent opening; gill laminae folded, the exterior one narrow; foot fairly small, without byssus; labial palps small; kidneys sack-shaped, connected with one another; pericardial limb fairly long.

Chama (Linné, 1758) Bruguière, 1789

Synonyms *Globus* Klein, 1753; *Jataronus* Adanson; 1757; *Maceris* Modeer, 1793; *Psilopus* + *Psilopoderma* Poli, 1795; *Lacinia* Mus. Calonn., 1797; *Planospirites* Lamarck, 1801; *Macerophyllum* (Meuschen) Herrmannsen 1847.

Characters of the family.

A few species, in warm seas.

Subgenus *Echinochama* P. Fischer, 1887 (synonym *Arcinella* Schumacher, 1817, non Oken, 1815). Shell fairly regular and equivalve, with radial rows of spines, cemented by the right valve in most cases only in the young; lunule distinctly delimited; embryonic shell large, equivalve, with concentric ribs. *C. (E.) arcinella* Linné, near the West Indies, and *californica* Dall.

Subgenus *Chama* s. s. Shell irregular, distinctly inequivalve, permanently cemented by one, in most cases, the left valve, without lunule. *C. (C.) lazarus* Linné (Fig. 831). *Pseudochama* N. Odhner, 1917, for *C. cristella* Lamarck, cemented by the right valve, is not recognized by Lamy.
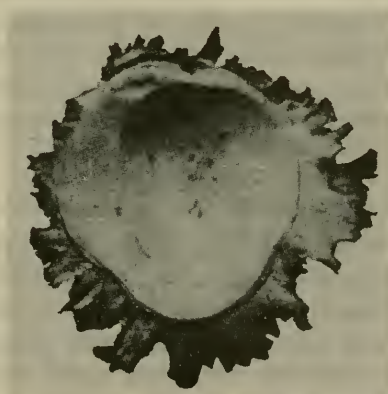
Fig. 831. Inner side of the right shell valve of *Chama lazarus* Linné. Length about 9 cm.

XII. STIRPS CARDIACEA

Shell of highly variable size, in most cases with radial sculpture, equivalve; ligament external; main teeth in most cases cone-shaped, on the right without central tooth; lateral teeth away from the main teeth, seldom the hinge teeth are reduced. Mantle line in most cases unindented;

siphons short as a rule; in tridacnids the anterior adductor muscle is reduced; gill laminae folded.

1. Family CARDIIDAE

Shell variable in size, in most cases roundish or oval, occasionally distinctly longer than broad, more often higher than long, frequently an edge is developed, which is sometimes very high; seldom lacking more or less strong radial ribs, which are frequently beset with transverse scales or spines; the periostracum is in most cases weak; the external ligament short and strong; as a rule 2 main teeth on either side, the median of which are stronger than the outer ones, and anterior and posterior lateral teeth; the anterior one often arising from the depression of the umbones. Mantle margin with papillae or smooth; incurrent and excurrent siphons fairly short, with the exception of *Adacna*, with tentacles, which sometimes contain eyes; the lower siphon is not separated from the anterior opening in a few groups, in which the mantle suture has a large valve, which extends below the posterior end of the gills; gill laminae folded, with large inner marginal filaments; outer laminae narrow, separated from the inner ones by a more or less large internal, below which runs the vas efferens; the septum broad beside and posterior to the foot, occasionally with a few folds; foot strong, long, bent; byssus occasionally rudimentary; labial palps fairly long, triangular; the sexes are seldom separate, in most cases hermaphroditic.

Microcardium n. gen.

Shell small and thin, translucent, inflated, only slightly longer than high, with numerous thread-shaped radial ribs, the intervening spaces of which show dense lamellae, and on which there are more to less numerous radial rows of pointed small projecting scales; at the ends of the ribs the margin is sharply denticulate; umbo projecting, rounded, situated nearly in the center; anterior margin curved; posterior margin in most cases somewhat flattened; ligament weak, on either side 2 main teeth, lateral teeth placed fairly far away, the left posterior one represents a narrow expansion of the hinge margin. Animal unknown.

M. torresi (Edg. Smith), distributed in the Indian Ocean. Smith placed this species in *Fragum*, which is hardly acceptable, whereas Dall named a similar West Indian species first *Cardium* (*Fulvia*) *peramabilis*, later *Protocardia* ♀, which again cannot be accepted. Dall mentions a few similar Tertiary species.

Nemocardium Meek, 1876

Shell fairly small, with densely placed ribs, which are spiny, warty, or lattice-shaped on the posterior part.

N. semiasperum (Deshayes) †. Grant and Gale placed the Californian species *centifilosum* (Carpenter) here, in which the posterior part, delimited by a weak edge, has a few concentric lamellae; the margin is denticulate because of the ribs. Dall considered *Nemocardium* as a section of *Protocardia* Beyrich, whereas Grant and Gale subordinated it under *Laevicardium*; both of these propositions appear unacceptable; the above-mentioned living species is most closely related with *Pratulum* and *Lophocardium*.

879

Pratulum Iredale, 1924

Shell fairly thin, medium-sized, transversely oval, posteriorly a little gaping; surface with numerous narrow radial ribs, the anterior and posterior of which are somewhat tuberculate; the posterior part is delimited by a somewhat stronger rib; margin at the ends of the ribs denticulate; lateral teeth fairly far away from the main teeth. Animal unknown.

P. thetidis (Hedley). A couple of species, near Australia and New Zealand.

Lophocardium P. Fischer, 1887

Shell thin, transversely oval, posteriorly somewhat gaping, very finely latticed, posterior part wrinkled, delimited by an elevated lamella; lateral teeth reduced. Dall states that the animal shows distinct anatomical differences, of which he mentions a thin septum, which anteriorly extends to beside the foot.

L. cumingi (Broderip), in Central America.

Laevicardium Swainson, 1840

Synonym *Liocardium* Mörch, 1853.

Shell of variable, sometimes considerable, size, strong, in most cases distinctly ribbed; umbo elevated; outline roundish without edge; hinge margin more or less curved, with distinctly developed teeth; posterior margins not gaping; genitalia hermaphroditic.

Subgenus *Discors* Deshayes, 1858 (synonyms *Lyrocardium* Meek, 1876; *Amphicardium* Martens, 1880; *Divaricardium* Dollfus &

Dautzenberg, 1886). Shell roundish, with distinct red or speckled periostracum; anterior part with weak ribs and sharp oblique ridges; posterior part with distinct radial ribs; lower margin denticulate. *L. (D.) subdiscors* (Orbigny) †, few living species, near the Philippines and near San Thomé.

Subgenus *Laevicardium* s. s. Shell moderately strong, in most cases higher than long, sometimes somewhat triangular, exterior sculpture weak, with distinct periostracum; hinge margin arched; ventral margin interiorly denticulate. *L. (L.) norvegicum* (Spengler). A few species, in various seas.

Subgenus *Vasticardium* Iredale, 1927. Shell large, higher than long; umbo elevated; surface with smooth, flat, dense ribs. *L. (V.) nebulosum* (Martyn), in the Pacific Ocean.

Subgenus *Mexicardia* Steward, 1930. Shell large, higher than long, with very strong umbones; surface with broad, flat, rib-like folds separated by deep furrows. *L. (M.) procerum* (Sowerby), near Central America.

Subgenus *Dinocardium* Dall, 1900. Shell large, obliquely triangular, ventricose, posteriorly somewhat flattened; umbo large; surface with strong, flattened ribs, scaly in the anterior part. *L. (D.) magnum* (Born), in the Gulf of Mexico.

Subgenus *Vepricardium* Iredale, 1929. Shell medium-sized, roundish, with rounded ribs which are beset with short thorns *L. (V.) pulchricostatum* (Iredale), near Australia.

Subgenus *Trachycardium* Mörch, 1853. Shell ventricose, higher than long, somewhat obliquely oval, with ribs bearing scales, the intervening spaces of which are finely transversely striated or granulose. *L. (T.) isocardia* (Linné). A few species, in warm seas.

880   *Papyridea* Swainson, 1840

Shell compressed, longer than high; umbo closer to the anterior end; surface with numerous, more or less scaly or spiny ribs, gaping; ligament short, borne on ridges; hinge margin weakly curved.

Few species, in warm seas.

Section *Papyridea* s. s. Shell fairly thin, gaping at both ends, distinctly longer than high; posterior margin sharply denticulate at the ends of the ribs. *P. (P.) spinosa* (Meuschen).—Section *Fulvia* Gray, 1853. Shell very thin, roundish, posteriorly gaping, with fine radial threads; anterior part finely warty; posterior margin not denticulate. *P. (F.) aperta* (Bruguière).

Serripes (Beck) Gould, 1841

Synonyms *Aphrodite* Lea, 1834, non Hübner, 1816; *Acardo* Swainson, 1840, non Bruguière, 1789, nec Lamarck, 1801.

Shell large, longer than high, triangular, with weak radial sculpture only at the ends; main teeth reduced; lateral teeth weak; mantle line posteriorly straight, foot compressed, ventrally cuspidate; genitalia hermaphroditic.

S. groenlandicus (Gmelin). 2 Nordic species.

Cardium Linné, 1758

Synonyms *Cordium* Gistel, 1848; *Eucardium* P. Fischer, 1887.

Shell roundish or somewhat elongated, with rib-like folds which are often tuberculate or spiny; umbo projecting, close to the center; hinge margin only slightly curved, with main and lateral teeth.

Several species, in various seas.

Subgenus *Cerastoderma* (Poli, 1795) Mörch, 1853 (synonym *Cerastes* Poli, 1795, non Laurenti, 1768). Shell in most cases somewhat longer than high; ribs often beset with tubercles, warts, or spines. Section *Parvicardium* Monterosato, 1884. Shell small, somewhat longish; radial folds anteriorly and posteriorly warty. *C.* (*P.*) *parvum* Philippi.—Section *Cerastoderma* s. s. Shell larger, longer than high; radial folds with weak tubercles. *C.* (*C.*) *edule* Linné.—Section *Rudicardium* Monterosato, 1917. Shell roundish, medium-sized; radial folds high, somewhat warty; intervening spaces with transverse wrinkles. *C.* (*R.*) *tuberculatum* Linné. —Section *Acanthocardia* Gray, 1851 (synonym *Acanthocardium* E. Römer, 1869). Shell large and fairly thin; rib-like folds warty or spiny; intervening spaces fairly broad, with dense transverse ridges. *C.* (*A.*) *aculeatum* Linné.

Subgenus *Cardium* s. s. (synonym *Tropidocardium* E. Römer, 1869). Shell large, fairly thin, inflated, somewhat longer than high, posteriorly gaping; rib-like folds broad and flat, with sharp keels or thorns or scales; 881 intervening spaces broad; lateral teeth thin. *C.* (*C.*) *costatum* Linné (Fig. 832). 2 species, near West and North Africa.

Subgenus *Ringicardium* P. Fischer, 1887. Shell strong, roundish, posteriorly gaping; rib-like folds flat; posterior intervening spaces tuberculate or wrinkled; posterior ribs with leaf-shaped elevated margins, separated by deep incisions. *C.* (*R.*) *ringens* Chemnitz, near West Africa.
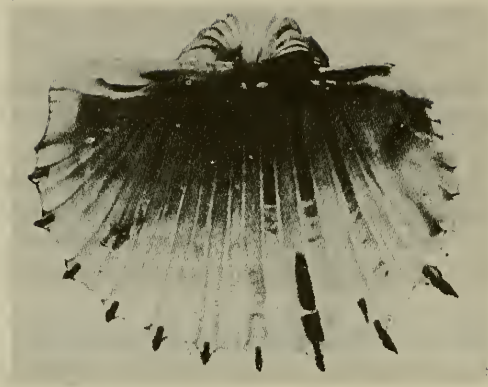
Fig. 832. Inner side of the right shell valve of *Cardium costatum* Linné. Length about 9 cm.

Corculum (Bolten) Röding, 1798

Synonym *Hemicardium* (Cuvier) Schweigger, 1820.

Shell higher than long, inclined, ribbed, with a more or less sharp edge descending from the umbones; hinge margin fairly short, curved. Incurrent opening of the mantle not separated from the opening for the foot; genitalia hermaphroditic.

Subgenus *Afrocardium* Tomlin, 1930. Shell fairly small, inclined, with rounded edge and several narrow, scaly ribs. *C. (A.) shepstonense* (Tomlin). A few species, in the Indian Ocean.

Subgenus *Papillicardium* Sacco, 1899. Shell fairly small, roundish, somewhat inclined, with weak, rounded edge and several tuberculate rib-like folds, the intervening spaces of which are regularly transversely striated. *C. (P.) papillosum* (Poli), in the Mediterranean Sea and Atlantic Ocean. This group is close to *Trigoniocardia*; the West Indian *Cardium guppyi* Thiele is intermediate between the typical species of the two.

Subgenus *Trigoniocardia* Dall, 1900. Shell fairly small, strong, with few strong, tuberculate ribs, the intervening spaces of which have dense transverse ridges; posterior part somewhat flattened, with weaker ribs. *C. (T.) graniferum* (Broderip & Sowerby). Few Central American species.

Subgenus *Ctenocardia* H. & A. Adams, 1857. Shell with several thorny ribs; posterior part with dense ribs, which bear only small scales. *C. (C.) hystrix* (Reeve), near the Philippines.

Subgenus *Fragum* (Bolten) Röding, 1798 (synonym *Loxocardium* Cossmann, 1887). Shell strong; posterior part delimited by a blunt edge,

with strong, tuberculate or scaly rib-like folds; intervening spaces smooth; margin denticulate. *C. (F.) unedo* (Linné). Few species, in warm seas.

Subgenus *Hemicardia* (Klein) Mörch, 1853. Shell with a keel-like edge, which ventrally forms an acute angle; ribs fairly broad and flat, on the sides of the body with tubercles; intervening spaces narrow, with dense transverse ridges. *C. (H.) hemicardium* (Linné), in the Indian Ocean.

Subgenus *Lunulicardia* Gray, 1853 (synonym *Opisocardium* Bayle, 1879). Shell similar to *Hemicardia*, but with a deeply sunken lunule. *C. (L.) retusum* (Linné). A couple of species, in the Indian Ocean.

Subgenus *Corculum* s. s. (synonym *Cardissa* Megerle von Mühlfeld, 1811). Shell thin, greatly shortened and laterally broadened, with a very high keel, without lunule, although with a small smooth area on the posterior side; surface with flat rib-like folds which are somewhat tuberculate in the upper part. *C. (C.) cardissa* (Linné) (Fig. 833). A couple of species, in the Indian Ocean and near Central America.

Fig. 833. Shell of *Corculum cardissa* (Linné).

881

882

Didacna Eichwald, 1838

Shell longer than broad, in most cases with a posterior edge, more or less strongly ribbed; lateral teeth rudimentary; 1 or 2 main teeth on either side; mantle line not or weakly indented. Mantle with 2 posterior openings, which form short siphons beset with papillae.

A few species in the Caspian Sea.

Subgenus *Didacna* s. s. Shell with posterior edge, posteriorly not gaping; hinge with 2 main teeth on either side, without mantle sinus. *D. (D.) trigonoides* (Pallas).

Subgenus *Monodacna* Eichwald, 1838. Shell transversely oval, without edge, posteriorly gaping; hinge with one main tooth on either side, with small mantle sinus. *D.* (*M.*) *caspia* (Eichwald).

Adacna Eichwald, 1838

Synonyms *Hypania* (Pander) Kupffer, 1831; *Hypanis* (Pander) Ménétries, 1832 (non Boisduval, 1833); *Hypnaxis* Gray, 1847.

Shell thin, laterally compressed, longish, anteriorly and posteriorly gaping, with more or less distinct rib-like folds, without distinct hinge teeth; mantle line deeply indented. Mantle with long siphons which are fused with one another, their ends bearing small warts; foot fairly short, compressed.

A. laeviuscula Eichwald. Few species, in the Caspian Sea.

2. Family TRIDACNIDAE

Shell thick, large, in some cases gigantic, with radial sculpture; anterior part of the hinge margin reduced, so that only one main tooth and the posterior lateral tooth are present; ligament external, the anterior margin is obliquely upwardly directed, in most cases interiorly denticulate. The animal is peculiarly twisted, so that the mantle opening for the foot is upwardly directed; the incurrent opening lies at the anterior part of the lower side, and the excurrent opening lies in the center; the anterior adductor muscle absent, whereas the posterior one lies in about the center, posterior to which is the attachment of the foot retractor; gill laminae fairly narrow, folded; gonads hermaphroditic.

The Tridacnidae connect with the cardiids through the fossil genus *Byssocardium* Munier-Chalmas, 1882.

Tridacna Bruguière, 1789

Shell very large and thick, longish triangular, with radial ribs and strong scaly folds, through which the tower margin is wavy; the upwardly directed anterior margin gapes just anterior to the umbones; it is interiorly denticulate; the hinge margin on either side has one main tooth and one posterior lateral tooth on the left, 2 on the right; below the main tooth is the sunken attachment of the anterior foot muscle. The mantle margin bears numerous warts; the excurrent opening is small; the small foot has a strongly developed byssus; labial palps narrow; gill folds high; posterior foot retractor strong.

T. gigas (Linné). Few species, in the Indo-Pacific region; they attach their byssus to stones or live in corals.

Hippopus Lamarck, 1799

Synonym *Cerceis* Gistel, 1848.

Shell similar to *Tridacna*, although without gaping opening; anterior end flattened and delimited by an edge. Foot larger, without byssus; posterior retractors small.

H. maculatus Lamarck (Fig. 834), in the Indo-Pacific region, living in sand.

Fig. 834. Inner side of the left shell valve of *Hippopus maculatus* Lamarck. Length about 11.5 cm.

XIII. STIRPS VENERACEA

Shell in most cases strong, smooth or sculptured, transversely oval or triangular, equivalve; right valve with central tooth and an anterior and posterior main tooth, catching between which are the teeth of the left valve; an anterior lateral tooth of the left valve is often rudimentary or absent; adductor muscle scars nearly symmetrical; a mantle sinus is more or less developed, seldom completely absent. The mantle in most cases widely open below, and posteriorly has sometimes shorter, sometimes longer, siphon fringed at the ends which are in most cases partly fused with one another; their partition wall often has a valve; gill laminae folded; foot in most cases without byssus.

1. Family VENERIDAE

Shell regularly formed, not gaping, often with a lunule, which is more or less distinctly delimited; the left valve, in addition to the bilobed main tooth, has a posterior main tooth and in a few genera a more or less strong anterior accessory tooth, corresponding to which in the right valve

is a socket with elevated margins. The mantle line is seldom unindented, in most cases it has an angular or rounded sinus, which is anteriorly or obliquely upwardly directed.

A division of this family into subfamilies has been attempted, based mainly on the presence or absence of the anterior lateral tooth, which however, is sometimes rudimentary; and through such a division some related forms would be separated from one another, therefore it does not seem to be useful. It is not certain whether different evolutionary lines can be recognized.

Gouldiopa Iredale, 1924

Shell small, bulging, somewhat slanting rounded-triangular, without sculpture; lunule only slightly deepened; in the right valve the anteriormost tooth is thin, the median somewhat triangular, the posteriormost large, longish, slanting, and cleft; in the left valve the thin, anterior main tooth and the stronger median one are joined above, the posteriormost very thin, and the anterior lateral tooth large and close to the anteriormost main tooth; mantle line fairly far from the margin, scarcely indented.

G. australis (Angas), near Australia.

Lioconcha Mörch, 1853

884

Shell medium sized, strong, oval, with projecting umbones, smooth or with fine concentric sculpture; lunule only slightly deepened; hinge margin thick; right anterior main tooth small, the posterior one occasionally weakly furrowed; left anterior main tooth weak, the posterior one partly joined with the ligamental ridge; mantle line unindented; margin smooth.

L. castrensis (Linné). Few species, in the Indo-Pacific Ocean.

? *Granicorium* Hedley, 1906

Shell roundish, posteriorly somewhat angulate. bulging; lunule deepened, although not delimited by a furrow; surface with concentric sculpture and with an attached cover of sand; hinge margin broad, on either side with 3 main teeth, the right median of which is triangular; the anterior one is short and the posterior one furrowed, without anterior lateral tooth, without distinct mantle sinus; inner margin smooth.

G. indutum Hedley, near eastern Australia.

Gouldia C. B. Adams, 1847

Shell fairly small, oval with somewhat elevated umbones; surface with concentric sculpture, at the ends sometimes finely radially striated; lunule shallow; hinge teeth broadly diverging; right posterior main tooth furrowed; left anterior lateral tooth separated from the anterior main tooth; mantle line weakly indented; margin smooth or somewhat rough; posterior dorsal margin furrowed.

G. cerina (C. B. Adams). A few species, in various seas.

Fluctiger Iredale, 1924

Shell small, strong, oval; umbo pointed, anteriorly inclined; lunule long and narrow; surface with a few wavy folds forming an angle in the center; hinge teeth similar to those in Circe.

F. royanus Iredale. A couple of Australian species.

Comus L.R. Cox, 1930

Shell thick, unequal-sided triangular, with broad concentric folds; umbo elevated; lunule long and narrow; ligament short; hinge margin thick, on the right with a posterior projecting main tooth joined with the ligamental ridge and a moderately developed median main tooth, whereas the anteriormost one is rudimentary; on the left with a thin posterior one, a very strong median one and a short anterior one, which touches the lateral tooth; mantle line unindented; margin interiorly finely denticulate.

C. platyaulax (Tomlin), near South and East Africa.

Gafrarium (Bolten) Röding, 1798

Shell roundish or transversely oval, strong, with concentric, sometimes also radial sculpture; lunule shallow, long and narrow; hinge margin broad, with 3 separate main teeth on either side; anterior lateral tooth more or less long; mantle line not or weakly indented.

Subgenus Circenita Jousseaume, 1888. Shell roundish, bulging, with concentric sculpture; main teeth fairly small and closely adjoining one another; anterior lateral tooth strong, short; mantle line weakly indented; margin smooth. G. (C.) arabicum (Chemnitz). Few species, in the Red Sea.

885   Subgenus Gafrarium s. s. (synonym Crista E. Römer, 1847). Shell transversely oval, moderately bulging, with radial, tuberculate ribs; hinge

margin short; left median main tooth furrowed; mantle line weakly indented; margin often denticulate. *G. (G.) pectinatum* (Linné) (Fig. 835).
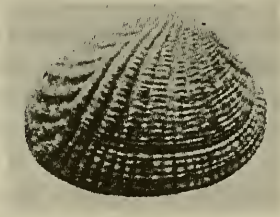
Fig. 835. Shell of *Gafrarium pectinatum* (Linné).
Length about 4 cm.

Subgenus *Circe* Schumacher, 1817. Shell with flattened initial part; umbo angulate, only slightly projecting; hinge margin strong; anterior lateral tooth fairly long and low; mantle line scarcely indented.

Section *Circe* s. s. Surface with concentric sculpture, often also with diverging ribs on the dorsal parts; left posterior main tooth long, the median one cleft; margin smooth. *G. (C.) scriptum* (Linné). A few species, in the Indian Ocean.—Section *Parmulina* Dall, 1902. Initial part wrinkled, the following with concentric sculpture; hinge teeth large, distinctly diverging; margin weakly denticulate. *G. (P.) corrugatum* (Chemnitz). Few species, in the Red Sea.

Callocardia A. Adams, 1864

Shell very thin, hinge margin weak; anterior and posterior main teeth joined arch-shaped; left posterior tooth long and free, the right one formed of 2 narrow plates; anterior lateral tooth pointed, arising from the margin; mantle line unindented.

C. guttata A. Adams, in the northern Pacific Ocean.

Samarangia Dall, 1902

Shell very strong, nearly colorless, roundly quadrangular, smooth; lunule somewhat depressed; ligament sunken; hinge margin strong, on the left with a fairly long posterior main tooth, a very thick, somewhat divided median one, and, joined with it, a weak anterior main tooth, anterior to which lies a distinct wart-shaped lateral tooth; on the right the posterior tooth is strong, distinctly furrowed, the median one triangular, the anterior one small, above a furrow with a minute pit corresponding to the anterior lateral tooth; the mantle line has no sinus; inner margin smooth.

S. quadrangularis (Adams & Reeve), in the northern Pacific Ocean. This species appears to have been misidentified to date, as shown by the diagnosis of the genus and its placement together with *Venus exalbida* and *lenticularis*, both of which are very different. The small lateral tooth is similar to that in some *Dosinia* species, although it seems this group is more closely related with *Callocardia* and *Pitaria*.

<p align="center">*Pitaria* E. Römer, 1857 (*Pitar*)</p>

Synonym *Caryatis* E. Römer, 1862, non Hübner, 1816.

Shell oval or rounded triangular, smooth or concentrically striated; lunule not deepened; hinge margin often with a groove-shaped depression below the right anterior main tooth; left posterior main tooth partly separated from the ligamental ridge or joined with it; anterior lateral tooth short.

Subgenus *Aphrodora* Jukes-Browne, 1914 (synonym *Leucothea* Jukes-Browne, 1913, non Rafinesque, 1815, nec Mertens, 1833). Shell thin, colorless, concentrically striated; hinge margin short, curved, posteriorly narrowed; teeth weak, left posterior one short and marginal in position, the right one joined arch-shaped; mantle sinus short and rounded. *P. (A.) birtsi* (Preston), in the Indian Ocean.

Subgenus *Tinctora* Jukes-Browne, 1914 (synonyms *Callizona* Jukes-Browne, 1913, non Doubleday, 1846; *Callizonata* Strand, 1928). Shell thick, roundish, shiny; left median main tooth very thick, the posterior one partly free; mantle sinus moderately deep, rounded; margin somewhat rough. *P. (T.) vulnerata* (Broderip).

Subgenus *Pitaria* s. s. Shell strong, rounded triangular or more oval. Section *Pitarina* Jukes-Browne, 1913. Right main teeth joined, the left posterior one free; ligamental ridges smooth; mantle sinus short, rounded. *P. (P.) citrina* (Lamarck).—Section *Calpitaria* Jukes-Browne, 1908. Right main teeth separate, the left median one triangular, the posterior one partly free; ligament ridges furrowed; mantle sinus short and rounded. *P. (C.) sulcataria* (Lamarck).—Section *Agriopoma* Dall, 1902. Shell colorless; right main teeth joined arch-shaped; the left posterior tooth long and partly free, ligamental ridges smooth; mantle sinus sharply angulate. *P. (A.) texasiana* (Dall).—Section *Pitaria* s. s. Right main teeth separate, the left median one triangular, the posterior one joined with the longitudinally furrowed ligamental ridge; mantle sinus deep and pointed. *P. (P.) tumens* (Gmelin).—Section *Megapitaria* Grant & Gale, 1931. Shell large, oval, smooth, hinge similar to that in *Pitaria* s. s. *P. (M.) aurantiaca* (Sowerby).

Subgenus *Amiantis* Carpenter, 1863. Shell with concentric rings or lamellae, oval; lunule somewhat deepened; ligament long, superficial;

886

anterior lateral tooth somewhat elongated; left posterior main tooth long, fused with the ligamental ridge; right anterior main tooth short. Section *Lamelliconcha* Dall, 1902 (synonyms *Dione* Gray, 1847, non Hübner, 1816; *Hysteroconcha* (Lang, 1722) Dall, 1902). Shell with more or less distinct posterior edge which sometimes bears spines; ligamental ridges longitudinally furrowed; hinge margin posteriorly narrowed; mantle sinus large, anteriorly rounded. *P.* (*L.*) *concinna* (Sowerby).—Section *Amiantis* s. s. (synonym *Eucallista* Dall, 1902). Shell thick, with broad concentric rings; hinge strong; ligamental ridges wrinkled; mantle sinus in most cases acutely angled. *P.* (*A.*) *callosa* (Conrad).

Subgenus *Macrocallista* Meek, 1876. Shell more or less elongated oval, smooth or with concentric furrows; lunule only slightly deepened; anterior lateral tooth in most cases not far from the main teeth; on the right in most cases without depression below the anterior main tooth, which is close to the median one; on the left the two anterior main teeth are joined above, the posterior one continuous with the ligamental ridge; margin not denticulate. Section *Notocallista* Iredale, 1924. Shell oval, only with growth lines; lunule indistinct; hinge similiar to that in *Lamelliconcha*; posterior right main tooth strong. *P.* (*N.*) *kingi* (Gray). —Section *Paradione* Dall, 1909 (synonyms *Chione* Gray, 1838, non Megerle von Mühlfeld, 1811; *Callista* (Poli, 1791) Mörch, 1853; *Chionella* Cossmann, 1886, non Swainson, 1840). Shell shiny, sometimes with weak radial striae; the socket for the strong anterior lateral tooth distinctly delineated; right posterior main tooth slender; mantle sinus broad, anteriorly angulate. Considering that according to Dall and Jukes-Browne, *Chionella*, proposed for the fossil species *Cytherea ovalina* Deshayes, is = *Chione*; it includes the group of *Venus chione* Linné.— Section *Macrocallista* s. s. Shell considerably elongated, large; posterior main teeth long; mantle sinus fairly short. *P.* (*M.*) *nimbosa* (Solander) 887 = *gigantea* (Gmelin).—Section *Lepidocardia* Dall, 1902. Shell fairly small, shiny, posteriorly with concentric furrows, anteriorly rounded, posteriorly pointed; hinge margin short, with closely adjoining teeth. *P.* (*L.*) *africana* (Philippi) = *floridella* (Gray).—Section *Transennella* Dall, 1883. Shell small; mantle sinus rounded; margin longitudinally furrowed. *P.* (*T.*) *conradina* (Dall).

Amiantis and *Macrocallista* are in most cases considered as genera, but their differences are only slight.

Saxidomus Conrad, 1837

Shell large and strong, elongated oval, with strong growth lines, posteriorly somewhat gaping, without distinct lunule; ligament long;

hinge margin fairly narrow, on the left with an oblique anterior lateral tooth and 3 slender closely adjoining main teeth, the posteriormost of which is separated from the ligamental ridge; on the right with 3 main teeth; mantle sinus deep; margin smooth. Siphons long.

S. nuttalli Conrad. 3 species, in the northern Pacific Ocean.

Sunetta Link, 1807

Synonyms *Cuneus* Megerle von Mühlfeld, 1811, non Da Costa, 1778; *Meroe* Schumacher, 1817.

Shell more or less elongated oval, strong, smooth or concentrically sculptured; lunule narrow; ligamental area deepened; hinge margin on either side with 3 main teeth; anterior lateral tooth fairly long; mantle sinus short, somewhat angular; margin denticulate.

A few species, in the Indo-Pacific region and on the African west coast.

Section *Sunetta* s. s. Shell longish; left posterior main tooth short, the right one smooth. *S. (S.) scripta* (Linné). *Sunettina* L. Pfeiffer, 1869 (synonym *Solanderina* Dall, 1902) [*solandri* (Gray)] is more bulging. —Section *Sunemeroe* Iredale, 1930 (synonym *Sunettina* Jousseaume, 1891, non L. Pfeiffer, 1869). Shell roundish, compressed; posterior side longer than the anterior; left posterior main tooth long and thin, the right one furrowed at the tip. *S. (S.) adelinae* Angas.

Meretrix Lamarck, 1799

Synonym *Nympha* Mörch, 1853, non Fitzinger, 1826.

Shell triangularly oval, thick, in most cases smooth, sometimes concentrically sculptured; lunule indistinct; ligament fairly short, on greatly projecting, wrinkled ridges; hinge margin strong, on either side with 3 separate main teeth; left posterior tooth joined with the ligamental ridge; right posterior one narrow and somewhat furrowed; lateral tooth strong, away from the main teeth; mantle sinus shallow; margin smooth.

M. meretrix (Linné). Few species, in the Indo-Pacific region.

Tivela Link, 1807

Synonyms *Trigona* Megerle von Mühlfeld, 1811, non Jurine, 1807; *Trigonella* Conrad, 1837, non Da Costa, 1778; *Pachydesma* Conrad, 1854.

Shell triangular, variable in size, smooth; lunule long; ligament short, projecting, on thick ridges, which are more or less strongly wrinkled or beset with tooth-shaped processes; hinge margin on either

side with 3 main teeth and a fairly long, more or less strong left anterior lateral tooth; mantle sinus in most cases only moderately deep.

A few species, in various seas.

888   Section *Tivela* s. s. Inner margin smooth. *T.* (*T.*) *mactroides* (Born). —Section *Eutivela* Dall, 1891. Inner margin denticulate. *T.* (*B.*) *perplexa* (Stearns), near Brazil.

Dosinia Scopoli, 1777

Synonyms *Pectunculus* Da Costa, 1778; *Artemis* (Poli) Oken, 1815; *Asa* (Leach) Basterot, 1825; *Arctoe* Risso, 1826; *Exoleta* T. Brown, 1827; *Cerana* Gistel, 1848; *Amphithaea* Leach, 1852.

Shell roundish, more or less compressed, with concentric sculpture; lunule in most cases small and deepened; ligament in most cases sunken; hinge margin strong, on either side with 3 main teeth, on the left with a more or less distinct anterior lateral tooth; right posterior tooth furrowed; left posterior tooth long, oblique.

Several species, in various seas.

Subgenus *Sinodia* Jukes-Browne, 1912. Shell bulging; lunule not depressed; anterior lateral tooth well developed, separated from the main teeth; left median main tooth strong; mantle sinus moderately deep, rounded. *D.* (*S.*) *trigona* Reeve.

Subgenus *Dosinia* s. s. Lunule distinctly depressed. Section *Dosinia* s. s. Ligamental surface depressed; anterior lateral tooth well developed; left median main tooth divided; mantle sinus deep and narrow, ascending. *D.* (*D.*) *africana* Gray.—Section *Austrodosinia* Dall, 1902. Ligamental surface indistinctly delimited; anterior lateral tooth strong and rough; left median main tooth strong, undivided; mantle sinus short, not ascending. *D.* (*A.*) *anus* Philippi.—Section *Dosinorbis* Dall, 1902 (synonym *Phacosoma* Jukes-Browne, 1912). Ligamental surface delimited by an elevated inner margin and lamellae-shaped ridges; anterior lateral tooth distinct; left median main tooth oblique, undivided; mantle sinus deep and angulate. *D.* (*D.*) *bilunulata* Gray.—Section *Orbiculus* Megerle von Mühlfeld, 1811. Ligamental surface not delimited; anterior lateral tooth small; left median main tooth indistinctly divided; mantle sinus deep, ascending, anteriorly rounded. *D.* (*O.*) *exoleta* (Linné).—Section *Dosinidia* Dall, 1902. Lunule only very slightly depressed; ligamental surface not delimited; anterior lateral tooth small, wart-shaped; left median main tooth broad and indistinctly divided; mantle sinus deep, angulate, ascending. *D.* (*D.*) *concentrica* (Born).—Section *Dosinella* Dall, 1902. Lunule shallow; ligamental surface indistinctly demarcated; anterior lateral tooth small or reduced; left median main tooth broad and cleft; mantle sinus very deep, ascending, rounded. *D.* (*D.*) *angulosa* (Philippi).

According to Jukes-Browne, *Dosinisca* Dall, 1902, is based on an abnormal specimen. Iredale has proposed the following "genera" for Australian species, without diagnoses; *Pardosinia*, 1929, for *colorata* Iredale; *Bonartemis*, 1929, for *stabilis* Iredale; *Meridosinia*, 1930, for *nedigna* Iredale; *Fallartemis*, 1930, for *amina* Iredale; and *Semelartemis*, 1930, for *aetha* Iredale.

Cyclina Deshayes, 1849

Synonym *Eocyclina* Dall, 1908.

Shell roundish, bulging, with more or less distinct growth lines, without deepened lunule; ligament strong; hinge margin broad, without lateral tooth; posterior main teeth short and oblique, the right one cleft; mantle sinus deep and ascending.

Subgenus *Cyclinella* Dall, 1902. Shell smaller, weaker and smoother than *Cyclina*; inner margin smooth; mantle sinus angulate. *C.* (*C.*) *tenuis* (Recluz), near Central America.

889 Subgenus *Cyclina* s. s. Shell strong, with rough growth lines and indistinct small radial ribs; hinge teeth strong, the left median one sometimes furrowed; inner margin denticulate. *C.* (*C.*) *sinensis* (Gmelin). Few species, near China.

Venus Linné, 1758

Synonyms *Dosina* Gray, 1838; *Omphaloclathrum* (Klein) Mörch, 1853.

Shell in most cases strong, roundish or oval, as a rule with distinct concentric, sometimes also radial sculpture; lunule distinct; hinge margin strong, on either side with 3 diverging main teeth, the left posterior of which is more or less joined with the ligamental ridge; anterior lateral tooth in most cases small, wart-shaped, or completely reduced; mantle sinus fairly small; inner margin denticulate.

Several species, in various seas.

Subgenus *Antigona* Schumacher, 1817. Shell oval, with radial ribs and strong concentric lamellae; lunule and ligamental surface distinctly delimited; main teeth widely diverging, the anteriormost ones anteriorly directed; anterior lateral tooth well developed; mantle sinus small and acutely angled. *V.* (*A.*) *lamellaris* (Schumacher). *Tigammona* Iredale, 1930 (*persimilis* Iredale), is very similar.

Subgenus *Ventricola* E. Römer, 1857. Shell roundish, strongly bulging, with concentric stronger and weaker lamellae, sometimes also with weak radial striae; anterior main teeth only slightly oblique; lateral

tooth distinct; mantle sinus small and acutely angled. *V.* (*V.*) *rugosa* Chemnitz. *Proxichione* Iredale, 1929 (*materna* Iredale), is scarcely different.

Subgenus *Dosinula* Finlay, 1927. Shell oval, with regular sharp concentric lamellae; left valve with long, fairly strong posterior main tooth, which is separated from the ligamental ridge by a deep pit, with strong, divided median and strong, triangular, anterior main tooth, and with small, wart-shaped lateral tooth; right valve with fairly strong, furrowed posterior, furrowed median, and slender anterior main tooth. *V.* (*D.*) *zelandica* Gray.

Subgenus *Venus* s. s. (synonym *Clausina* T. Brown, 1827). Shell roundish, bulging, with stronger and weaker concentric lamellae and irregular radial ribs, by which the lamellae are tuberculate; anterior lateral tooth very small, wart-shaped, close to the anterior main tooth. *V.* (*V.*) *verrucosa* Linné (Fig. 836).
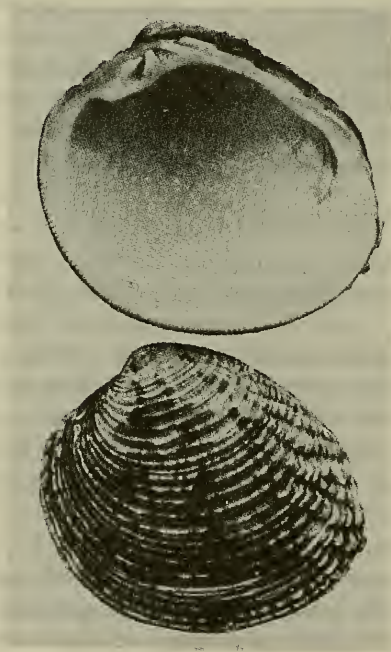
Fig. 836. Inner and outer side of the right shell valve of *Venus verrucosa* Linne. Length about 6 cm.

Subgenus *Periglypta* Jukes-Browne, 1914 (synonym *Cytherea* (Bolten) Röding, 1798, non Fabricius, 1794). Shell strongly bulging, with radial

ribs and concentric lamellae; ligamental surface somewhat asymmetrical; ligament sunken; anterior lateral tooth very small and close to the anterior main tooth; mantle sinus broad and rounded. *V. (P.) puerpera* Linné.

Subgenus *Circomphalus* Mörch, 1853. Shell compressed and flattened, with high, posteriorly canal-shaped elongated, concentric lamellae; hinge margin strongly curved and posteriorly narrowed; anterior lateral tooth very weak; mantle sinus acutely angled. *V. (C.) plicata* Gmelin.

Subgenus *Mercenaria* Schumacher, 1817 (synonym *Crassivenus* Perkins, 1869). Shell oval, bulging, with more or less elevated, thin, concentric lamellae; teeth moderately diverging; median main teeth and right posterior one in most cases furrowed; mantle sinus acutely angled. *V. (M.) mercenaria* Linné.

Subgenus *Chione* Megerle von Mühlfeld, 1811. Shell oval or somewhat triangular, with radial ribs and more or less high concentric lamellae; hinge margin short, with strong main teeth, without lateral tooth; mantle sinus small and angular. Section *Chione* s. s. Ligamental surface distinctly delimited; concentric lamellae well developed. *V. (C.) cancellata* Linné. Dall, 1902, proposed a section *Anomalodiscus* for *Venus squamosa* Linné, which Jukes-Browne did not want to separate from *Chione* s. s., although it may be distinguished by the sharp posterior point and the tuberculate radial ribs.—Section *Austrovenus* Finlay, 1927. Ligamental surface not delimited; concentric lamellae weak. *V. (A.) stuchburyi* Gray.—Section *Veremolpa* Iredale, 1930. Shell small, without delimited ligamental surface, with radial ribs and low concentric rings; mantle sinus short and roundish. *V. (V.) ethica* Iredale.—Section *Timoclea* T. Brown, 1827 (synonyms *Pasiphae* Leach, 1852, non Risso, 1826; *Leukoma* E. Römer, 1857 = *Leucoma* Stoliczka, 1871, non Stephens, 1829; *Murcia* E. Römer, 1857, non Koch, 1835). Shell fairly small, oval, without delimited ligamental surface, with radial ribs and sometimes only weak concentric rings; hinge teeth widely diverging; mantle sinus blunt or rounded. *V. (T.) ovata* Pennant.

Subgenus *Chioneryx* Iredale, 1924. Shell small, oval, with narrow radial ribs and fine concentric lamellae; ligamental surface somewhat deepened; the two anterior main teeth of the right valve anteriorly directed, the median one greatly elongated, the posterior one cleft; on the left the anteriormost one is long, parallel to the margin; the median one thick, cleft, the posteriormost one weak; mantle sinus angular. *V. (C.) striatissima* Sowerby.

Subgenus *Clausinella* Gray, 1851 (synonym *Zucleica* Leach, 1852). Shell with concentric sculpture; lunule and ligamental surface distinctly delimited; hinge teeth widely diverging, without lateral tooth; mantle

sinus very small. Section *Clausinella* s. s. Shell with regular concentric ridges without elevated lamellae. *V.* (*C.*) *fasciata* Da Costa.—Section *Lirophora* Conrad, 1864 (synonyms *Clausina* E. Römer, 1857, non T. Brown, 1827; *Anaitis* E. Römer, 1857, non Duponchel, 1829). The concentric ridges posteriorly form upwardly directed lamellae. *V.* (*L.*) *athleta* Conrad †, the living *V. paphia* Linné, and other mainly American species. Section *Chamelea* Mörch, 1853 (synonyms *Ortygia* T. Brown, 1827, non Boie, 1826; *Hermione* Leach, 1852, non Blainville, 1828; *Parvivenus* Sacco, 1900). Shell with narrow, densely placed, rounded concentric rings; mantle sinus angulate. *V.* (*C.*) *gallina* Linné.—Section *Tawera* Marwick, 1927. Shell with fairly fine, rounded, more or less densely placed rings. *V.* (*T.*) *spissa* Deshayes †, the living *bollonsi* (Powell), near New Zealand.—Section *Plurigens* Finlay, 1930. Shell with partly somewhat irregular, fairly densely placed concentric rings; ligamental surface fairly narrow and deep; mantle sinus fairly large. *V.* (*P.*) *phenax* (Finaly), near New Zealand.—Section *Placamen* Iredale, 1925. Ligamental surface broad, asymmetrical; rings blunt, as broad as their intervals; mantle sinus small. *V.* (*P.*) *placida* Philippi, near Tasmania.

Subgenus *Bassina* Jukes-Browne, 1914. Shell with not very densely placed, concentric lamellae; left median tooth broad, divided; right teeth narrow; lunule narrow. *V.* (*B.*) *pachyphylla* Jonas = *paucilamellata* Dunker. *Salacia* Jukes-Browne, 1914 (non Lamouroux, 1816, nec Brandt, 1835, nec Boie, 1841, nec Milne-Edwards & Lucas, 1844) = *Callanaitis* Iredale, 1917, is scarcely separable according to Marwick.

Anomalocardia Schumacher, 1817

Synonyms *Triquetra* (Blainville) Anton, 1839; *Cryptogramma* Mörch, 1853.

Shell bulging, anteriorly rounded, posteriorly pointed, mainly with broad, rounded concentric rings; ligamental ridge wrinkled; main teeth strong and widely diverging; mantle sinus very small.

Section *Anomalocardia* s. s. Inner margin denticulate. *A.* (*A.*) *flexuosa* (Linné). Few American species.—Section *Cryptonema* Jukes-Browne, 1914. Inner margin smooth. *A.* (*C.*) *impressa* (Anton), near the Mollucas.

Gomphina Mörch, 1853

Shell oval or triangular, fairly thick, smooth or concentrically striated; hinge margin broad and short, with 3 main teeth on either side; ligament short; mantle sinus rounded; inner margin smooth.

Few species, in the Pacific Ocean.

Section *Gomphinella* Marwick, 1927. Shell fairly small, oval, posteriorly shorter than anteriorly; lunule indistinct; right median main tooth anteriorly curved; mantle sinus shallow. *G. (G.) maorum* Edg. Smith, near New Zealand. Section *Gomphina* s. s. (synonym *Macridiscus* Dall, 1902). Shell triangular, posteriorly flattened; lunule long and narrow; hinge margin on the right with a narrow, furrowed posterior tooth, a broadly triangular, furrowed median one, and a thin anterior main tooth; on the left with 3 narrow diverging teeth, the median of which is furrowed; mantle sinus moderately deep. *G. (G.) donacina* (Chemnitz) = *veneriformis* (Lamarck).

Subgenus *Psephidia* Dall, 1902 (synonym *Psephis* Carpenter, 1864, non Guenée, 1854). Shell small, smooth, rounded triangular; left posterior tooth free; inner margin very finely denticulate; mantle sinus short and triangular. *G. (P.) lordi* (Baird), near California.

Subgenus *Jukesena* Iredale, 1915 (synonym *Acolus* Jukes-Browne, 1913, non Förster, 1856). Shell small, elongated triangular; hinge on the left with 3, on the right with 2 teeth; mantle line scarcely indented; inner margin smooth. *G. (J.) foveolata* (Cooper & Preston), near the Falkland Islands.

Subgenus *Liocyma* Dall, 1870. Shell fairly small, triangular oval, concentrically striated; hinge margin on either side with 3 teeth; mantle sinus short; inner margin smooth. *G. (L.) fluctuosa* (Gould). Few species, in the northern Pacific and Atlantic Oceans.

892   *Gemma* Deshayes, 1853

Shell small, oval or triangular, smooth or concentrically striated; lunule superficial; hinge margin short, on the right with 3 diverging teeth, the median of which is large and triangular; on the left with 2 or 3 teeth; left anterior dorsal margin and right posterior one with a furrow corresponding to the margin of the other side; ventral margin denticulate. With brood care.

Subgenus *Gemma* s. s. (synonym *Tottenia* Perkins, 1869). Shell roundish, striated; hinge margin on either side with 3 teeth; marginal furrows distinct; mantle sinus more or less deep. *G. (G.) gemma* (Totten), near North America.

Subgenus *Parastarte* Conrad, 1862 (synonym *Callicistronia* Dall, 1883). Shell strong, high triangular, smooth; hinge margin on the right with 3, on the left with 2 teeth; ligament very short; marginal furrows narrow; mantle sinus weak. *G. (P.) triquetra* (Conrad), near Florida.

Protothaca Dall, 1902

Shell strong, oval, with radial and partly concentric sculpture; lunule distinctly delimited; teeth strong, the two median ones and the right posterior one furrowed; ligament large and strong; mantle sinus acutely angled; inner margin denticulate.

Section *Protothaca* s. s. Anterior and posterior parts with distinct concentric sculpture; left valve somewhat flattened next to the ligament; mantle sinus moderately deep. *P. (P.) thaca* (Molina) = *dombeyi* (Lamarck). Few species on the west coast of America.—Section *Tuangia* Marwick, 1927. The concentric sculpture is more extensive, without flattening beside the ligament; mantle sinus short. *P. (T.) crassicosta* (Deshayes), near New Zealand.

Catelysia E. Römer, 1857 (*Katelysia*)

Shell more or less elongated oval; umbo closer to the anterior end, smooth or concentrically sculptured; lunule somewhat depressed; hinge margin with 3 strong, diverging, often rough teeth, of which the right median and posterior and the left median are furrowed; anterior left and posterior right margin furrowed; mantle sinus rounded; ventral margin smooth.

A few species, in the Indo-Pacific region.

Subgenus *Eumarcia* Iredale, 1924 (synonym *Marcia* H. & A. Adams, 1857, non Warlow, 1833). Shell oval, bulging, smooth or indistinctly sculptured; hinge teeth widely diverging, the two anterior ones of the left side furrowed. *C. (E.) fumigata* (Sowerby).

Subgenus *Hemitapes* E. Römer, 1864. Shell oval or more or less triangular, bulging, sculptured with concentric rings; both anterior main teeth simple. *C. (H.) rimularis* (Lamarck).

Subgenus *Catelysia* s. s. (synonyms *Metis* H. & A. Adams, 1857, non 1856; *Myrsus* H. & A. Adams, 1858; *Myrsopsis* Sacco, 1900). Shell obliquely oval, more or less bulging, with strong, sometimes somewhat tuberculate concentric rings; mantle sinus moderately deep. *C. (C.) scalarina* (Lamarck).

Venerupis Lamarck, 1818

Shell angulate oval, with more or less distinct sculpture; umbo close to the anterior margin; hinge margin fairly narrow, with 3 teeth on either side, mantle sinus rounded; ventral margin smooth.

893   Several species, in various seas.

Subgenus *Venerupis* s. s. (synonym *Pullastra* Sowerby, 1826). Surface with fine sculpture, which is stronger in the posterior part. *V. (V.) perforans* (Montagu) = *pullastra* (Montagu).

Subgenus *Amygdala* E. Römer, 1857 (synonym *Ruditapes* Chiamenti, 1900). Shell with fine radial ribs and more or less distinct concentric rings; hinge margin narrow; posterior teeth very short; mantle sinus deep. *V. (A.) decussata* (Linné).

Subgenus *Polititapes* Chiamenti, 1900. Shell longish, posteriorly not angulate, with fine concentric rings and indistinct radial ribs; lunule narrow and long; mantle sinus fairly short, rounded. *V. (P.) aurea* (Gmelin).

Callithaca Dall, 1902

Shell oval, in most cases with narrow concentric lamellae, sometimes with fine radial striae; ligament large; lunule more or less depressed; posterior hinge teeth short; mantle sinus angular; ventral margin smooth.

Subgenus *Rhomalea* Jukes-Browne, 1914. Shell roundish, with weak radial striae and in the ventral part with stronger concentric rings; mantle sinus acutely angled. *C. (R.) rufa* (Lamarck), near Peru.

Subgenus *Humilaria* Grant & Gale, 1931. Shell medium-sized, longish oval; umbo close to the anterior end; surface with concentric lamellae, without radial sculpture; mantle sinus moderately deep. *C. (H.) kennerleyi* (Reeve), on the American west coast.

Subgenus *Callithaca* s. s. Shell large, longish oval; umbo close to anterior end; surface with narrow concentric rings and fine, densely-placed radial striae; mantle sinus very deep and acutely angled. *C. (C.) tenerrima* (Carpenter), near California.

Paphia (Bolten) Röding, 1798

Shell more or less elongated, smooth or concentrically sculptured; lunule distinct; hinge margin narrow, with short, fairly closely placed and moderately diverging teeth; mantle sinus moderately deep, rounded; inner margin smooth.

A few species, in the Indian Ocean.

Section *Protapes* Dall, 1902. Shell triangular, with narrow concentric rings; lunule large, long; median hinge teeth and the right posterior one cleft. *P. (P.) gallus* (Gmelin) = *malabarica* (Dillwyn).—Section *Paphia* s. s. (synonyms *Eutapes* Chiamenti, 1900; *Callistotapes* Sacco,

1900). Shell long, compressed, with flat concentric rings; lunule long and narrow; mantle sinus obliquely ascending. *P. (P.) alapapilionis* Röding (Fig. 837).—Section *Paratapes* Stoliczka, 1871 (synonym *Textrix* E. Römer, 1857, non Sundeval, 1833). Shell long, smooth or with weak concentric sculpture; lunule narrow; mantle sinus fairly short. *P. (P.) textile* (Gmelin) = *textrix* (Chemnitz).
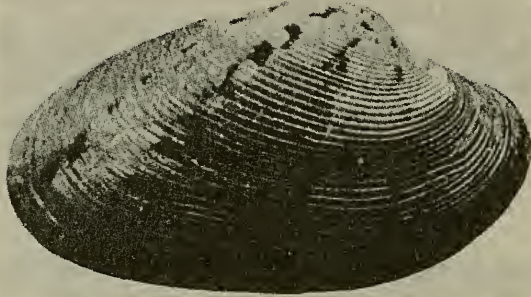
Fig. 837. Shell of *Paphia alapapilionis* Röding. Length 8.5 cm.

894   *Tapes* Megerle von Mühlfeld, 1811

Synonym *Parembola* E. Römer, 1870.
Shell elongated oval, with umbones close to the anterior end, anteriorly somewhat pointed, posteriorly broadly flattened, with densely placed concentric rings; lunule long and narrow; left median tooth broad and deeply cleft, the remaining teeth simple; mantle sinus moderately deep, rounded, not ascending; margin smooth.
T. litterata (Linné). Few species, in the Indo-Pacific region.

Clementia Gray, 1842

Synonym *Blainvillia* Hupé, 1854, non Desvoidy, 1830.
Shell oval, bulging, thin; umbo more or less close to anterior end, projecting; lunule indistinct; ligament short; hinge margin weak, anterior to the teeth deepened pit-like, on either side with 3 teeth, the right posterior of which is in most cases cleft; mantle sinus variable. Animal with long siphons, which are completely fused; mantle margin smooth; foot compressed.
Few species, in various seas.
Subgenus *Compsomyax* Stewart, 1930. Shell fairly elongated oval, not very thin; umbo moderately elevated; right posterior tooth deeply cleft, its parts diverging. *C. (C.) subdiaphana* Carpenter, on the west coast of North America.

Subgenus *Clementia* s. s. Shell very thin, with irregular concentric folds; umbo high, close to the anterior end; right posterior tooth long, straight, narrowly forked. *C. (C.) papyracea* (Gray), in the Indo-Pacific region.

Subgenus *Terentia* Jukes-Browne, 1914. Shell longish, with irregular, obliquely crossed striae; hinge teeth short, all undivided, right posterior one thin; mantle sinus very large and deep. *C. (T.) granulifera* Sowerby.

Notopaphia Oliver, 1923

Shell long and low; umbo blunt, closer to the anterior end; lunule distinctly delimited; ligamental surface narrow; surface with fine radial ribs and concentric rings, which in the posterior part expand into lamellae; teeth short, on the right the 2 posterior ones cleft; on the left the median is distinct, the anterior one indistinctly furrowed, the posterior one joined with the ligamental ridge; mantle sinus acutely angled; margin denticulate.

N. elegans (Deshayes), near New Zealand.

Irus Oken, 1815

Shell in most cases fairly small, longish, often more or less irregular, variously sculptured; umbo closer to the anterior end; lunule not delimited; hinge margin narrow and very short; teeth often irregular, in most cases 2 on either side are furrowed; lower margin smooth.

A few species, in various seas, in most cases living in holes.

Subgenus *Paphirus* Finlay, 1927. Shell fairly large, longish oval, with concentric threads and weak radial striae; median hinge teeth furrowed, as well as the right posterior one; mantle sinus broadly rounded. *I. (P.) largillierti* (Philippi), near New Zealand.

Subgenus *Notirus* Finlay, 1928 (synonyms *Irona* Finlay, 1927, non *Ironus* Bastian, 1865). Shell longish, with concentric lamellae; hinge teeth somewhat downwardly prolonged. *I. (N.) reflexus* (Gray), near New Zealand.

895   Subgenus *Irus* s. s. Shell with narrow radial ribs and more or less elevated concentric lamellae; mantle sinus in most cases short, somewhat angular. *I. (I.) irus* (Linné).

2. Family PETRICOLIDAE

Shell in most cases fairly small and colorless, roundish or elongated; ligament external, fairly short; hinge margin on the right with 2, on the

left with 3, sometimes irregular main teeth, without lateral teeth; mantle sinus more or less deep. Siphons long; gill laminae folded; foot with or without byssal furrow.

Mysia (Leach) Lamarck, 1818

Synonym *Lucinopsis* Forbes & Hanley, 1848.
Shell thin, roundish, colorless, concentrically striated; umbo fairly pointed, anteriorly inclined; hinge margin on the right with 2 thin teeth, on the left with 3 teeth, the median of which is fairly broad and forked; mantle line large, rounded. Siphons long and separate.
M. undata (Pennant), near Europe.

Lajonkairea Deshayes, 1854

Shell short, somewhat quadrangular, anteriorly shortly rounded, posteriorly high; surface with fine, rough radial ribs; ligament sunken; hinge teeth similar to those in *Mysia*; mantle sinus very broad. Siphons fused.
L. lajonkairei (Payraudeau). A couple of European species and one in the Red Sea.

Cooperella Carpenter, 1864

Synonyms *Oedalia* Carpenter, 1864, non Meigen, 1820; *Oedalina* Carpenter, 1865.
Shell small and very thin, roundish, inflated, nearly smooth; hinge margin on the left with 3, on the right with 2 teeth; mantle sinus deep.
C. subdiaphana Carpenter, near California.

Petricola Lamarck, 1801

Shell more or less elongated, often irregular, anteriorly short and rounded, posteriorly narrowed, with variably strong, sometimes oblique radial ribs; anterior hinge teeth are sometimes reduced; mantle sinus variable. Mantle with a small opening for the foot and 2 long, largely separate siphons; foot small, with byssal groove.
Few species, in various seas.
The animals bore into mud, soft limestone, or corals.
Subgenus *Velargilla* Iredale, 1931. Shell moderately long, reddish with brown rays, thin, with dense, oblique, irregular small ribs; umbo not close to the anterior end. *P. (V.) rubiginosa* (Adams & Angas), near Port Jackson.

Subgenus *Naranio* Gray, 1853. Shell fairly short oval, with oblique or zig-zag-shaped threads; mantle sinus very broad. *P. (N.) lapicida* (Chemnitz).

Subgenus *Petricola* s. s. (synonyms *Rupellaria* Fleuriau de Bellevue, 1802; *Choristodon* Jonas, 1844). Shell anteriorly short and inflated, posteriorly thinned and elongated; sculpture radial; mantle sinus broad, rounded. *P. (P.) lithophaga* Retzius.

896   Subgenus *Claudiconcha* P. Fischer, 1887. Shell irregularly roundish, inequivalve, with radial ribs and in part broadened concentric rings; posterior margin of the right shell widened and enclosing that of the left shell; mantle sinus fairly short and angular. *P. (C.) monstrosa* (Chemnitz).

Subgenus *Petricolaria* Stoliczka, 1871 (synonym *Gastranella* Verrill, 1872). Shell in most cases greatly elongated, similar to that in *Pholas* with radial ribs, in the anterior part, with stronger, rough radial ribs; mantle sinus very deep. *P. (P.) pholadiformis* Lamarck (Fig. 838).
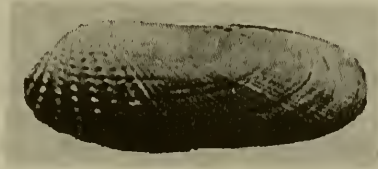
Fig. 838. *Petricola (Petricolaria) pholadiformis* Lamarck.
Length 5.5 cm.

XIV. STIRPS MACTRACEA

Shell equivalve, triangular or oval or more elongated, closed or gaping; ligament with large internal cartilage posterior to the main teeth; hinge margin on the left with an often cleft or angle-shaped main tooth, on the right with 2 teeth clasping it, on the left also with an anterior and a posterior lateral tooth, and corresponding to them on the right having furrows with elevated margins; mantle sinus variable. Siphons partly or completely fused, in most cases with a cuticula and with tentacles at the end ; mantle more or less widely open; gill laminae smooth; oral lobes long and narrow; foot large, without byssus.

1. Family MESODESMATIDAE

Shell equivalve, in most cases longish triangular; posteriorly shorter than anteriorly, seldom transversely oval, strong, smooth ,or concentrically striated, with distinct periostracum; external ligament small,

internal one in a more or less inwardly projecting pit; the hinge margin has an anterior and posterior lateral tooth in the left valve and corresponding pits in the right valve and mainly below them with teeth, on the left with one main tooth anterior to the ligamental cartilage and sometimes posterior to it with a smaller or larger lamella, on the right with 2 main teeth, the anterior of which is in most cases joined with the lower anterior lateral tooth; muscle scars fairly large; mantle line in most cases with a small angular or roundish indentation. Siphons completely separate, on the ends with papillae; mantle margin smooth; foot large, triangular, without byssus; gill laminae folded, unequally broad; labial palps triangular.

? *Nesis* Monterosato, 1875

Shell small, colorless, smooth and shiny, transversely oval; umbo close to the posterior end; ligamental cartilage weak, posterior to it with a short, angularly projecting ridge; hinge margin on the left with a simple, on the right with a forked main tooth, without lateral teeth; adductor muscle scars large, oval; mantle line close to the margin, unindented.

N. prima Monterosato, in the Mediterranean Sea.

Davila Gray, 1853

Shell fairly small, rounded triangular, compressed; ligamental cartilage moderately large, in the left valve its anterior and posterior margins are elevated tooth-shaped and the lateral teeth are short and close to the center; in the right valve the main tooth is very weak, the posterior lateral tooth is strong, furrowed; mantle line unindented.

897

D. plana (Hanley). A couple of species, near the Philippines, Sunda Islands, and eastern Australia.

Anapella Dall, 1895

Synonym *Anapa* Gray, 1853, non 1847.

Shell triangular oval, inflated, concentrically sculptured, posteriorly longer than anteriorly and somewhat pointed; ligamental cartilage strong; left valve with a strong, furrowed main tooth, and with long lateral teeth; right valve with a forked main tooth and distinct lower lateral teeth; mantle line unindented, posteriorly straight.

A. triquetra (Hanley) (Fig. 839). Few species, near South Australia and Tasmania.

Fig. 839. Hinge margins of *Anapella triquetra* (Hanley), enlarged.

Ervilia Turton, 1822

Shell small, compressed, elongate oval, posteriorly longer than anteriorly, moderately thick, smooth or concentrically sculptured; umbo somewhat projecting; external ligament more or less rudimentary; cartilage triangular, scarcely projecting interiorly; left valve with a weak main tooth and a similar adjacent anterior lateral tooth, as well as a short and strong posterior lateral tooth; right valve with one main tooth and a short posterior lateral tooth; mantle sinus fairly deep, oval.

E. nitens (Laskey). A few species, in various seas.

Iredale, 1930, proposed a "genus" *Spondervilia* for the anteriorly and posteriorly radially striated *E. australis* Angas.

? *Caecella* Gray, 1853

Shell fairly large and thin, somewhat inflated, elongated oval, finely concentrically striated; umbo close to the center, more or less projecting; external ligament rudimentary; cartilage pit downwardly projecting; left valve with one main tooth and short lateral teeth; right valve with a divided main tooth, the anterior cusp of which is fused with the lateral tooth, and a somewhat longer posterior lateral tooth; mantle sinus fairly small.

C. horsfieldi Gray. Few species, in the Pacific Ocean.

Argyrodonax Dall, 1911

Shell small, somewhat triangular, posteriorly pointed, shorter than anteriorly, exteriorly concentrically sculptured; ligamental cartilage narrow, but strong; main teeth weak; lateral teeth on the right fitting below the margin of the left shell, the anterior one short and strong, the posterior one elongated, high and thin; mantle sinus deep, fused with the mantle line.

A. haycocki Dall, near the Bermudas.

Mesodesma Deshayes, 1830

Shell in most cases compressed, triangular, anteriorly longer than posteriorly; hinge margin strong, with variably long lateral teeth' and more or less strong main teeth; mantle sinus small.

Several species, in various seas.

898   Section *Atactodea* Dall, 1895 (synonym *Paphia* Lamarck, 1801, non Röding, 1798). Shell fairly short triangular, anteriorly scarcely longer than posteriorly, bulging; hinge strong, although ligamental pit only slightly projecting downward, on the left its two margins, especially the anterior one, are distinctly elevated; the anterior lateral tooth longer than the posterior; on the right the posterior part of the main tooth is scarcely developed; the inner lateral teeth strong. *M. (A.) glabratum* (Gmelin). —Section *Paphies* Lesson, 1830 (synonym *Machaena* (Leach) Gray, 1843). Shell elongated oval, anteriorly somewhat longer than posteriorly, compressed; cartilage pit interiorly distinctly projecting; left valve with a simple main tooth and fairly short lateral teeth; right valve with strong inner lateral teeth; posterior part of the main tooth rudimentary; mantle sinus small, angular. *M. (P.) novaezelandiae* (Chemnitz). —Section *Donacilla* (Lamarck) Philippi, 1836. Shell compressed, anteriorly distinctly elongated; ligamental pit scarcely projecting below, anterior to it on the left a weak main tooth, posterior to it a strong lamella and a very short posterior lateral tooth, whereas the anterior one is elongated; right valve with a forked main tooth, with double anterior lateral teeth and a short thick posterior lateral tooth; mantle sinus roundish. *M. (D.) corneum* (Poli).—Section *Taria* Gray, 1853. Shell oval to triangular, anteriorly more or less elongated; ligamental cartilage strong; left valve with the one main tooth and fairly short, smooth lateral teeth; right main tooth merging into the anterior lateral tooth; mantle sinus sometimes deep. *M. (T.) quoyi* Deshayes. Iredale, 1930, proposed the "genus" *Amesodesma* for the eastern Australian species *perfuga*. Section *Mesodesma* s. s. (synonym *Ceronia* Gray, 1853). Differing from *Taria* mainly by the transverse grooves on the lateral teeth; main teeth fairly weak; mantle sinus roundish. *M. (M.) donacium* (Lamarck) (Fig. 840).

2. Family MACTRIDAE

Lateral teeth present as a rule and mantle sinus of variable size.

Fig. 840. Internal side of the right shell valve of *Mesodesma donacium* (Lamarck).
Length about 8 cm.

Rangianella Conrad, 1868

Shell fairly small and strong, triangular, posteriorly angular; umbo projecting, close to the center; cartilage not separated from the external ligament, fairly small, not projecting inwardly; main teeth weak. Lateral teeth moderately long; mantle sinus small.

Subgenus *Rangianella* s. s. In the right valve the taller anterior main tooth and a small angle arch over the weak main tooth anterior to the cartilage; on the left with a cleft main tooth and an angle anterior to the upper part of the cartilage; lateral teeth not distinctly grooved; mantle sinus scarcely deepened. *R.* (*R.*) *mendica* (Gould). On the coasts of North and Central Amercia.

Subgenus *Notospisula* Iredale, 1930. Main teeth of right valve weak, the posterior one short; left valve with a distinctly forked main tooth and with a short tooth at the corner anterior to the cartilage; lateral teeth distinctly grooved; mantle sinus fairly shallow. *R.* (*N.*) *parva* (Petit). A couple of Australian species.

899

Rangia Des Moulins, 1832

Synonyms ? *Clathrodon* (nom. nud.) Conrad, 1830; *Gnathodon* (Gray) Sowerby, 1831, non Oken, 1816.

Shell very thick, with high umbones close to the anterior end; cartilage strong, not separated from the ligament; the hook-shaped main tooth of left valve clasps the posterior main tooth of right valve and is embraced anteriorly by the other tooth; lateral teeth distinctly grooved, the posterior one very long, parallel to the margin, the anterior one less

long, on the left enclosing hook-shaped the initially high lateral tooth of the right valve; mantle sinus small, but distinct. Siphons short, fused at base.

R. cuneata (Gray), in the Gulf of Mexico.

Mulinia Gray, 1837

Shell strong, greatly bulging, oval with high umbones situated close to the middle, with strong periostracum; ligament and cartilage enclosed in a common pit and not exteriorly visible; left valve with a forked main tooth and a small posterior lamella; right valve with 2 thin main teeth forming a right angle and a small denticle above the cartilage pit; mantle sinus distinctly deepened, tongue-shaped.

M. edulis (King). A few American species and one from East Africa.

Spisula Gray, 1837

Shell of medium to considerable size, more or less bulging, rounded triangular, in most cases closed; umbo somewhat elevated and close to the center, concentrically striated; external ligament not separated from the cartilage by a calcareous lamella; lateral teeth often grooved; mantle sinus more or less large.

Subgenus *Spisula* s. s. (synonym *Spisulina* P. Fischer, 1887). Shell fairly small, triangular, bulging, closed; upper part distinctly striated; umbo close to the center; left valve with an angle-shaped main tooth, which is covered above by the main teeth of the right valve; lateral teeth grooved; mantle sinus fairly small, tongue-shaped. *S. (S.) solida* (Linné). A few mainly European species.

Subgenus *Hemimactra* Swainson, 1840. Shell large, oval triangular, closed; anterior lateral teeth very close to the main teeth. Section *Hemimactra* s. s. Right anterior main tooth joined with the lower lateral tooth; lateral teeth grooved; mantle sinus short, rounded. *S. (H.) solidissima* (Chemnitz). Few species, near North America.—Section *Mactromeris* Conrad, 1868. Lateral teeth smooth, the lower ones of the right valve weak, without junction with the main tooth; mantle sinus large. *S. (M.) polynyma* (Stimpson) (Fig. 841), near North America.—Dall, 1894, proposed the section *Symmorphomactra* for *S. falcata* Gould from the North American west coast; according to Finlay, 1928, belonging here are his "genera" *Scalpomactra* (*scalpellum* Deshayes) and *Longimactra* (*elongata* Quoy & Gaimard) from New Zealand. The relationship of *Hemimactra versicolor* Tate from South Australia, for which Iredale, 1930, proposed the genus *Diaphoromactra*, seems doubtful.—Section *Austromactra* Iredale, 1930. Shell triangular, with distinct concentric

900

rings; lateral teeth smooth, moderately long, without connection to the main teeth; mantle sinus short, roundish. *S. (A.) caloundra* Iredale, near Australia.—Section *Oxyperas* Mörch, 1853. Shell elongated triangular, with concentric rings; in the left valve the posterior end of the anterior lateral tooth is separated by a depression and forms a lamella just anterior to the main tooth; lateral teeth grooved; mantle sinus deep. *S. (O.) triangularis* (Lamarck). Few species, in the Pacific Ocean.

Fig. 841. Shell margins of *Spisula* (*Mactromeris*) *polynyma* (Stimpson) (after Lamy).

Subgenus *Leptospisula* Dall, 1895. Shell large, bulging, gaping; umbo closer to the anterior end; lateral teeth short, smooth; mantle sinus deep, tongue-shaped. *S. (L.) striatella* (Lamarck), near West Africa and on the east coast of South America.

Subgenus *Schizodesma* (Gray, 1837) Swainson, 1840 (*Scissodesma*). Shell triangular, posteriorly angulate; umbones far away from one another, between them lies the external ligament in a half-moon-shaped cleft, below this the cartilage in very deep pits; the posterior margin of the cleft is thickened and projects at the end as roundish tooth; the angle-shaped left main tooth high; lateral teeth short, granulose; mantle sinus tongue-shaped. *S. (S.) spengleri* (Linné), near South Africa.

Mactra Linné, 1767

Shell triangular or oval, often somewhat gaping; cartilage separated from the ligament by a calcareous lamella; lateral teeth not grooved; mantle sinus variable in size, rounded. Siphons completely fused, partly enveloped by a cuticula.

Numerous species, in various seas.

Subgenus *Mactra* s. s. (synonym *Trigonella* Da Costa, 1778, non Walch, 1762, nec Schröter, 1776). Shell bulging, triangular, posteriorly scarcely gaping; umbo close to the center, more or less high; mantle sinus short. Section *Nannomactra* Iredale, 1930. Shell small and thin, fairly long, dorsally not more strongly sculptured; hinge margin weak; cartilage pit small; main teeth diverging at a right angle; lateral teeth thin. *M. (N.) jacksonensis* Edg. Smith, near eastern Australia.—Section

Mactra s. s. Shell larger and stronger; umbo elevated, dorsal parts not grooved; main teeth of the right valve not connected; lateral teeth fairly large. *M.* (*M.*) *stultorum* Linné (Fig. 842).—Section *Maorimactra* Finlay, 1928. Shell small and thin, anteriorly shorter, dorsally sharply ribbed; cartilage small; lateral teeth long; mantle sinus broad and shallow. *M.* (*M.*) *ordinaria* Edg. Smith, from New Zealand.—Section *Calorimactra* Iredale, 1929. Shell fairly short, anteriorly rounded, posteriorly angulate, thin; umbo high, with stronger striae; lateral teeth short, close to the main teeth; mantle sinus short. *M.* (*C.*) *queenslandica* Edg. Smith, near Queensland.—Section *Telemactra* Iredale, 1929. Shell triangular, thin, inflated, with dorsal folded striae; mantle sinus very short. *M.* (*T.*) *obesa* Deshayes.—Section *Coelomactra* Dall, 1894. Shell fairly large and thin, longish triangular, bulging; hinge margin fairly broad, the anteriormost main teeth of both valves situated on a lamella, which covers the posterior, strongly depressed part with the thin anterior lateral teeth. *M.* (*C.*) *violacea* Chemnitz.

901

Fig. 842. Shell of *Mactra stultorum* (Linné).

Subgenus *Mactroderma* Dall, 1894. Umbo close to the anterior end; hinge margin broad with large, triangular cartilage; mantle sinus large. Section *Cyclomactra* Dall, 1894. Shell roundish; anterior main teeth situated in the prolongation of the anterior lateral teeth. *M.* (*C.*) *tristis* Deshayes, near New Zealand and Australia.—Section *Mactroderma* s. s. Shell large and strong, longish triangular; anterior right main tooth extending to the short anterior lateral tooth; posterior lateral teeth short and strong; mantle sinus broadly rounded. *M.* (*M.*) *velata* Philippi, on the American west coast.

Subgenus *Mactrotoma* Dall, 1894. Shell compressed, longish, posteriorly often distinctly gaping; cartilage pit large; anterior lateral teeth very short, continuing posteriorly and dorsally by a lamella. Section

Micromactra Dall, 1894. Shell small and strong; umbo furrowed. *M. (M.)
californica* Conrad.—Section *Simomactra* Dall, 1894. Shell only slightly
gaping; accessory lamellae separated from the lateral teeth, mantle sinus
fairly small. *M. (S.) dolabriformis* Conrad.—Section *Mactrotoma* s. s.
Shell distinctly gaping, posterior part delimited by a depressed band;
anterior lateral teeth joined with the lamellae; mantle sinus large and
broad. *M. (M.) fragilis* Chemnitz. *Pseudoxyperas* Sacco, 1900, was
proposed for the Tertiary species still living on the West African coast,
M. proaspera Sacco, which is considered by Lamy as *M. (Mactrotoma)
aspera* Sowerby forma *egena* Deshayes.

Subgenus *Mactrella* Gray, 1853 (synonym *Papyrina* Mörch, 1853).
Shell triangular, thin, colorless, indented anterior to the umbones,
posteriorly with a more or less high lamella; surface with weak concentric
lines or strong folds; mantle sinus fairly large. Section *Mactrella* s. s.
Shell longish, with fine concentric threads, without delimited lunule,
posteriorly gaping; left valve with a pit above the anterior cusp of the
main tooth and below its anterior end with a pointed lamella, which is
separated from the anterior lateral tooth by an indentation; pits are also
present above and anterior to the anterior main tooth of the right valve.
M. (M.) alata Spengler. In tropical America.—Section *Electromactra*
Iredale, 1930. Shell smooth and shiny; lunule not distinctly delimited;
anterior to the main teeth on either side, a depression divided by the
lateral tooth. *M. (E.) parkesiana* Hedley, near eastern Australia.
—Section *Harvella* Gray, 1853. Shell roundish, strongly bulging, with
strong concentric folds; lunule distinctly deepened; hinge margin similar
to that in *Mactrella*; lateral teeth short; mantle sinus large. *M. (H.)
elegans* Sowerby, near Panama.—Section *Mactrinula* Gray, 1853. Shell
compressed, longish, with strong concentric folds and distinct lunule;
hinge margin broad, below the anterior main tooth on either side with a
short accessory lamella, which is not continuous with the lateral
tooth; posterior lateral tooth high. *M. (M.) plicataria* Linné. Near southern
Asia.

902

Labiosa (Schmidt) Möller, 1832

Synonyms *Anatina* Schumacher, 1817, non Lamarck, 1816; *Cypricia*
Gray, 1847; *Leucoparia* C. Mayer, 1867.

Shell thin, posteriorly gaping, anteriorly bulging, posteriorly
compressed; umbo projecting, situated behind the center; cartilage
separated from the ligament by a calcareous lamella; hinge margin broad
and short; main teeth similar to those in *Mactra*; lateral teeth more or

less rudimentary. Siphons naked, completely retractile; mantle partly closed below.

A few species, in warm seas.

Subgenus *Labiosa* s. s. Shell longish oval, fairly large, concentrically striated, with a posterior radial ridge, broadly gaping; lunule delimited by a flat furrow; lateral teeth very short and close to the main teeth, on either side with an anterior one and a posterior one; mantle sinus broad, anteriorly rounded. *L. (L.) anatina* (Spengler). A couple of American species.

Subgenus *Raeta* Gray, 1853 (synonym *Lovellia* C. Mayer, 1867). Shell inflated, posteriorly angulate and somewhat gaping, with concentric folds; a ridge parallel to the margin extending posteriorly from the ligamental pit; mantle sinus deep, anteriorly angulate. Section *Raeta* s. s. Shell variable in size; small posterior lateral teeth present. *L. (R.) canaliculata* (Say).—Section *Raetina* Dall, 1894. Shell small, without posterior lateral teeth. *L. (R.) indica* (Dall).

Subgenus *Raetella* Dall, 1894. Shell very small and thin, shiny, roundish, with short beak, without lateral teeth. *L. (R.) tenuis* (Dall), from China.

Standella Gray, 1853

Shell oval, anteriorly and posteriorly gaping, often with radial sculpture; umbo situated anterior to the center; ligament not separated from the cartilage by a calcareous lamella; anterior lateral teeth short and close to the main tooth; lateral teeth smooth, double in the right valve; mantle sinus deep and anteriorly rounded.

Subgenus *Standella* s. s. (synonym *Merope* H. & A. Adams, 1856). Shell fairly thin, posteriorly elongated; left main tooth angle-shaped; anterior lower lateral tooth of the right valve joined with the anterior main tooth. Few species, in the Indo-Pacific area. Section *Standella* s. s. Shell without distinct radial sculpture. *S. (S.) pellucida* (Chemnitz). —Section *Meropesta* Iredale, 1929. Shell with numerous radial threads. *S. (M.) meridiana* Iredale.

Subgenus *Eastonia* Gray, 1853. Shell strong, bulging, roundish oval, with distinct radial sculpture; left main tooth scarcely diverging; right anterior main tooth very short; the lower lateral tooth high, adjoining the anterior main tooth. *S. (E.) rugosa* (Helbling),·in the Mediterranean Sea and the neighboring Atlantic Ocean.

Heterocardia Deshayes, 1854

Shell triangular oval; umbo close to the center; surface concentrically striated; cartilage large, separated from the ligament by a calcareous lamella; left valve with a high angle-shaped main tooth the short high lateral teeth; right anterior main tooth joined with the lower or upper lateral tooth; mantle sinus large.

H. gibbosula Deshayes. A couple of species near the Philippines.

Schizothaerus Conrad, 1853

Synonyms *Cryptodon* Conrad, 1837, non Turton, 1822, nec Latreille, 1833; *Tresus* Gray, 1853, non Walkenaer, 1833.

Shell very large and strong, oval, bulging, concentrically striated, posteriorly widely gaping; umbo situated anterior to the center; cartilage strong, separated from the ligament by a calcareous lamella; hinge teeth weak; left main tooth angle-shaped; right anterior main tooth joined with the short lower lateral tooth; mantle sinus very large.

S. nuttalli (Conrad), in the northern Pacific Ocean.

Lutraria Lamarck, 1799

Synonyms *Cacophonia* + *Eustylon* Gistel, 1848.

Shell elongated, more or less compressed, broadly gaping at the ends, concentrically striated, with distinct periostracum; umbo only slightly elevated, situated anterior to the center; cartilage pit obliquely posteriorly directed; left main tooth high; right anterior main tooth joined with the short anterior lateral tooth; posterior lateral teeth weak or absent; mantle sinus very deep, anteriorly rounded.

A few species, in various seas.

Subgenus *Lutraria* s. s. Shell elongated oval; ligament separated from the cartilage by a calcareous lamella; right anterior lateral tooth situated in the process of the main tooth. Section *Lutraria* s. s. Shell posteriorly moderately elongated; right posterior main tooth fairly high; posterior lateral teeth very weak. *L. (L.) lutraria* (Linné) (Fig. 843). *Lutromactra* Iredale, 1929 [*impedita* Iredale = *elongata* (Gray)] is smaller, but is otherwise scarcely different.—Section *Goniomactra* C. Mayer, 1867, is different by the greatly elongated shell with nearly parallel dorsal and ventral margins. *L. (G.) impar* Deshayes.—Section *Lutrophora* Dall, 1894. Shell greatly compressed, elongated oval, with strong concentric sculpture; right posterior main tooth posteriorly appressed; posterior lateral teeth distinctly developed, but without the upper ones of the right side. *L. (L.) planata* (Chemnitz).
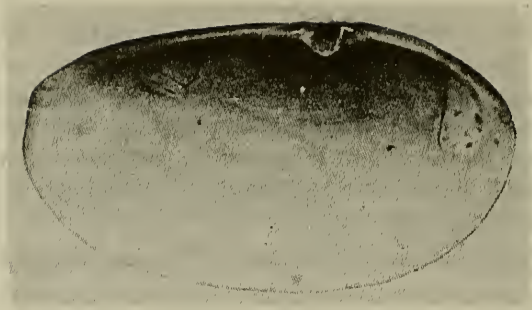
Fig. 843. Inner side of the left shell valve of *Lutraria lutraria* (Linné).
Length about 12.5 cm.

Subgenus *Psammophila* (Leach) T. Brown, 1827. Shell elongated, dorsally somewhat concave; umbo close to the anterior end; ligament not **904** separated from the cartilage by a lamella; left main tooth compressed; right posterior main tooth high, the anterior one situated close beside the anterior lateral tooth, separated by a cleft. *L. (P.) oblonga* (Chemnitz).

Darina Gray, 1853

Shell fairly small, thin, elongated oval, compressed, somewhat gaping at both ends, smooth, with distinct periostracum; umbo scarcely elevated, situated posterior to the center; cartilage only slightly oblique, not separated from the ligament by a calcareous lamella; left main tooth with larger anterior limb and small posterior limb; right anterior main tooth joined with the small lateral tooth; posterior lateral teeth short; mantle sinus moderately deep, anteriorly rounded, joined with the mantle line.

D. solenoides (King), near Tierra del Fuego.

Vanganella Gray, 1851

Synonyms *Resania* Gray, 1853; *Myomactra* + *Laminaria* C. Mayer, 1867.

Shell fairly large, thin, compressed, elongated oval, anteriorly somewhat pointed, concentrically striated, with yellowish periostracum; umbo not projecting, situated somewhat posterior to the center; cartilage large, obliquely posteriorly directed, not separated from the ligament by a calcareous lamella; the cartilage bearer is fused with a strong ridge, which descends from the ligament anterior to the posterior adductor muscle scar; a flatter ridge lies posterior to the anterior adductor muscle scar; left main tooth strong, with equal limbs; lateral teeth weak; right main teeth fairly thin, diverging at a right angle, the anterior one fused with the

small lateral tooth; mantle sinus broad, extending to the posterior ridge, joined with the mantle line.

V. taylori Gray, near New Zealand.

Zenatia Gray, 1853

Synonym *Metabola* C. Mayer, 1867.

Shell compressed, thin, gaping at the ends, with brownish periostracum; umbo not projecting, more or less close to the anterior end; the triangular cartilage bearer is posteriorly attached to the shell; ligament not separated from the cartilage by a calcareous lamella; left main tooth with equal limbs, its anterior limb is parallel to the short anterior lateral tooth, the posterior one very weak; right main teeth fairly strong; lateral teeth rudimentary; mantle sinus deep, joined with the mantle line.

Z. acinaces (Quoy & Gaymard) near New Zealand, and one species (*victoriae* Pritchard & Gatliff) near South Australia.

3. Family ANATINELLIDAE

Shell roundish oval, bulging, fairly thin, colorless, anteriorly rounded, posteriorly angulate and only slightly gaping; surface concentrically striated and with very fine radial lines; umbo elevated, close to the center; ligament small, not separated from the large club-shaped cartilage; the cartilage bearer projects far downward and somewhat backward; the fairly strong left main tooth is weakly cleft, parallel to its anterior margin runs a rudimentary anterior lateral tooth; the two right main teeth form an acute angle; probably a small lateral tooth is completely fused with the anterior tooth; posterior lateral teeth absent; the anterior margin of the posterior adductor muscle scar is thickened; the two scars and the mantle line situated very close to the margin, this line posteriorly runs parallel to the margin without indentation. Animal unknown.

905

Anatinella Sowerby, 1834

Characters of the family.
A. candida (Chemnitz), in the Indo-Pacific region.

? 4. Family CARDILIIDAE

Shell greatly bulging, higher than long, with very strong, anteriorly spirally inrolled umbones, colorless; external ligament short; cartilage on

a short and broad, anteriorly deepened plate, which below the cartilage bears high and narrow teeth, and on the right with a triangular main tooth and between it and the cartilage a half-moon-shaped tooth; between them fits the channel-shaped left tooth; a weak ridge on the anterior margin of the right valve is perhaps a rudimentary lateral tooth; the anterior adductor muscle scar is long and narrow, close to the anterior margin; the posterior adductor muscle is attached to an erect lamella; a mantle sinus absent.

Cardilia Deshayes, 1835

Synonyms ? *Hemicyclonosta* (Deshayes) Michelin, 1828; *Hemicyclostera* Bronn, 1838; *Hemicyclodonta* Deshayes, 1850; *Leptina* (Bonelli) Pictet, 1855.
Characters of the family.
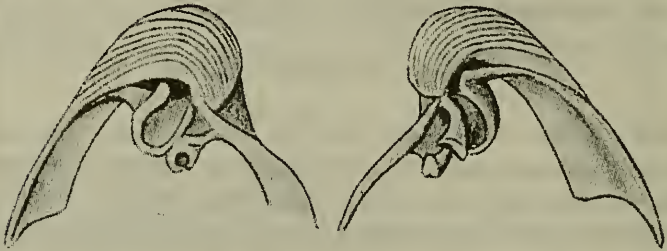
Fig. 844. Hinge margins of *Cardilia semisulcata* (Lamarck) (after Lamy).

C. semisulcata (Lamarck) (Fig. 844). Few species in the Pacific Ocean (Japan to Australia).

XV. STIRPS TELLINACEA

Shell in most cases somewhat asymmetrical, compressed, oval or triangular, as a rule on either side with 2 main teeth and often also with lateral teeth; mantle sinus deep, not seldom completely or largely continuous with the mantle line. Siphons long, separate; mantle ventrally more or less open; foot in most cases without byssus; gill laminae smooth or folded, in the posterior part of the mantle as a rule with a cross-shaped muscle.

1. Family DONACIDAE

Shell equivalve, triangular or elongated, more or less compressed, smooth or sculptured; ligament short, bulging, attached in a furrow; cartilage on short ridges; hinge margin as a rule with 2 main teeth on either side; lateral teeth may be reduced; the right anterior dorsal margin is often distinctly furrowed; mantle line in most cases strongly indented; inner margin often denticulate. Mantle completely open below.

906   *Hemidonax* Mörch, 1870

Synonym *Donacicardium* Vest, 1875.
Shell strong, triangular, anteriorly somewhat longer and rounded, posteriorly flattened and delimited by an edge; surface radially ribbed; umbo strong; hinge margin on the left with 2 main teeth and an anterior and a posterior lateral tooth, on the right with 2 diverging main teeth and 2 anterior and 2 posterior lateral teeth; mantle line not indented; inner margin strongly denticulate. Animal unknown.
H. donaciformis (Spengler), near Australia and the Philippines.
Because of the unindented mantle line, this species was earlier included with the cardiids, but recently with the donacids; Fischer has placed it with the fossil genus *Tancredia* Lycett in a family Tancrediidae, which is similar to the donacids.

Donax Linné, 1758

Synonyms *Cuneus* Da Costa, 1778; *Capisteria* Meuschen, 1787.
Shell triangular or elongated, posteriorly shorter than anteriorly; umbo fairly small; ligamental cartilage sometimes somewhat sunken; lateral teeth more or less distinctly developed, 2 main teeth on either side; mantle sinus deep and rounded; margin in most cases denticulate. Siphons fairly long, separate, unequal; mantle margin beset with papillae; gill laminae variable, sometimes smooth and with identical filaments, sometimes folded with large inner border filaments; outermost lamella broadened; foot without byssus.
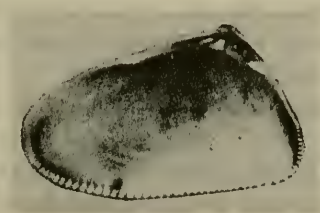
Fig. 845. Inner side of the left shell valve of *Donax rugosus* Linné.

Several species in temperate and warm seas, living in sand close to the shore.

Section *Chion* Scopoli, 1777. Shell fairly strong, triangular, posteriorly sharply truncated; surface with punctate radial furrows; lateral teeth distinctly developed; ventral margin sharply denticulate. *D. (C.) denticulatus* Linné.—Section *Deltachion* Iredale, 1930. Shell scarcely different from *Chion. D. (D.) virilis* Iredale—Section *Donax* s. s. Shell strong, posteriorly very short, anteriorly long, with simple radial furrows; anterior lateral tooth long; ventral margin sharply denticulate. *D. (D.) rugosus* Linné (Fig. 845).—Section *Grammatodonax* Dall, 1900. Shell short triangular; surface with deep oblique furrows; right valve with a cleft main tooth; the left one with 2 simple main teeth and an anterior and posterior lateral tooth; ventral margin finely denticulate. *D. (G.) madagascariensis* Lamarck.—Section *Hecuba* Schumacher, 1817. Shell large, posteriorly with a sharp keel ending in an acute angle, anterior to it with concentric threads and lamellae; hinge teeth similar to those in *Serrula*; anterior dorsal margin of the right valve with a distinct furrow; ventral margin with very fine transverse wrinkles. *D. (H.) scortum* Linné. —Section *Serrula* (Chemnitz) Mörch, 1853. Shell compressed, long, smooth, without posterior keel, 2 main teeth on either side; on the left with weak lateral teeth; ventral margin sometimes only weakly denticulate. *D. (S.) trunculus* Linné.—Section *Platydonax* Dall, 1900. Shell long, compressed, without distinct keel; hinge teeth similar to those in *Serrula*, but without lateral teeth. *D. (P.) finchii* Sowerby. —Section *Machaerodonax* E. Römer, 1870. Shell smooth and shiny, thin, long and low, posteriorly with a sharp keel; hinge margin on the right with a weak tooth posterior to the 2 normal teeth; anterior dorsal margin with a furrow; ventral margin finely denticulate. *D. (M.) scalpellum* Gray. —Section *Plebidonax* Iredale, 1930. Shell large and strong, unequally triangular, with rounded edge; surface finely radially sculptured; lateral teeth distinct; right anterior dorsal margin furrowed; ventral margin smooth. *D. (P.) deltoides* Lamarck.—Section *Latona* Schumacher, 1817 (synonym *Liodonax* P. Fischer, 1887). Shell compressed, rounded triangular, posteriorly not distinctly truncated; surface with weak, posteriorly sometimes rough sculpture; left valve with 2 main teeth and a weak posterior lateral tooth; the right one with one strong and one rudimentary anterior main tooth, as well as one anterior and posterior lateral tooth; ventral margin not denticulate. *D. (L.) cuneatus* Linné. —Section *Tentidonax* Iredale, 1930, appears to be intermediate between *Latona* and *Capsella. D. (T.) veruinus* Hedley (= *nitidus* Reeve non Lamarck).—Section *Capsella* Gray, 1851 (synonym *Peraeonoderma* Mörch, 1853). Shell long and low, thin, smooth, without posterior edge;

on the left with a short anterior lateral tooth just anterior to the 2 main teeth and a longer marginal posterior lateral tooth; on the right the posterior main tooth is cleft, anterior and above the anterior one lies a short lateral tooth and the anterior dorsal margin is furrowed. *D. (C.) politus* (Poli) = *violaceus* (Meuschen).

Iphigenia Schumacher, 1817

Synonyms *Capsa* Lamarck, 1818, non 1799; ? *Donacina* Férussac, 1821; *Procos* Gistel, 1848.

Shell fairly thin, elliptical to triangular, with yellowish or olive-brown periostracum, without sculpture; umbo close to the center; ligament external, short; left valve with 2 main teeth, the right with one strong, cleft main tooth and one weak anterior main tooth and with long and narrow anterior and posterior lateral teeth; mantle sinus deep. Siphons long, free, exteriorly with longitudinal threads; and with terminal papillae; gill laminae free; labial palps long.

A few species on the coast and in rivers of tropical West Africa and both coasts of Central and South America.

Section *Iphigenia* s. s. Shell medium-sized, interiorly with white or violet flecks, mainly in brackish water. *I. (I.) laevigata* [(Chemnitz) Gmelin].—Section *Profischeria* Dall, 1903 (synonym *Fischeria* Bernardi, 1860, non Robineau-Desvoidy, 1830). Shell small, interiorly violet, mainly in rivers. *I. (P.) delesserti* Bernardi.

Egeria Roissy, 1805

Synonym *Galatea* Bruguière, 1797 = *Galathea* Lamarck, 1804, non Fabricius, 1793; *Potamophila* J. Sowerby, 1821; *Megadesma* Bowdich, 1822; *Galateola* (Fleming) Herrmannsen, 1847.

Shell thick, triangular to longish, with strong periostracum; hinge margin broad, with 2 or 3 often irregularly furrowed diverging main teeth and on the right with low and short anterior and posterior lateral teeth, which are often indistinct in old shells; mantle sinus moderately deep, rounded.

E. radiata (Lamarck). A few species, in brackish water of tropical West Africa.

908

2. Family PSAMMOBIIDAE

Shell equivalve, oval or elongated, smooth or sculptured; ligament external, on thick ridges; hinge margin as a rule with 2 main teeth on

either side, without lateral teeth; muscle scars close to the dorsum; mantle sinus deep, often continuous with the ventral mantle line; lower margin smooth. Mantle margin widely open, with papillae; siphons very long and separate; foot tongue-shaped, without byssus; gill laminae folded with larger inner border filaments; outermost lamella broadened; oral lóbes large, triangular.

Heterodonax Mörch, 1853

Shell compressed, oval, anteriorly somewhat longer than posteriorly, exteriorly only with growth lines; anterior left and posterior right hinge tooth cleft, left posterior one weak; mantle sinus broad, roundish, separated from the mantle line.

H. bimaculatus (Linné). Few species, on American coasts.

Asaphis Modeer, 1793

Synonyms *Corbula* (Bolten) Röding, 1798; *Capsa* Lamarck, 1801, non 1799; *Capsula* Schumacher, 1817; *Pleiorhytis* Conrad, 1863.

Shell large and strong, oval, bulging, with slender radiating ribs; umbo situated somewhat anterior to the center; ligament fairly long and thick; anterior left and posterior right tooth furrowed, the 2 other ones weak; mantle sinus large, rounded, separated from the mantle line.

Few species, in warm seas.

Section *Asaphis* s. s. Ribs uniformly radial. *A. (A.) deflorata* (Linné). —? Section *Heteroglypta* Martens, 1880. Ribs converging in angles. *A. (H.) contraria* (Deshayes). This group is in most cases placed in *Psammobia*.

According to Winckworth, 1930, *Corbula* Röding—sp. typ. *anomala* Bolten—is synonymous with *Asaphis*.

Elizia Gray, 1854

Shell thin, greatly compressed, with strong periostracum, oval; umbo not projecting, close to the anterior end; hinge margin very narrow, on the left with 3 teeth, the median of which is very broad and furrowed, on the right with 2 widely diverging teeth; mantle sinus completely separated from the mantle line.

E. orbiculata (Wood), near Indochina and the Greater Sunda Islands.

Sanguinolaria Lamarck, 1799

Synonyms *Aulus* Oken, 1815; *Lobaria* Schumacher, 1817, non Müller, 1776; *Isarcha* Gistel, 1848.

Shell oval or more elongated, compressed, smooth; umbo only slightly projecting, situated close to the center hinge margin weak, on either side with 2 unequal teeth; mantle sinus deep, ventrally not or only slightly separated from the mantle line.

A few species, in various seas.

Section *Nuttallia* Dall, 1898. Shell fairly large, oval; right valve somewhat flatter than the left, with strong, smooth periostracum; umbo scarcely projecting, situated somewhat anterior to the center; ligamental ridges broad; mantle sinus posteriorly very broad, anteriorly narrowed. *S. (N.) nuttallii* Conrad. Few species, near Japan and California.—
Section *Psammotellina* P. Fischer, 1887. Shell only slightly elongated, greatly compressed; ligamental ridges with broad, more or less excavated roughenings; right posterior hinge tooth rudimentary; mantle sinus long and narrow. *S. (P.) ambigua* (Deshayes).—Section *Solenotellina* Blainville, 1824 (*Soletelllina*) (synonym *Hiatula* Modeer, 1793, non Martini, 1774). Shell fairly large, equivalve, more or less elongated, with strong periostracum; ligamental ridges short and broad; hinge margin with 2 teeth on either side; mantle sinus very deep, anteriorly narrowed. *S. (S.) diphos* (Gmelin).—Section *Psammotaea* Lamarck, 1818 (synonyms *Psammocola* Blainville, 1824; *Capsella* Deshayes, 1854, non Gray, 1851). Shell elongated oval, concentrically striated; ligamental ridges fairly long and projecting; left posterior hinge tooth rudimentary. *S. (P.) serotina* Lamarck. *Psammosphaerita* Jousseaume, 1894 (*psammosphaerita* Jousseaume) differs from *Psammotaea* by the nongaping shell. —Section *Sanguinolaria* s. s. Shell moderately sized, thin, equivalve, oval, rose-red, or white, with narrow ligamental ridges; hinge margin on either side with 2 cleft teeth; mantle sinus deep, anteriorly widened. *S. (S.) sanguinolenta* (Gmelin). —Section *Psammotella* (Blainvelle) Herrmannsen, 1852. Shell long, beaked; left valve flatter than the right; hinge as in *Sanguinolaria* s. s.; mantle sinus anteriorly narrowed, unequal in the two valves. *S. (P.) operculata* (Gmelin).

Psammobia Lamarck, 1818

Synonym *Haplomochlia* Gistel, 1848.

Shell more or less long, smooth or striated, somewhat gaping, anteriorly rounded, posteriorly in most cases somewhat flattened or angulate; hinge margin on either side with 2 teeth, of which the left and

the anterior right ones are cleft; umbo not projecting; mantle sinus largely fused with the mantle line. Siphons very long and thin.

Several species, in various seas, living close to the shore.

Subgenus *Gobraeus* Leach, 1852. Shell somewhat bulging, posteriorly more or less truncated, smooth or concentrically striated; umbo close to the center; hinge teeth variable; mantle sinus more or less deep and often partly detached from the mantle line. *P. (G.) vespertina* (Gmelin) (Fig. 846).—? Section *Psammobella* Gray, 1851. Shell small; hinge weak; mantle sinus connected with the mantle line; *P. (P.) tellinella* Lamarck.
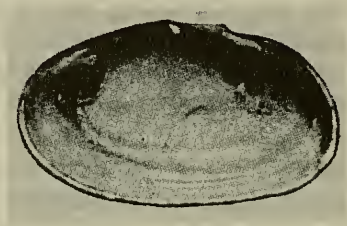
Fig. 846. Inner side of the right shell valve of *Psammobia (Gobraeus) vespertina* (Gmelin).

Subgenus *Psammobia* s. s. Shell long, posteriorly more or less pointed, with concentric or oblique sculpture; mantle sinus largely connected with the mantle line. Section *Psammobia* s. s. Surface concentrically sculptured. *P. (P.) feroensis* (Gmelin).—Section *Grammatomya* Dall, 1898. Shell with oblique, posteriorly strengthened and scaly ridges; hinge margin on either side with 2 teeth; mantle sinus short, rounded, anteriorly detached from the mantle line. *P. (G.) squamosa* Lamarck.

The genus name *Gari* Schumacher, 1817, for *Tellina gari* Linné, can hardly be used, since gari is the genitive of the garum, which was a sharp spice used by Romans, a fact presumably not known to Schumacher.

910   *Amphichaena* Philippi, 1847

Shell elongated; dorsal and ventral margins nearly parallel; anterior end rounded; posterior end truncated; umbo situated in the center; surface smooth; ligamental ridges short and thin; hinge margin on the right with 2 on the left with 3 teeth; mantle sinus rounded, ventrally partly free; anterior margin interiorly crenated.

A. kindermanni Philippi, near Mazatlan (Mexico).

Tagelus Gray, 1847

Synonyms *Siliquaria* Schumacher, 1817, non Bruguière, 1789; *Tagalus* P. Fischer, 1887.

Shell elongated; dorsal and ventral margins nearly parallel, the ends rounded or somewhat truncated; hinge margin on either side with 2 teeth. Anterior mantle opening long, closed only at the cross-shaped muscle; siphons long and separate; foot large.

Few species, on American coasts.

Subgenus *Mesopleura* Conrad, 1867 (synonym *Subtagelus* Ghosh, 1920). Shell thin; umbo situated nearly in the center; ends rounded; inner side with a weak rib descending from umbo; mantle sinus moderately deep, rounded, not separated from the mantle line. *T.* (*M.*) *divisus* (Spengler).

Subgenus *Clunaculum* Dall, 1899. Umbo closer to the rounded anterior end; posterior end truncated; in the center with an oblique furrow corresponding to an internal thickening; mantle sinus not reaching the umbones; posterior adductor muscle scar triangular. *T.* (*C.*) *mollis* (Sowerby).

Subgenus *Tagelus* s. s. Umbo at or posterior to the center, without exterior furrow; mantle sinus deep; posterior adductor muscle scar roundish. *T.* (*T.*) *gibbus* (Spengler) (Fig. 847).
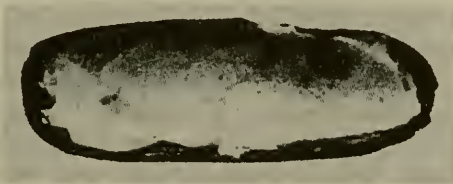
Fig. 847. Inner side of the right shell valve of *Tagelus gibbus* (Spengler). Length 6.5 cm.

Solenocurtellus Ghosh, 1920 (*Solecurtellus*)

Shell elongated; umbo close to the center; both ends rounded and gaping; surface with strong, smooth periostracum; mantle sinus not reaching the center. Mantle margins fused only posteriorly; a short common space anterior to the siphons.

S. dombeyi (Lamarck), on the west coast of South America.

Zozia Winckworth, 1930

Synonym *Azor* (Leach) T. Brown, 1844, non Sowerby, 1824.

Shell fairly small and thin, moderately long, anteriorly and posteriorly gaping; umbo situated somewhat anterior to the center; both ends rounded; surface with somewhat lamellose periostracum, with concentric growth lines; mantle sinus broad, rounded. Mantle margin anteriorly with tentacles, posteriorly closed, anterior to the siphons with a short common part with ridge on either side on the mantle, to which the gill bases adjoin.

Z. chamasolen (Da Costa) = *antiquata* (Donovan), in European seas.

911   *Solenocurtus* Blainville, 1825 (*Solecurtus*)

Synonyms *Psammosolen* Risso, 1826; *Macha* Oken, 1835; *Cyrtosolen* Herrmannsen, 1848; *Adasius* Leach, 1852.

Shell moderately long; umbo situated anterior to the center; both ends rounded and gaping; surface with oblique lines; hinge margin on either side with 2 teeth; mantle sinus large, extending beyond the center. Mantle anteriorly open, without tentacles, posterior half closed; anterior to the siphons with a large common portion; foot very large; labial palps narrow, triangular.

S. strigillatus (Linné). A few species, in various seas.

3. Family SEMELIDAE

Shell in most cases roundish or oval; ligament not on projecting ridges, with an interior, more or less strong cartilage situated posterior to the main teeth; hinge margin as a rule with 1 or 2 main teeth and lateral teeth; mantle sinus posteriorly narrowed. Animal with long, completely separated siphons; mantle widely open below; foot large, without byssus; labial palps large; outer gill lamina narrow, upwardly directed, without reflected lamella; in most cases the gill laminae are smooth.

Semele Schumacher, 1817

Synonym *Amphidesma* Lamarck, 1818.

Shell roundish or elliptical, anteriorly and posteriorly somewhat gaping, often strong; umbo situated sometimes somewhat anterior, sometimes posterior to the center, only slightly elevated; surface with more or less strong concentric and weaker radial sculpture; external ligament small; cartilage in an oblique pit which does not project inwardly; anterior to this on either side with 2 small main teeth, on the right with distinct, on the left with weaker anterior and posterior lateral

teeth; muscle scars large; mantle sinus elliptical, anteriorly ascending and completely separated from the mantle line. Gill laminae folded.

Several species, in warm seas.

Section *Semele* s. s. Shell with weak sculpture; umbo close to the center; hinge margin on either side with 2 main teeth; lateral teeth on the left weak. *S. (S.) proficua* (Pulteney) (Fig. 848).—Section *Élegantula* Gregorio, 1884. Shell with fairly broad concentric lamellae; umbo close to the anterior end. *S. (E.) striata* [(Rüppell Reeve].—Section *Semelina* Dall, 1900. Shell small, *Nucula*-like, with dense concentric sculpture; cartilage short; anterior left main tooth cleft, posterior one rudimentary; left lateral teeth indistinct. *S. (S.) nuculoides* Conrad.
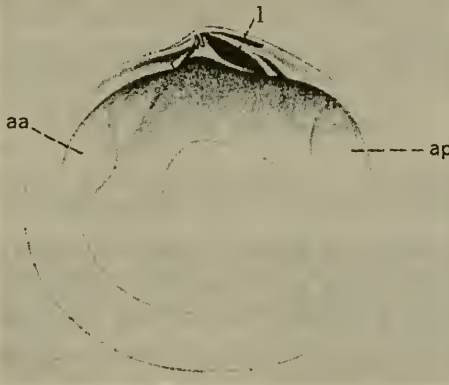
Fig. 848. Inner side of the right shell valve of *Semele flavescens* Gould. aa, ap, anterior and posterior adductor muscle; l, ligamental cartilage.

Punigapia Iredale, 1930

Shell small and thin, oval, white or purplish; umbo scarcely elevated, closer to the posterior end; ligamental cartilage weak, very oblique, not projecting inwardly; right valve with 2 main teeth and distinct lateral teeth; left valve with 2 dissimilar main teeth; mantle sinus not very deep, anteriorly flattened, free to about one-half.

P. subelliptica (Sowerby), near eastern Australia.

Semelangulus Iredale, 1924

Shell small, white or pink, anteriorly elongated and rounded, posteriorly obliquely truncated; surface concentrically striated; ligament weak; cartilage thin, interiorly not projecting, oblique; right valve with

912

2 main teeth and 2 fairly long lateral teeth; left valve with one main tooth; mantle sinus nearly reaching the anterior adductor muscle scar.

S. tenuiliratus (Sowerby), near eastern Australia and the Fiji Islands.

Cumingia Sowerby, 1833

Synonyms *Harpax* Gistel, 1848, non Parkinson, 1811; *Mikrola* O. Meyer, 1887.

Shell somewhat triangular, anteriorly rounded, posteriorly angulate; umbo only slightly projecting; ligamental cartilage large, somewhat posteriorly inclined and interiorly projecting, anterior to it on either side with a weak main tooth; lateral teeth of the right valve large, those of the left valve weak or absent; mantle sinus very deep and broad, joined with the mantle line.

C. mutica Sowerby. Few American species, living in holes of rocks.

Eumontrouziera Hedley, 1915

Synonym *Montrouzieria* Souverbie, 1863, non *Montrouziera* Bigot 1860.

Shell longish, posteriorly shorter, angulate, anteriorly bulging, straight below; surface with radial and concentric threads; cartilage narrow triangular, obliquely posteriorly directed and interiorly projecting; 2 main teeth anterior to it on the right, the anterior of which is thick and triangular; on the left a triangular tooth, on both sides one posterior lateral tooth; anterior muscle scar narrow; mantle sinus deep, joined with the mantle line.

E. clathrata (Souverbie), near New Caledonia.

Thyella H. Adams, 1865

Shell somewhat triangular, posteriorly somewhat shorter and flattened, with concentric threads or lamellae and fine radial lines; ligamental bands obliquely interiorially projecting; main teeth similar to those in *Eumontrouziera*; lateral teeth absent; mantle sinus broad, partly separated from the mantle line.

T. pulchra H. Adams. Few species, in the Indo-Australia region.

Theora H. & A. Adams, 1856

Shell thin and translucent, compressed, elongated oval, smooth and shiny, posteriorly or also anteriorly gaping; ligamental cartilage oblique,

interiorly projecting, on the left with one, on the right with 2 very small main teeth and thin lateral teeth of the right valve; mantle sinus deep. *T. lata* (Hinds). Few species, mainly near Japan to Australia.

Endopleura A. Adams, 1864 (*lubrica* Gould), interiorly has an oblique anteriorly-descending rib.

Souleyetia Recluz, 1869, seems to differ from *Theora* only by reduction of the hinge teeth. *S. moulinsi* Recluz, near Borneo.

913   *Abra* (Leach) Lamarck, 1818

Synonym *Syndosmya* Recluz, 1843 = *Syndesmia* L. Agassiz, 1846.

Shell thin, colorless, oval or somewhat triangular, often anteriorly somewhat longer than posteriorly; umbo only slightly projecting; external ligament weak; cartilage interiorly only slightly projecting, anterior to it on the left with 1, on the right 2 weak main teeth; in the right valve with an anterior and posterior thin lateral tooth; mantle sinus posteriorly greatly narrowed, joined with the mantle line.

A few species, in various seas.

Subgenus *Abra* s. s. (synonyms *Orixa* + ? *Dorvillea* Leach, 1852). Shell smooth or weakly concentrically sculptured, somewhat triangular or oval. *A. (A.) tenuis* (Montagu); Monterosato, 1884, proposed a group *Lutricularia* for the oval species (*ovata* Philippi), and Iredale, 1924, proposed a "genus" *Abranda* for the Australian *A. rex* Iredale = *elliptica* (Sowerby).

Subgenus *Iacra* H. & A. Adams, 1856 (synonym *Strigillina* Dunker, 1861). Shell with angle-shaped sculpture; hinge margin on either side with a small main tooth and with lateral teeth, which are stronger on the right. *A. (I.) seychellarum* (A. Adams).

Scrobicularia Schumacher, 1817

Synonyms *Arenaria* Megerle von Mühlfeld, 1811, non Brisson, 1760; *Listera* Turton, 1822.

Shell compressed, oval, posteriorly somewhat angulate; external ligament small; cartilage triangular, only slightly interiorly projecting; on the left with 1, on the right with 2 small main teeth, without lateral teeth; mantle sinus large, joined with the mantle line. Gill laminae smooth.

Subgenus *Leptomya* A. Adams, 1864. Shell somewhat bulging and posteriorly pointed. *S. (L.) cochlearis* (Hinds). Few species, in the Indo-Australian region and near New Zealand.

Subgenus *Scrobicularia* s. s. Shell flattened, oval. *S. (S.) plana* (Da Costa). 2 European species. *S. ceylonica* Edg. Smith does not seem to belong here.

4. Family TELLINIDAE

Shell in most cases oval, sometimes elongated and posteriorly rostrate, often somewhat asymmetrical, externally smooth or variably sculptured; ligament external, in the right valve in most cases with lateral teeth in addition to the main teeth; mantle sinus large, often more or less joined with the mantle line, occasionally differing on the two sides. Siphons separate; gill laminae smooth, the outer upwardly directed, sometimes very small; labial palps large; foot sometimes with a sole and a small byssal groove at the posterior end.

Arcopagia (Leach) T. Brown, 1827

Synonym *Cydippe* Leach, 1852, non Eschscholtz, 1829.
Shell oval, in most cases with concentric sculpture; umbo very slightly projecting; hinge margin with 2 main teeth on either side, one of which is furrowed, and with lateral teeth, of which the posterior one of the left side may be absent; mantle sinus freely ascending or partly joined with the mantle line.
A few species, in warm seas.

914 Subgenus *Arcopagia* s. s. Shell moderately bulging, roundly oval, concentrically sculptured; mantle sinus free. Section *Arcopella* Monterosato, in sched. Shell fairly small and weak; anterior end only slightly longer than the posterior; lateral teeth fairly long, weak in the left valve. *A. (A.) balaustina* (Linné).—Section *Arcopagia* s. s. Shell fairly large and strong, anteriorly distinctly longer than posteriorly; left posterior lateral tooth rudimentary. *A. (A.) crassa* (Pennant).

Subgenus *Elliptotellina* Cossmann, 1886. Shell small, bulging, longish oval, anteriorly and posteriorly rounded; the concentric sculpture at the ends often crossed by radial lines; left lateral teeth absent; mantle sinus free, obliquely ascending. *A. (E.) tellinella* (Lamarck) †; Dall described a couple of living species from American coasts. *Maoritellina* Finlay, 1927, may be a related group, whose typical New Zealand species *charlottae* (Edg. Smith), according to Finlay, has a short, free, steeply ascending mantle sinus.

Subgenus *Pinguitellina* Iredale, 1927. Shell small, strongly bulging, short triangular, with concentric threads; left lateral teeth present;

mantle sinus partly continuous with the mantle line. *A. (P.) robusta* (Hanley).

Subgenus *Arcopaginula* Jousseaume, 1918. Shell medium-sized, colorless, posteriorly with a flattening delimited by an edge, asymmetrical; left valve more strongly bulging; anterior lateral teeth fairly short, posterior ones long, those of the left valve weak; mantle sinus partly joined with the mantle line. *A. (A.) inflata* (Chemnitz).

Strigilla Turton, 1822

Shell roundish, bulging; umbo angular, scarcely elevated, situated somewhat anterior to the center, with oblique sculpture on a part or the entire surface; lunule narrow, asymmetrical; ligament small and weak; hinge margin on the right with 2 main teeth and 2 moderately long lateral teeth, on the left with one main tooth and 2 weak lateral teeth; mantle sinus not separated from the mantle line.

A few species, in warm seas.

Section *Rombergia* Dall, 1900. The entire surface with oblique lines, which form angles anteriorly and posteriorly; mantle sinus equal on both sides, not reaching the anterior adductor muscle scar. *S. (R.) rombergi* Mörch.—Section *Strigilla* s. s. Surface sculptured as in *Rombergia*; mantle sinus not completely symmetrical. *S. (S.) carnaria* (Linné). Both sections near America.—Section *Aeretica* Dall, 1900. Surface with more or less strong concentric sculpture and on the larger posterior half with oblique lines; mantle sinus greatly differing on the two sides, on the left almost or fully reaching the anterior adductor muscle scar, considerably shorter on the right. *S. (A.) senegalensis* (Hanley). Few species, near the Philippines, Java, Sandwich Islands, and Senegambia.

Pseudarcopagia Bertin, 1878

Shell roundish oval, medium-sized, moderately bulging, posteriorly somewhat asymmetrical, with concentric and weaker radial sculpture; ligament fairly long; anterior lateral teeth shorter than the posterior ones, weaker on the left than on the right; mantle sinus largely joined with the mantle line.

Section *Pseudarcopagia* s. s. Surface distinctly latticed. *P. (P.) decussato* (Lamarck) = *victoriae* (Gatliff & Gabriel). A couple of Australian species.—Section *Zearcopagia* Finlay, 1927. Shell smaller and more finely sculptured. *P. (Z.) disculus* (Deshayes), near New Zealand.

Cyclotellina Cossmann, 1886

Shell large and strong, roundish, inequivalve; ligament large; left valve without distinct lateral teeth; mantle sinus partly joined with the mantle line, anteriorly angulate and joined with the anterior muscle scar by an impressed line.

Subgenus *Cyclotellina* s. s. Shell with distinct concentric and weak radial sculpture; right anterior lateral tooth short. *C. (C.) lunulata* (Deshayes) †. Dall included here the Recent species *fausta* (Pultney) from the West Indies and *remies* (Linné) and *discus* (Hanley) from the Indo-Australian region.

Subgenus *Scutarcopagia* Pilsbry, 1918. Shell nearly circular, with small warts which are joined with one another more or less net-shaped; right anterior lateral tooth fairly long. *C. (S.) scobinata* (Linné), in the Pacific Ocean.

Apolymetis Salisbury, 1929

Synonyms ? *Capsa* Bruguière, 1797; *Metis* H. & A. Adams, 1856, non Philippi, 1843, nec Gistel, 1848; *Polymetis* Salisbury, 1929, non Walsingham, 1903.

Shell thin, colorless, oval, with a narrow depressed lunule, in the posterior part asymmetrical and folded; surface with concentric threads; ligament strong; hinge margin on either side with 2 unequal main teeth, the larger of which is cleft; mantle sinus more or less steeply ascending, completely or largely free.

Few species, in warm seas.

Subgenus *Hemimetis* n. Right valve with a thin lateral tooth posterior to the ligament and a weak one below the anterior part of the lunule; mantle sinus largely free, obliquely ascending. *A. (H.) plicata* (Valenciennes).

Subgenus *Apolymetis* s. s. Right valve without lateral teeth; mantle sinus free, more or less steeply ascending. *A. (A.) meyeri* (Dunker).

Iredale, 1930, proposed a genus *Leporimetis* for the posteriorly steeply descending *Tellina spectabilis* Hanley, the mantle sinus of which is largely joined with the mantle line; it appears to be intermediate between *Apolymetis* and *Macoma*, but closer to the latter.

Gastrana Schumacher, 1817

Synonyms *Diodonta* Deshayes, 1846; *Fragilia* Deshayes, 1848.
Shell bulging, fairly thin, oval, posteriorly elongated, with concentric

threads and weak radial lines; ligament weak; hinge margin on the right with 2 greatly diverging main teeth, on the left with 2 dissimilar main teeth; without lateral teeth; mantle sinus moderately deep, rounded, scarcely ascending, free.

G. *fragilis* (Linné). Few species, in various seas.

Macoma Leach, 1819

Synonym *Limicola* Leach, 1852, non Koch, 1816.

Shell in most cases fairly thin, somewhat triangular, posteriorly shorter, flattened and folded; surface with growth lines; hinge margin without lateral teeth; mantle sinus partly free.

916   Numerous species, in various seas.

Subgenus *Macoma* s. s. Shell anteriorly moderately elongated, with distinct periostracum; mantle sinus often differing in the two valves. M. (M.) *tenera* Leach = *calcarea* (Gmelin). Mainly in the colder northern seas.

Subgenus *Salmacoma* Iredale, 1929. Shell inequivalve, anteriorly only slightly elongated, thin; hinge teeth small, on the right with only one; mantle sinus differing on the two sides. M. (S.) *vappa* (Iredale), near eastern Australia.

Subgenus *Macalia* H. Adams, 1860 (synonym *Tellinungula* E. Römer, 1872). Shell anteriorly only slightly longer; hinge margin with strikingly large teeth. M. (M.) *bruguieri* (Hanley). In warm seas.

Subgenus *Rexithaerus* Conrad, 1869. Shell large, inequivalve, smooth; margin distinctly elevated and gaping posterior to the strong, somewhat sunken ligament.

Subgenus *Psammacoma* Dall, 1900. Shell anteriorly longer and rounded, posteriorly truncated, smooth; the two valves only slightly different. Section *Psammacoma* s. s. Shell anteriorly significantly elongated, thin; ligament completely external; mantle sinus moderately deep. M. (P.) *candida* (Lamarck).—Section *Pseudometis* Jousseaume, 1918. Shell fairly strong, more triangular; ligament somewhat sunken; pallial sinus moderately deep. M. (P.) *truncata* (Jonas).—Section *Temnoconcha* Dall, 1921. Shell thin, anteriorly and posteriorly only slightly different; in the anterior part with oblique impressed lines; ligament short; mantle sinus largely free, reaching almost to the anterior adductor muscle scar. M. (T.) *brasiliana* Dall. Dall, 1900, proposed a section *Cydippina* for M. *brevifrons* Say, but later seems to have discarded it.—Section *Psammotreta* Dall, 1900. Shell moderately long, with an internal cartilage, partly separated from the ligament. M. (P.) *aurora* (Hanley).

Subgenus *Tellinimactra* Jousseaume, 1918. Shell thin, bulging, smooth anteriorly not greatly elongated; hinge teeth weak; ligament short, sunken; mantle sinus deep, largely joined with the mantle line, anteriorly almost reaching the narrow anterior adductor muscle scar. *M.* (*T.*) *edentula* (Spengler).

Subgenus *Cymatoica* Dall, 1889. Shell small and very thin, with concentric wrinkled folds; posterior end oblique. *M.* (*C.*) *undulata* (Hanley).

Tellidora (Mörch) H. & A. Adams, 1856

Shell colorless, thin, compressed, inequivalve, triangular, concentrically sculptured; lunule and ligamental surface narrow, with elevated, denticulate margins; ligament short; right valve with 2 main teeth and 2 long lateral teeth; left valve with one main tooth; lateral teeth not separated from the margin; mantle sinus free.

T. burneti (Broderip & Sowerby). Few species, in warm seas.

Merisca Dall, 1900

Shell colorless, fairly small, more or less triangular, in most cases distinctly inequivalve, posteriorly truncated or with short beak, with concentric lamellae and often fine radial lines; umbo close to the center, not projecting; right valve with distinct elongated lateral teeth; mantle sinus large, completely joined with the mantle line.

Subgenus *Merisca* s. s. Shell more or less distinctly beaked, with weak radial sculpture. *M.* (*M.*) *crystallina* (Wood). A few American species and one from Singapore.

917   Subgenus *Clathrotellina* n. Shell nearly equivalve, posteriorly somewhat pointed, with numerous fine radial threads, whose point of intersection with the concentric threads bear small elevated scales. *M.* (*C.*) *pretiosa* (Deshayes), near the Philippines. The Californian *M. reclusa* (Dall) seems to be intermediate between the two subgenera.

Quadrans (Klein) Bertin, 1878

Shell medium-sized, fairly strong, rounded triangular, anteriorly rounded; umbo in most cases close to the center, scarcely elevated, a narrow depressed lunule anterior to it; surface with concentric and in most cases weak radial sculpture; ligament external, fairly long; hinge margin on either side with 2 main teeth, the stronger of which is furrowed, and an anterior and posterior lateral tooth, which in the left

valve are not separated from the margin; mantle sinus large, nearly reaching the narrow anterior adductor muscle scar.

Few species, mainly in the Indo-Pacific region.

Section *Striotellina* n. Shell longish triangular, with dense concentric threads, which posteriorly become coarser and more irregular and at the edges of the depressed ligamental surface form irregular cusps; radial sculpture scarcely indicated; mantle sinus nearly reaching the anterior adductor muscle scar, in its posterior half separated from the mantle line by a very narrow interval. *Q. (S.) serratus* (Renieri), in the Mediterranean Sea and the neighboring Atlantic Ocean.—Section *Obtellina* Iredale, 1929. Umbo closer to the posterior end; surface with fine, oblique, anteriorly ascending lines, in the posterior part with irregular wrinkles, which form cusps at the margin; mantle sinus largely joined with the mantle line. *Q. (O.) bourgei* (Sowerby), near New Caledonia. *Tellina obtusalis* Deshayes, also placed by Iredale in *Obtellina*, is very different. —Section *Quadrans* s. s. Ligamental surface depressed, with cuspidate margins; surface with somewhat oblique threads which are in most cases wrinkled in the posterior part; radial lines indistinct; mantle sinus almost completely joined with the mantle line. *Q. (Q.) gargadia* (Linné). —Section *Pistris* n. nom. (synonyms *Pristis* (Jousseaume, Lamy, 1918, non Latham, 1794, nec Müller & Henle, 1837)). Shell relatively high; ligamental surface depressed, with cuspidate margins; surface with concentric, somewhat wavy threads and fine radial impressed lines; mantle sinus partly free. *Q. (P.) pristis* (Lamarck).—Section *Quidnipagus* Iredale, 1929. Shell posteriorly somewhat beaked; lunule and area very narrow, somewhat asymmetrical; surface with wavy or cuspidate discontinuous wrinkles and fine radial furrows; mantle sinus free in about one-half. *Q. (Q.) palatum* (Martyn) = *rugosus* (Born).

Homalina Stoliczka, 1871

Shell compressed, triangular, anteriorly rounded, posteriorly pointed and somewhat asymmetrical, externally smooth and colorless; umbo not elevated, closer to the anterior end; hinge margin on either side with 2 main teeth and on the right with a short anterior and a weak posterior lateral tooth at the end of the ligament; mantle sinus deep, completely joined with the mantle line, almost or fully reaching the narrow anterior adductor muscle scar.

Subgenus *Homalina* s. s. Shell thin, shiny; hinge line weak; anterior lateral tooth very short, occasionally joined with the anterior main tooth; posterior lateral tooth posterior to the end of the ligament; mantle sinus

918   asymmetrical, on the right reaching the anterior adductor muscle scar, *H. (H.) triangularis* (Chemnitz), in the Indian Ocean.

Subgenus *Macomona* Finlay, 1927. Shell fairly strong; anterior lateral tooth distinctly separated from the main teeth; mantle sinus on both sides reaching the ventral end of anterior adductor muscle scar. *H. (M.) liliana* (Iredale), near New Zealand.

Phylloda Schumacher, 1817

Shell thin, greatly compressed, longish, anteriorly rounded, posteriorly obliquely truncate and somewhat asymmetrical; umbo not projecting, close to the center; surface finely concentrically sculptured; ligament long and thin; mantle sinus short, ascending, largely free.

Subgenus *Phyllodina* Dall, 1900. Shell small; surface with concentric threads, the ends of which form tooth-shaped lamellae on the sides of the very narrow lunule and ligamental surface; lateral teeth of the right valve distinctly developed, fairly long. *P. (P.) squamifera* (Deshayes), near America.

Subgenus *Phylloda* s. s. Shell fairly large, with fine and dense sculpture, the posterior part, which is delimited by an edge, with small tubercles and denticulate on the dorsal margin; lunule and ligamental surface extremely narrow; lateral teeth indistinct; a short anterior one of the right valve joined with the anterior main tooth; anterior corner of the mantle sinus joined with the anterior adductor muscle scar through a weak depression. *P. (P.) foliacea* (Linné), in the Indo-Pacific region.

Eurytellina P. Fischer, 1887

Shell compressed, fairly long, posteriorly somewhat pointed and only slightly asymmetrical, weakly concentrically sculptured; umbo not projecting, close to the center; ligament fairly long and thin, not sunken; anterior lateral tooth of the right valve very short and close to the anterior main tooth, the posterior one below the end of the ligament; mantle sinus joined with the mantle line, almost reaching the anterior adductor muscle scar, posterior to which runs a radial thickening.

E. punicea (Born), in warm seas.

Scrobiculina Dall, 1900, may be a subgenus of *Eurytellina*; the thin shell is weakly sculptured; ligament with short, internal cartilage; right anterior lateral tooth short, the posterior one weak; mantle sinus moderately deep, joined with the mantle line.

S. viridotincta (Carpenter). A couple of Californian species.

Angulus Megerle von Mühlfeld, 1811

Shell more or less elongated, compressed, in most cases fairly small, posteriorly angulate and only slightly asymmetrical; ligament short; hinge margin in most cases on the right with a short anterior lateral tooth; mantle sinus not separated from the mantle line.

Several species, in warmer seas.

Subgenus *Moerella* P. Fischer, 1887 (synonyms *Moera* H. & A. Adams, 1856, non Hübner, 1816; *Donacilla* Gray, 1851, non Lamarck, 1812). Shell anteriorly elongated and rounded, posteriorly obliquely truncated; surface finely concentrically striated; right valve with a short anterior lateral tooth and a posterior one below the end of ligament. *A. (M.) donacinus* (Linné).

919 Subgenus *Fabulina* Gray, 1851. Shell small and moderately elongated, in most cases thin and transparent; a right posterior lateral tooth absent. Section *Scissula* Dall, 1900. Shell similar to *Moerella*, but with fine oblique striae on the surface and without posterior lateral tooth. *A. (S.) decorus* (Say).—Section *Fabulina* s. s. Shell thin; umbo close to the center; posterior end pointed; only the right valve sculptured with fine oblique lines; anterior lateral tooth short. *A. (F.) fabula* (Gronovius), in the Mediterranean Sea and eastern Atlantic Ocean.—Section *Oudardia* Monterosato, 1884. Shell thin, greatly compressed; umbo closer to the posterior end; surface with gradually ascending oblique lines, which leave the posterior part free, in the interior with a radial thickening posterior to the anterior adductor muscle scar; anterior lateral tooth somewhat away from the main teeth. *A. (O.) compressus* (Brocchi), in the Mediterranean Sea, and one species (*buttoni* Dall) from California. —Section *Exotica* Jousseaume, 1918. Shell very similarly formed and sculptured to that in *Oudardia*, but without anterior lateral tooth and without internal ridge-shaped thickening. *A. (E.) rhomboides* (Quoy & Gaimard), in the Indo-Pacific region.—Section *Jactellina* Iredale, 1929. Shell fairly short oval, posteriorly somewhat flattened; surface with fine oblique lines, which leave only the posterior part free; the posterior of the 2 main teeth of the right valve is sometimes rudimentary, also on the left in most cases only one well developed tooth; lateral teeth absent. *A. (J.) obliquarius* (Deshayes), from Polynesia.

Subgenus *Tellinangulus* n. Shell small, anteriorly rounded, posteriorly with short beak and distinctly asymmetrical, with concentric, not very densely placed threads, the intervening spaces of which are finely radially striated; left anterior and right posterior main tooth cleft; right

anterior main tooth very short, joined with the anterior main tooth. *A.* (*T.*) *aethiopicus* (Jäckel & Thiele), near East Africa.

Subgenus *Angulus* s. s. Shell medium-sized, longish, greatly compressed, concentrically striated; right anterior lateral tooth short or absent. Section *Angulus* s. s. Shell long and fairly low; umbo close to the center; anterior lateral tooth distinctly separated from the main teeth. *A.* (*A.*) *lanceolatus* (Linné).—Section *Tellinides* Lamarck, 1818. Shell elongated oval; umbo only slightly anterior to the center; anterior lateral tooth close to the anterior main tooth. *A.* (*T.*) *timorensis* (Lamarck). —Section *Homala* Schumacher, 1817 (*Omala*). Shell anteriorly short and posteriorly greatly elongated; right anterior lateral tooth very short and close to the anterior main tooth; anterior to it in the left valve a bulge-shaped thickening is present. *A.* (*H.*) *hyalinus* (Gmelin).—Section *Peronidia* Dall, 1900 (synonym *Peronea* (Poli) Mörch, 1853, non *Peronea* Curtis, 1824, nec *Peronia* Blainville, 1824). Shell longish, posteriorly pointed to blunt; umbo situated in the center; hinge margin without lateral teeth. *A.* (*P.*) *albicans* (Gmelin) = *nitidus* (Poli).

Tellina Linné, 1758

Synonyms *Tellinella* Mörch, 1853; *Eutellina* (part.) P. Fischer, 1887.
Shell fairly large, compressed, elongated, posteriorly beaked and asymmetrical, anteriorly rounded; as a rule on the left with one, on the right with 2 main teeth; right valve with long lateral teeth away from the main teeth; mantle sinus deep, more or less joined with the mantle line.
Several species, in warm seas.

920   Section *Tellina* s. s. Shell fairly strong; surface with distinct, mainly concentric sculpture. *T.* (*T.*) *virgata* Linné (Fig. 849).—Section *Liotellina* P. Fischer, 1887. Surface smooth and shiny. *T.* (*L.*) *radiata* Linné. —Section *Pharaonella* (Jousseaume) Lamy, 1918. Shell thin, long and fairly low, distinctly beaked, with fine concentric sculpture. *T.* (*P.*) *pharaonis* Hanley.
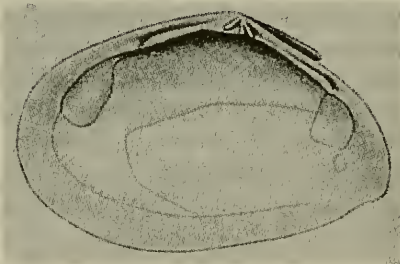
Fig. 849. Inner side of the right shell valve of *Tellina staurella* Lamarck.

Subgenus *Scissulina* Dall, 1924. Oblique sculpture only on one valve; hinge as in *Macoma*. *T. (S.) dispar* Conrad, near the Hawaiian Islands.

Suborder ADAPEDONTA

Shell without distinct hinge plate, with or without main teeth, always without lateral teeth; ligament variable.

1. STIRPS SOLENACEA

Shell in most cases laterally compressed and more or less considerably elongated, gaping at the ends; ligament external, attached on a ridge; hinge margin variable, without lateral teeth; mantle sinus in most cases only not very deep. Mantle closed below, sometimes with a small opening, anteriorly open, posteriorly with 2 short, separate or united siphons; gill laminae smooth or folded; foot strong, more or less long, swollen at the end.

1. Family GLAUCOMYIDAE

Shell elongated oval, gaping at the ends, with distinct periostracum; umbo situated anterior to the center, only slightly projecting; ligament short, external or somewhat sunken; hinge margin without lateral teeth; mantle sinus deep. Siphons long, retractile, almost completely united, covered by a membrane; mantle closed below, anteriorly open; foot anteriorly directed; labial palps broad.

The animals live in fresh or brackish water.

Glaucomya Bronn, 1838

Synonym *Glauconome* Gray, 1828, non Goldfuss, 1826.

Shell more or less elongated, bulging, with strong, in most cases olive-green periostracum; umbo closer to the anterior end; ligament external, projecting, moderately long, attached on one side; hinge margin fairly narrow, on either side with 3 main teeth, one of which is furrowed and the posteriormost is obliquely directed; mantle sinus narrow and deep. Siphons very long, almost completely united, fringed at the end; gill laminae folded; foot fairly thick, tongue-shaped.

G. chinensis (Gray). A few species, in east and south Asian rivers.

Tanysiphon Benson, 1855

Shell small and thin, elongated oval, with a brownish periostracum; umbo situated anterior to the center; ligament very short, with an internal cartilage borne on very short ridges; hinge margin on the right with 2, on the left with one tooth; mantle sinus large, rounded. At the end of the siphonal envelope is a series of tentacles and a series of shorter threads at the end of the lower siphon.

921

T. rivalis Benson, in India.

The systematic position of these broad[1] genera is uncertain; they are sometimes considered close to the venerids, sometimes close to the solenids.

2. Family SOLENIDAE

Shell in most cases elongated; foot large and strong, without byssus; siphons in most cases short; living almost only in the sea.

A. Subfamily Novaculininae

Shell with strong periostracum, fairly bulging; umbo away from the anterior end, but situated anterior to the center; ligament short; hinge margin on the right with 2, on the left with 3 sometimes rudimentary teeth; posterior adductor muscle scar roundish. The fused ventral surface of the mantle more or less broad, with numerous muscle bands; siphons completely separate; foot short, with disk-shaped end; gill laminae smooth; labial palps broad; intestine with a few long limbs.

Novaculina Benson, 1830

Synonym ? *Loncosilla* Rafinesque, 1820.

Shell fairly small and thin, moderately long; umbo somewhat projecting; hinge teeth weak; mantle sinus without connection with the mantle line, anteriorly angulate. Siphons without tentacles; anterior mantle opening smooth; ventral mantle surface very broad.

N. gangetica Benson, in the Ganges.

[1] Correction from Part 4, 1935: 1154.
The original German "breiten" was corrected to "beiden," meaning "both."

Sinonovacula Prashad, 1924

Shell larger and stronger, more elongated; umbo scarcely projecting; an impression extending obliquely from it toward the posterior to the ventral margin; mantle sinus short and rounded, joined below with the mantle line. Siphons with small tentacles; anterior mantle opening with 2–3 rows of short tentacles; ventral mantle surface narrow.

S. *constricta* (Lamarck), in the sea near China and Japan.

B. Subfamily Soleninae

Shell in most cases very long and laterally compressed; umbo more or less close to the anterior end; hinge margin variable; mantle sinus flat. Ventral mantle surface very narrow; foot long and narrow; gill laminae occasionally smooth, more often folded; intestine with 2 limbs.

Siliqua Megerle von Mühlfeld, 1811

Synonyms *Leguminaria* Schumacher, 1817; *Solecurtoides* Desmoulins, 1832; *Machaera* Gould, 1841, non Cuvier, 1832.
Shell compressed, moderately long, thin, anteriorly and posteriorly rounded and gaping; umbo not elevated, situated anterior to the center; hinge margin on the right with 2, on the left with 3 main teeth, from which an accessory ridge extends to the ventral margin; mantle sinus joined with the mantle line. Siphons united, with tentacles at the end; mantle margin with leafy fringes; foot obliquely truncated at the end; gill laminae smooth; labial palps long and pointed.

S. *radiata* (Linné). A few species, in various seas.

Pharus (Leach) T. Brown, 1844

Synonyms *Polia* Orbigny, 1843, non Ochsenhausen, 1816; *Ceratisolen* Forbes & Hanley, 1848; *Artusius* Leach, 1852.
Shell long, anteriorly rounded, posteriorly somewhat truncated; umbo not projecting, fairly close to the center; hinge margin on the right with 2, on the right with 3 teeth[1], the posterior of which are very oblique, from which an accessory ridge extends anteriorly and a short one

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[1] Apparently an error in the original text, indicating 2 teeth *on the right* and also 3 teeth *on the right.*—Editors.

ventrally; between them lies the elongated scar of the anterior adductor muscle; the posterior scar is triangular, close to the posterior end of the shell; mantle sinus shallow, joined with the lower mantle line. Anterior mantle opening with tentacles only dorsally and ventrally; siphons separated from one another, long and thin; gill laminae smooth; foot long; oral lobes broad.

P. legumen (Linné), near Europe and West Africa.

Phaxas Leach, 1852

Synonym *Subcultellus* Ghosh, 1920.

Shell similarly formed to that in *Pharus*, but shorter; umbo and hinge teeth close to the anterior end, in the interior a short anterior accessory ridge anterior to the long scar of the anterior adductor muscle; posterior scar very small. Posterior part of the mantle opening with tentacles; siphons short, separated from one another; gill laminae folded; foot anteriorly thickened.

P. pellucidus (Pennant), near Europe.

The group of "*Solen*" *cultellus* Linné is to be considered as the subgenus *Ensiculus* H. Adams, 1860, with similar muscle scars; the shell is often speckled, and is somewhat concave posterior to the umbones. The siphons are very short and largely united, with tentacles at the margin. Few species, mainly near the Philippines.

Cultellus Schumacher, 1817

Shell not greatly elongated, anteriorly and posteriorly rounded, sometimes large and strong; umbo closer to the anterior end, somewhat posterior to the anteriormost quarter; ligament more or less long; upper margin of the roundish anterior adductor muscle scar thickened; posterior scar pear-shaped; the anterior border of the mantle sinus extends from the center of this muscle scar almost in a straight line downward to the mantle line, with which the sinus joins. Siphons short and separate, with tentacles; gill laminae folded; labial palps short and broad; foot strong.

C. lacteus (Spengler). A few species, in the Indo-Pacific region.

Coen, 1933, erected a subgenus *Cultrensis* for *C. adriaticus* Coen, with straight dorsal margin, small and very thin, on either side with 2 lines from the umbo to the posterior corners.

Pharella Gray, 1854

Shell elongated, not greatly compressed, thin, anteriorly and posteriorly rounded and gaping, with strong, somewhat folded

periostracum; umbo situated somewhat posterior to the anterior third; hinge margin on the right with 2, on the left with 3 thin and sometimes strikingly high teeth; adductor muscle scars long and narrow; from the center of the posterior one the boundary of the mantle sinus extends obliquely downward to the posterior end of the mantle line. Siphons short, with free ends which bear tentacles; gill laminae narrow, somewhat folded; labial palps broad; foot long.

P. javanica (Lamarck). Few species, on the coasts of the Indo-Pacific regions.

923

Neosolen Ghosh, 1929

Shell small, thin and transparent, about 3½ times longer than high, anteriorly truncated, posteriorly somewhat rounded, on the right with a long and narrow tooth; anterior muscle scar elongated triangular; posterior one small, roundish. Siphons long, with several rows of tentacles, completely united with one another; gill laminae folded; labial palps short and broad; foot weakly compressed, with a ring-shaped thickening.

N. aquaedulcioris Ghosh, in Chilka Lake.

Solen Linné, 1758

Synonyms *Hypogaea* + *Hypogaeoderma* Poli, 1791, and 1795; *Solenarius* Dumeril, 1811; *Vagina* Megerle von Mühlfeld, 1811, *Listera* Leach, 1852; *Fistula* (Martini) Mörch, 1853.

Shell very long, nearly cylindrical, anteriorly truncated, open at both ends; umbo very close to the anterior margin; hinge margin on either side with one tooth; posterior adductor muscle scar and boundary of the mantle sinus far from the posterior margin. Siphons short, completely united with one another, with tentacles on the ends, without ventral mantle opening; gill laminae folded; labial palps long and narrow; foot cylindrical, swollen at the end.

A few species, in various seas.

Subgenus *Solena* (Browne) Mörch, 1853 (synonym *Hypogella* Gray, 1854). Shell with strong, folded periostracum, without anterior furrow; umbo and hinge teeth somewhat away from the anterior margin; anterior muscle scar oval. *S. (S.) obliquus* Spengler.

Fig. 850. Shell of *Solen siliqua* (Linné).

Subgenus *Solen* s. s. Surface smooth, often with an anterior furrow; umbo and hinge teeth nearly terminal; ligament long. *S. (S.) marginatus* Pulteney (Fig. 850).

Ensis Schumacher, 1817

Synonym *Ensatella* Swainson, 1840.

Shell greatly elongated, weak, curved; umbo nearly terminal; ligament long; hinge margin on the right with one erect and one posterior appressed tooth, on the left with 2 erect and one posterior ridge-shaped tooth; adductor muscle scars greatly elongated; boundary of the mantle sinus not very far from the posterior margin. Siphons short, with tentacles at the margin; mantle with a small ventral opening, which is separated from the anterior one; gill laminae folded; foot long and narrow.

E. magnus Schumacher. Few species, in the Atlantic and Pacific Oceans.

II. STIRPS SAXICAVACEA

Shell more or less longish, in most cases gaping at the ends, often irregular, with concentric striae and a periostracum; ligament external, attached on ridges; main tooth in most cases weak or reduced; lateral teeth absent; mantle line sometimes not continuous; sinus variable. Mantle with small opening for the foot and with large, completely or largely united siphons which in most cases are covered by a membrane; gill laminae smooth or folded, unequally broad, posteriorly fused; foot small.

924

1. Family SAXICAVIDAE

Characters of the stirps.

Saxicava Fleuriau de Bellevue, 1802

Synonyms *Hiatella* (Daudin) Bosc, 1802; *Clotho* Faujas S. Fond, 1808; *Didonta* + *Glycimeris* Schumacher, 1817, non Da Costa, 1778, nec Lamarck, 1799; *Byssomya* Cuvier, 1817; *Rhombus* Blainville, 1818; *Pholeobia* Leach, 1819; *Agina* Turton, 1822; *Rhomboides* Blainville, 1825; *Biapholius* (Leach) Blainville, 1825.

Shell fairly small, longish, often irregularly formed and striated; in the young state with 2 posterior scale-bearing edges; umbo situated

anterior to the center; ligament attached on strong ridges; hinge margin with 1 or 2 weak main teeth which disappear with age; mantle line interrupted, with more or less deep sinus. Siphons largely united, the lower one longer; gill laminae smooth; foot in the young state with byssus. The animals live sometimes on the surface of the substratum, sometimes in preformed caverns of stones; sometimes they bore more or less deep into limestone by an acid secreted from glands in the mantle.

Few species, in all seas.

Subgenus *Saxicava* s. s. Shell fairly thick, more or less irregular, longish, often gaping; mantle sinus deep. *S. (S.) arctica* (Linné).

Subgenus *Saxicavella* P. Fischer, 1887 (synonym *Arcinella* Philippi, 1844, non Oken, 1815, nec Schumacher, 1817). Shell small and thin, gaping, oval, posteriorly somewhat angulate; umbo only slightly elevated; ligament short; mantle sinus broad, not deep. *S. (S.) plicata* (Montagu).

Panomya Gray, 1853

Synonym *Chaenopaea* C. Mayer, 1885.

Shell fairly large and strong, irregular, gaping at both ends, posteriorly truncated, irregularly concentrically striated, with yellowish periostracum; ligament short; hinge margin on either side with one tooth; mantle line fairly far from the margin, not continuous. Living in sand or mud.

P. spengleri (Valenciennes). Few species, in the Arctic Ocean.

Panopea Ménard de la Groye, 1807

Synonym *Glycimeris* Lamarck, 1799, non da Costa, 1778.

Shell sometimes very large and thick, longish, in most cases posteriorly truncated, greatly bulging, gaping mainly posteriorly, irregularly striated; umbo depressed; ligament on very strong ridges; hinge margin on either side with a high, cone-shaped tooth; mantle line not interrupted, with more or less deep sinus. Mantle closed except for a small aperture for the foot; siphons very long, completely united and covered by a strong membrane; gill laminae folded.

P. glycymeris (Born). Few species, in various seas, living at considerable depth in sand or mud.

Cyrtodaria Daudin, 1799

Shell elongated oval, thick, widely gaping, with strong, dark periostracum projecting at the margin; umbo scarcely projecting, situated posterior to the center; ligament on very thick ridges; hinge margin

toothless; posterior adductor muscle scar close to the posterior margin, below which the mantle line is broadened, but scarcely indented. Mantle closed, leaving a small opening at the anterior end; siphons large, not retractile, with a thick membrane; gill laminae folded; labial palps large, triangular; foot weak.

C. siliqua (Spengler), in the Arctic Ocean.

III. STIRPS MYACEA

Shell in most cases fairly small, not nacreous; ligament with internal cartilage borne asymmetrically on a process of one valve, which extends below the dorsal margin of the other valve; hinge teeth variable; mantle sinus sometimes small or absent, sometimes large. Siphons largely united; mantle closed below, anteriorly with small opening.

1. Family ALOIDIDAE

Shell fairly small, more or less asymmetrical, closed in most cases posteriorly angulate or rostrate, often with distinct concentric sculpture; the cartilage bearer of one valve is more or less projecting; the right valve anterior to the cartilage has in most cases a strong tooth, corresponding to which is a pit in the left valve, which posterior to the cartilage bearer has a more or less distinct tooth; mantle line posteriorly as a rule not or weakly indented. Siphons short, surrounded at the base by a common sheath, which in most cases bears tentacles at the margin, as also does the incurrent siphon; mantle margin with papillae; gill laminae smooth; foot with byssus.

Aloidis Megerle von Mühlfeld, 1811

Synonyms *Corbula* (Bruguière) Lamarck, 1799, non Röding, 1798; ? *Harlea* + *Raleta* + *Tomala* Gray, 1844 (nom. nuda).

Shell asymmetrical; left valve with projecting cartilage bearer; mantle sinus absent or weak.

Several species, mainly in warmer seas, a few in fresh water.

Subgenus *Lentidium* Cristofori & Jan, 1832 (synonym *Corbulomya* Nyst, 1846). Shell small and thin, longish, flatly bulging, smooth; right valve only slightly larger than the left; umbo close to the center, only slightly elevated; posterior margin somewhat obliquely truncated; the cartilage of the right valve is visible near the umbo through an internal cleft; the posterior margin of the left cartilage bearer forms a somewhat

convex triangular plate and the anterior margin of the tooth pit forms a triangular tooth; the mantle line extends obliquely backward, without distinct indentation. Siphons without ring of tentacles. *A. (L.) mediterranea* (Costa), in the Mediterranean Sea.

Subgenus *Anticorbula* Dall, 1898 (synonym *Himella* H. Adams, 1860, non Dallas, 1854). Shell thin; left valve larger than the right; right main tooth rudimentary; external ligament present; cartilage on either side affixed on a nearly horizontal process; mantle sinus weak. *A. (A.) fluviatilis* (H. Adams), in the Amazon River.

926   Subgenus *Aloidis* s. s. Shell inequivalve; right valve larger than the left, with distinct concentric sculpture. Section *Anisocorbula* Iredale, 1930. Shell compressed, longish, posteriorly with 2 corners; umbo only slightly elevated, situated somewhat anterior to the center; right valve only slightly larger than the left, both with concentric rings and a posterior edge; left valve without distinct anterior tooth. *A. (A.) macgillivrayi* (Edg. Smith), in the Indo-Australian region. —Section *Cuneocorbula* Cossmann, 1886. Shell elongated oval; the two valves only slightly different, bulging, with an edge to the posterior corner. *A. (C.) biangulata* (Deshayes) †, the living *A. contracta* (Say) on the North American east coast.—Section *Bothrocorbula* Gabb, 1872. Shell oval, strong, posteriorly pointed; both valves with strong concentric rings; lunular area more or less depressed. *A. (B.) viminea* (Guppy) †, also species living in the West Indies.—Section *Aloidis* s. s. Shell distinctly inequivalve; right valve larger and more strongly sculptured, fairly short, with more or less distinct posterior beak and an edge, often very thick, with strong, triangular hinge tooth; in the left valve the posterior margin of the cartilage bearer is elevated hump-like and is sometimes produced tooth-shaped. *A. (A.) sulcata* (Lamarck). *Notocorbula* Iredale, 1930, for the Australian *N. vicaria* Iredale, is scarcely different; *Varicorbula* Grant & Gale, 1931 [*gibba* (Olivi)] (Fig. 851) is distinguished only by a weaker edge of the right valve.

Fig. 851. Inner side of the right shell valve of *Aloidis* (*Varicorbula*) *gibba* (Olivi).

Subgenus *Panamicorbula* Pilsbry, ·1932. Shell not beaked; right valve only slightly larger, with deeply sunken cartilage bearer, an erect anterior main tooth, and long lateral teeth, the posterior of which is strong; left valve with broad, somewhat erect cartilage bearer and a deep pit anterior to it. *A. (P.) inflata* (C. B. Adams).

Subgenus *Erodona* (Daudin) Bosc, 1802 (synonyms *Potamomya* Sowerby, 1839; *Azara* Orbigny, 1839). Shell longish triangular, weakly sculptured, nearly equivalve; left valve with a strong, obliquely projecting cartilage bearer, the margins of which are elevated ridge-like; right valve with a corresponding indentation of the hinge margin with elevated margins, the pits of which correspond to the other valve. *A. (E.) labiata* (Maton), in South American rivers.

Grippina Dall, 1912

Shell small, triangular, nearly equivalve; umbo moderately elevated; right valve with 2 projecting teeth, between which the cartilage rests, and with furrows corresponding to the dorsal margin of left valve; the latter has no hinge margin; mantle sinus distinctly developed, roundish.

G. california Dall, near California.

2. Family MYIDAE

Shell somewhat inequivalve, posteriorly more or less gaping; ligamental cartilage on the left attached to a projecting process, which is posteriorly fused with the margin and extends below the margin of the right valve; hinge margin without distinct teeth; mantle sinus more or less large. Siphons long, united, with a conchin membrane and a ring of tentacles; gill laminae folded.

927

? *Paramya* Conrad, 1860

Synonym *Myalina* Conrad, 1845, non Koninck, 1842.
Shell small, somewhat quadrangular; umbo situated anterior to the center; both valves with a vertical cartilage bearer without hinge teeth; mantle line posteriorly obliquely descending, without sinus.

P. subovata (Conrad), near Florida and South Carolina.

Sphenia Turton, 1822

Shell fairly small and thin; umbo closer to the somewhat pointed anterior end; right valve only slightly larger than the left; cartilage bearer

obliquely projecting, with a ridge on its posterior part; right valve with a weak roundish denticle anterior to the cartilage; mantle sinus moderately deep, roundish. Siphons fairly long and thick; foot with byssus.

S. binghami Turton. A few species, in various seas.

Cryptomya Conrad, 1848

Shell fairly small and thin, oval, nearly equivalve, sometimes with fine radial threads; cartilage bearer of the left valve with elevated anterior margin and posteriorly with a ridge; mantle sinus very shallow.

Few species, in various seas.

Subgenus *Cryptomya* s. s. Without distinct indentation anterior to the cartilage bearer of the left valve. *C. (C.) california* (Conrad).

Subgenus *Tugonella* Jousseaume, 1891 (synonym *Venatomya* Iredale, 1930). Left valve with an incision anterior to the cartilage bearer, whereby an anterior tooth is separated. *C. (T.) tugonella* (Jousseaume).

Tugonia Gray, 1842

Shell fairly small and thin, greatly bulging, posteriorly greatly shortened and widely gaping, anteriorly rounded and closed, exterioly with radial threads, in one species only in the posterior part; umbo posteriorly inclined; cartilage bearer projecting toward the left, posteriorly with a tooth-shaped process, elevated on the right, but obliquely receding, posteriorly with a pit which corresponds to the tooth of the left valve; mantle line close to the margin, posteriorly not indented.

T. anatina (Gmelin). 2 species, near West and East Africa.

Mya Linné, 1758

Shell nearly equivalve, oval or posteriorly broadly truncated, gaping at both ends; umbo only slightly elevated; external ligament thin; cartilage strong, attached on the left to a horizontal process, which lies below the margin of the right valve and posteriorly has a slanting ridge, whereas its anterior margin is upwardly curved; the right valve anterior to the cartilage has a weak tubercular thickening; mantle sinus large; siphons very long, with a conchin membrane and at its end with a ring of tentacles; foot small, tongue-shaped, without byssus.

928

Few species, in the northern and Arctic seas.

Section *Arenomya* Winckworth, 1930. Shell posteriorly not shortened. *M. (A.) arenaria* Linné.—Section *Mya* s. s. Shell posteriorly broadly truncated and widely gaping. *M. (M.) truncata* Linné (Fig. 852).

Fig. 852. Inner side of the left shell valve of *Mya truncata* Linné.

Platyodon Conrad, 1837

Shell fairly large and strong, elongated oval, bulging, posteriorly truncated and widely gaping, with distinct concentric and weak radial sculpture; cartilage bearer horizontal, anteriorly and posteriorly indented; the right valve has a tuberculate thickening posterior to the cartilage; mantle sinus large. The siphons at the ends have 4 horny, sometimes somewhat calcified processes.

P. cancellatus (Conrad), near California.

IV. STIRPS GASTROCHAENACEA

Shell more or less elongated, fairly small, widely gaping in the anterior part of the lower side; ligament external, attached to a only slightly projecting ridge; hinge margin toothless; mantle sinus deep. Siphons variably long; mantle closed, leaving a, in most cases small, opening for the foot. The animals either live freely in sand and build a club-shaped tube surrounding the shell and siphons or they bore into limestone or molluscan shells.

1. Family GASTROCHAENIDAE

Characters of the stirps.

Spengleria Tryon, 1862

Shell anteriorly somewhat rounded, posteriorly broadly truncated; umbo not situated very far forward; extending from them toward the

ventral posterior corner is a furrow and the part lying above it is more or less distinctly concentrically sculptured; anterior muscle scar fairly large. Siphons fairly short, separate; gill laminae folded; foot thick cylinder-shaped, without anterior tip, with protractor muscles, ventrally with a byssus gland; the mantle contains no acid-secreting glands.

S. mytiloides (Lamarck). Few species, in warm seas, living in sand.

Gastrochaena Spengler, 1783

Synonyms *Chaena* Retzius, 1788; *Rocellaria* Blainville, 1828.

Umbo very close to the pointed anterior end, posteriorly rounded, with uniform concentric sculpture; anterior muscle scar small. Siphons long, united with one another; gill laminae smooth, sometimes extending into the ventral siphon; foot with a more or less large anterior tip, without protractor muscles; the mantle contains an acid-secreting gland. 929 *G. cuneiformis* Spengler. A few species, in warm seas (Fig. 853), boring into limestone. *Dufoichaena* (Jousseaume) Lamy, 1925 (*G. dentifera* Dufo), is not substantially different. *Cucurbitula* Gould, 1861, was proposed for animals which bore into shells, from which they more or less project and form an envelope of roundish capsules arranged in a row.
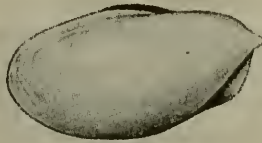
Fig. 853. *Gastrochaena ovata* Sowerby, seen from the right, somewhat enlarged.

Fistulana Bruguière, 1792

Shell thin, narrow and elongated; umbo nearly terminal, anterior part small, angular, ribbed, delimited by an edge; posterior part greatly elongated, concentrically striated, widely gaping below; anterior muscle scar small; mantle sinus deep. The calcareous tube, in which the animal lies, is club-shaped, closed at the anterior end, in the interior with a thickening posterior to the shell, exteriorly sometimes with attached sand grains; the posterior part contains the very long united siphons; the mantle has an opening anteriorly for the very small foot; labial palps small.

F. mumia (Spengler). 3 species, in the Indo-Pacific region.

V. STIRPS ADESMACEA

Shell colorless, equivalve, sometimes elongated, sometimes spherical, exteriorly in most cases ribbed and denticulate especially in the anterior part, gaping at both ends, sometimes anteriorly widely open, without ligament and hinge margin, so that the two valves are joined together only by muscles; anterior part of the dorsal margin broadened and reflected outward; attached to it is the anterior adductor muscle, which however does not work together with the posterior one but is antagonistic to it, thus producing rasping movements of the valves; projecting from the umbones into the interior of the shell is a band- or spoon-shaped process, to which the body musculature attaches; in addition to the shell, the animals produce various accessory calcareous plates or tubes, which sometimes remain unconnected to the shell, sometimes fuse with it. Siphons more or less long, largely united; mantle closed except for an anterior opening for the sometimes rudimentary foot.

The animals bore into wood and rock.

1. Family PHOLADIDAE

Shell variable in size, in most cases more or less elongated, seldom spherical, anteriorly and posteriorly gaping, sometimes anteriorly wide open; surface with denticulate ribs or rings, which in most cases on the posterior part become weaker or are completely absent; the expansions of the anterior dorsal margins are sometimes nearly parallel, but in most cases outwardly reflected; overlying the dorsal parts are plates produced by the reflected mantle, the anterior of which are known as the protoplax, the median one as the mesoplax, and the posterior one as the metaplax; only the central one has the same structure as the shell. Occasionally there are accessory shell pieces at the posterior end and in a few genera the wide anterior opening is closed by plates which are firmly joined with the shell; mantle sinus more or less deep. Siphons moderately long, without calcareous plates (pallets) at the ends; gill laminae in most cases scarcely folded, sometimes the outer one is rudimentary; labial palps fairly large, triangular; foot short, without byssus, sometimes rudimentary.

A. Subfamily Pholadinae

930

Shell anteriorly more or less gaping and not closed in older shells by a secondary expansion, in most cases without accessory plates at the posterior end.

Barnea (Leach) Risso, 1826

Synonym *Holopholas* P. Fischer, 1887.

Shell elongated; umbo situated anterior to the center; surface sculptured throughout the length with tuberculate radial ribs; expansions of the anterior dorsal margin simple or posteriorly cleft, without transverse septa; mantle sinus fairly shallow, but away from the posterior end.

Several species, in various seas.

Subgenus *Barnea* s. s. Dorsally only a protoplax is present. Section *Barnea* s. s. Shell anteriorly rounded and only slightly gaping. *B. (B.) candida* (Linné).—Section *Anchomasa* Leach, 1852. Shell anteriorly pointed and widely gaping. *B. (A.) parva* (Pennant).

Subgenus *Cyrtopleura* Tryon, 1862. Shell anteriorly rounded, gaping below, the dorsal expansions demarcating a cross-shaped area, which is covered by a horny lamella. *B. (C.) crucigera* (Sowerby).

Subgenus *Scobinopholas* Grant & Gale, 1931 (synonym *Scobina* Bayle, 1880, non Lepeletier, 1825). Shell large and strong, strongly sculptured, anteriorly rounded, with a triangular protoplax and a small mesoplax. *B. (S.) costata* (Linné).

Zirfaea (Leach) Gray, 1842

Synonym *Thurlosia* (Leach) Scudder, 1882.

Shell fairly small, anteriorly pointed and very widely gaping, posteriorly truncated, a groove descending from the umbo dividing each valve into an anterior part sculptured with pointed teeth and a posterior part with smooth rings; the dorsal expansion is reflected and is largely appressed, simple; 2 triangular accessory plates are rudimentary; mantle sinus large.
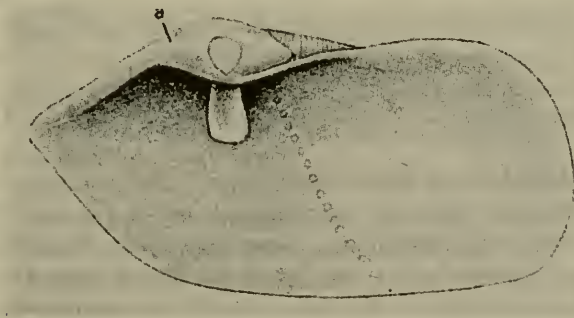
Fig. 854. Inner side of the right shell valve of *Zirphaea crispata* (Linné).
a, the outwardly reflected part.

Z. crispata (Linné) (Fig. 854). Few species, in various seas.

Pholas Linné, 1758

Shell elongated; posterior part more weakly or not denticulate; the reflected dorsal margin consisting of 2 lamellae, one of which is largely appressed, whereas the other is free; the two are connected with one another by a few transverse septa, in most cases the protoplax, mesoplax, and metaplax are developed; mantle sinus large, rounded.

Few species, in various seas.

Subgenus *Monothyra* Tryon, 1862. Shell anteriorly rounded and only slightly gaping; posterior part smooth; dorsally a protoplax and a very narrow metaplax are present. *P. (M.) orientalis* Gmelin.

931   Subgenus *Thovana* Gray, 1847 (synonym *Gitocentrum* Tryon, 1862). Shell anteriorly rounded and only slightly gaping; protoplax paired, with nuclei on the inner side; mesoplax small and transverse; metaplax long and narrow. *P. (T.) campechiensis* Gmelin.

Subgenus *Pholas* s. s. (synonym *Dactylina* Gray, 1847). Shell anteriorly pointed and widely gaping; protoplax paired, with nuclei on the outer side posterior to the center; mesoplax and metaplax present. *P. (P.) dactylus* Linné.

Talona Gray, 1842

Shell thin and moderately long, bulging, a major part sculptured with tuberculate concentric rings; the elevated dorsal margins are simple, parallel to one another, not appressed; 2 symmetrical accessory plates are present, which overlie the umbones, and a few half calcified ones at the posterior ends; mantle sinus moderately deep, tongue-shaped.

T. explanata (Spengler), near West Africa.

Xylophaga Turton, 1822

Synonyms ? *Xylotrya* (Leach) Menke, 1830, nom. nud.; *Xylotomea* Dall, 1898.

Shell fairly small, spherical, similar to *Teredo* with a large angular anterior indentation, posteriorly only slightly gaping; the anterior part is sculptured with finely denticulate ridges parallel to the margins; the posterior part, separated by a flat furrow descending from the elevated umbones, is sculptured with very dense, smooth, concentric striae; below the outer furrow extends an internal rib which projects wart-like at the end; the anterior dorsal margin is outwardly curved and bears 2 small

obtusely angled plates; inner process small. Siphons fairly thin, united nearly to the end; their retractor is short; below their attachments extends a fairly strong muscle from one valve to the other; the posterior adductor muscle is large, the anterior one very weak; mantle anteriorly widely open; foot disk-shaped, short; outer gill lamina absent.

X. dorsalis (Turton). Few species, some of which are doubtful, in various seas. Because the name *Xylophagus* was proposed earlier, Dall suggested the name *Xylotomea* for *Xylophaga*.

B. Subfamily Martesiinae

Shell in the young state anteriorly widely open, later closed by an sculptureless expansion, the margins of which are firmly joined and dorsally send out a more or less broadened, in most cases appressed process; the anterior part, sculptured with wavy or denticulate concentric threads, is separated by a descending furrow from the posterior part, which often bears horny or calcareous plates at the end.

Nettastomella Carpenter, 1865 (= *Nettastoma* Conrad, 1864, non Rafinesque, 1810) and *Navea* Gray, 1851, were proposed for juvenile shells, which probably belong to this subfamily.

Pholadidea (Goodall) Turton, 1819

Synonym *Cadmusia* Leach, 1852.

Shell longish, anteriorly bulging; upper part with wave-shaped concentric threads, lower part indistinctly sculptured; posterior half only slightly bulging, and concentrically striated; protoplax only in fully grown shells of variable size, single or paired; mesoplax and metaplax rudimentary; at the posterior end each valve has a horny process and 932 sometimes a calcareous groove, which may be fused with the opposite one to form a tube. Siphons completely united and with a fringed disk at the end; mantle nearly completely closed. Foot becoming rudimentary with age; gill laminae not folded, very unequal; labial palps long and narrow.

A few species, in various seas.

Section *Pholadidea* s. s. Shell with a radial furrow; protoplax paired, very small; posterior processes cup-shaped, not folded, without calcareous tube. *P. (P.) loscombiana* Goodall.—Section *Talonella* Gray, 1851. Shell posteriorly with 2 curved swellings and processes, the inner side of which shows a tripartite callus. *P. (T.) tridens* (Gray).—Section *Hatasia* Gray, 1851. Shell posteriorly with 2 horny processes and a calcareous tube. *P. (H.) melanura* (Sowerby).—Section *Penitella* Valenciennes,

1846. Shell posteriorly with 2 diverging horny plates, anteriorly with a broad appressed reflection; protoplax formed of 2 plates largely joined with one another; mesoplax small, triangular *P. (P.) penita* (Conrad). —Section *Calyptopholas* Lamy, 1928. Shell fairly short, with a very large protoplax enveloping the anterior part; at the posterior end with a calcareous, rounded process of each valve and around the siphons with a calcareous tube which lines the wall of the cavity produced by the animal in a coral *(Porites)*. *P. (C.) cheveyi* Lamy, near Annam.

Parapholas Conrad, 1848

Shell longish, on either side divided into 3 sections by 2 radial furrows, the anterior section is sculptured above with wavy lamellae, below with weak striae, whereas the middle one bears a thick periostracum, the posterior one horny lamellae; the paired protoplax sometimes attains considerable size, posterior to it lies a long paired metaplax, occasionally there also a ventral, paired, narrow hypoplax; whereas the posterior end lacks processes joined with the shell, the surrounding cavity is lined by a calcareous tube; posterior adductor muscle scar elongated; mantle sinus very flat, but away from the posterior end.

P. californica (Conrad). A few species, in warm seas.

Martesia (Leach) Blainville, 1825

Shell in most cases fairly small and thin, with a descending furrow on either side; dorsally with a paired, more or less large protoplax, a narrow metaplax, and seldom a mesoplax; ventrally with a narrow paired hypoplax; sometimes the valves are posteriorly elongated into thin calcareous lamellae. Siphon as in *Pholadidea*; their retractors are divided into 2 bundles on either side.

A few species, in warm seas; one, *M. rivicola* (Sowerby), in rivers near the mouth.

Section *Martesia* s. s. (synonym *Martesiella* Verrill & Bush, 1898). Protoplax moderately large; a mesoplax absent. *M. (M.) striata* (Linné). —Section *Diplothyra* Tryon, 1863. A mesoplax present. *M. (D.) caribaea* (Orbigny).—Section *Aspidopholas* P. Fischer, 1887 (synonym *Scutigera* Cossmann, 1886, non Lamarck, 1801). Protoplax very large; a calcareous tube lining the surrounding cavity. *M. (A.) scutata* (Deshayes) †; the living *M. yoshimurai* (Kuroda & Teremachi), near Japan.

For *Pholas semicostata* H. C. Lea, the shell of which is posteriorly produced as a short, cone-shaped tube, Dall, 1898, proposed a genus 933 *Scyphomya*, whereas Tryon and Lynge considered the species identical

with *Martesia striata*; the dorsal plates are said to be similar to those in *Pholadidea*.

Jouannetia Des Moulins, 1828

Shell nearly spherical, inequivalve; right valve divided by a furrow into a large anterior and a small posterior part, the former consisting of one part sculptured with more or less wavy concentric threads and in the adult animal a broad, dorsal posteriorly reflected and appressed, indistinctly sculptured part; adjoining the posterior margin of the narrow posterior part is a tongue-shaped process; the larger left valve has no tongue-shaped process posteriorly; the posterior part is further divided by a second radial furrow; the dorsal reflection is greatly expanded and also covers a part of the right valve. The mantle is anteriorly closed, leaving a small opening; foot reduced in the adult animal; gill laminae distinctly folded.

Few species, in warm seas.

Subgenus *Jouannetia* s. s. Posterior processes of the right valve smooth margined; a lamella extending between the short internal process and the posterior dorsal part in both valves, attached to which is the posterior adductor muscle. *J. (J.) semicaudata* Des Moulins †; the living *J. cumingi* Sowerby.

Subgenus *Triomphalia* Sowerby, 1849 (synonym *Pholadopsis* Conrad, 1849). Posterior process of the right valve with cuspidate margin; in the interior without lamellae for the posterior adductor muscles. *J. (T.) globulosa* (Quoy & Gaimard).

2. Family TEREDINIDAE

Shell very small in comparison with the animal and covering only its anteriormost part, equivalve, without accessory pieces; it consists of a strongly curved triangular part and an anterior and posterior piece; the anterior plate is triangular, separated from the central part by a large angulate indentation and externally sculptured with finely denticulate concentric ridges; the central part shows 3 fields, the anterior of which is beset with denticulate ridges, whereas the centralmost is narrow and somewhat deepened, and the posteriormost field is concentrically striated; the posteriormost piece is ear-shaped, on the inner side in most cases delimited by a strong infolding; it serves for attachment of the strong posterior adductor muscle, where as the weak anterior adductor muscle attaches to a reflection of the anterior dorsal margin; the inner side shows a narrow free process and a median rib ending in a knob. The animal is

greatly elongated, with partially united siphons, which are characterized by the presence of a pair of peculiar, in most cases spoon- or feather-shaped calcareous structures (pallets); the visceral sac, which is otherwise situated ventral to the adductor muscles, is here posteriorly turned and elongated, so that the stomach and intestine are the most ventral; pericardium and kidney are situated above them and posterior to the posterior adductor muscle; the ventricle is not traversed by the intestine; the outer gill lamina is rudimentary, the inner one very long and narrow; the foot weak; oval lobes very narrow.

934   The animals are known as ship worms, boring into the destroying wood in marine construction and embankments; the cavities produced by them through rasping movements of the shell valves are lined with calcareous tubes.

<div align="center">

Teredo Linné, 1758

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Synonym *Xylophagus* Meuschen, 1781.

Pallets stalked, simple, not plumose, rounded at the end, truncate or forked (Fig. 855a).
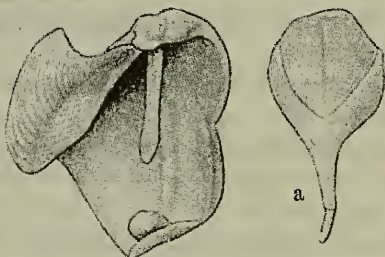
Fig. 855. Inner side of the left shell valve of *Teredo petersi* Roch. Height 1 cm. a, pallet of the same species.

Several species, in various seas.

Subgenus *Teredo* s. s. Shell valves about as long as high (Fig. 855). Section *Psiloteredo* Bartsch, 1922. The posterior ear-shaped piece of the shell not separated from the central part by infolding; pallets spoon-shaped, with a weak depression at the end of outer side. *T. (P.) dilatata* Stimpson.—Section *Zopoteredo* Bartsch, 1923. The posterior piece of the shell separated from the central part only by a distinct line; distal part of the pallets very short and broad, distally with a horny part infolded in the center. *T. (Z.) clappi* Bartsch.—Section *Teredora* Bartsch, 1921 (synonym *Malleolus* Gray, 1847, non Rafinesque, 1815, nec Ehrenberg,

1838). Posterior shell piece separated from the central part by an infolding, as also in all following groups; pallets exteriorly with an elevated margin, which proximally and laterally surrounds a fingernail-shaped part. *T. (T.) malleolus* Turton.—Section *Nototeredo* Bartsch, 1923. Shell as in *Teredora*; pallets similar to those in *Psiloteredo*. *T. (N.) edax* Hedley.—Section *Neoteredo* Bartsch, 1920. Pallets spoon-shaped, depressed cup-like at the end. *T. (N.) reynei* Bartsch.—Section *Teredops* Bartsch, 1921. Pallets leaf-shaped, with a calcareous knob at the end. *T. (T.) diegensis* Bartsch.— Section *Coeloteredo* Bartsch, 1923. Pallets with a thin, exteriorly bulging, interiorly nearly flat, distally somewhat concave lamina. *T. (C.) mindanensis* Bartsch.—Section *Spathoteredo* Moll, 1928. Pallets long-stalked, with broad, nearly quadratic lamina. *T. (S.) batilliformis* Clapp.—Section *Lyrodus* Gould, 1870. Pallets leaf-shaped forked at the end. *T. (L.) chlorotica* Gould.—Section *Teredo* s. s. Pallets deepened bowl-shaped at the end. *T. (T.) navalis* Linné.—Section *Teredothyra* Bartsch, 1921. Pallets fairly long, with a double cup at the end. *T. (T.) dominicensis* Bartsch.—Section *Ungoteredo* Bartsch, 1927. Pallets with a fairly short plate, which at the end has 2 deep, cup-shaped depressions separated by a slit. *T. (U.) matocotana* Bartsch.

Subgenus *Hyperotus* Guettard, 1770 (*Uperotus*) (synonym *Guetera* Gray, 1847). Shell considerably higher than long, with small anterior and posterior parts, the posterior one freely projecting; pallets with fairly long, exteriorly concave lamina, which is sculptured in the distal half with irregular, radiating, somewhat prominent ridges at the end. *T. (H.) clava* Gmelin. The animals bore into floating fruits of *Carapa moluccensis*; their calcareous tubes are strongly coiled and fairly short and strong.

Eoteredo Bartsch, 1923, is said to be characterized by the internal process arising not from the umbones but from the infolding separating the posterior ear-shaped part from the median part of the shell, but this is evidently only due to strong erosion of the umbonal area and may also happen otherwise; the pallets are unknown. *E. philippinensis* Bartsch.

A genus *Kuphus* Guettard, 1770 (= *Cyphus* P. Fischer, 1887; synonyms *Furcella* Lamarck, 1801; *Septaria* Lamarck, 1818, non Férussac, 1807; *Clossonnaria* Férussac, 1822; *Clausaria* Menke, 1828) was proposed for *T. arenaria* (Linné); the tubes attain considerable size, and are cleft at the posterior end or separated by a partition; they do not live in wood but free in sand, for which reason Lamy places them in subfamily Kuphinae; the shells are not sufficiently known; the pallets are long stalked with a triangular plate, the distal cavity of which is divided into two halves by a median rib.

Bactronophorus Tapparone Canefri, 1877

Synonym *Calobates* Gould, 1862, non Kaup, 1829, nec Temminck, 1839.

Anteriormost part of the shell very large in comparison with the posterior ear-shaped part; pallets long stalked, with a short, broad, triangular plate, rooted in the distal cavity of which is a band-like, distally somewhat broadened lamella, which is nearly as long as the stalk (Fig. 856a); siphons nearly completely united.

B. thoracites (Gould), near eastern Asia.

Fig. 856a. Pallet of *Bactronophorus thoracites* (Gould).

Zachsia Bulatoff & Rjabtschikoff, 1933

Shell very weak, its anterior part forming no projecting angle, but is convex, somewhat incurved at the margin, with a few ribs which bear unequal oblique teeth; the posterior ear-shaped part is very small and weak; the internal process thin, needle-shaped. Only the small anterior part of the shell is free, the posterior covered by a mantle fold. Pallets broad and simple as in *Teredo*. The larvae develop into elongated forms within the maternal mantle cavity.

Z. zenkewitschi Bulatoff & Rjabtschikoff. 2 species in the roots of *Phylospadix ruprechti*, near eastern Asia (Vladivostok).

Bankia Gray, 1842

Shell similar to that in *Teredo*; pallets more or less long, formed of several small funnel-shaped calcareous structures fitting into one another (Fig. 856b).
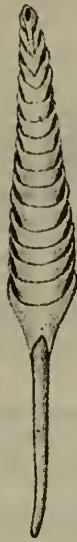
Fig. 856b. Pallet of *Bankia* (*Bankiella*) *gouldi* Bartsch
(after Bartsch).

A few species, in various seas.

Subgenus *Nausitora* Wright, 1864. The funnel-shaped parts are more or less densely placed, united on the external surface and covered by a calcareous layer. *B.* (*N.*) *dunlopi* (Wright).

936 Subgenus *Bankia* s. s. The funnel-shaped parts are distally free, covered by a thin membrane. Section *Bankiella* Bartsch, 1921. This membrane is smooth at the free margin. *B.* (*B.*) *mexicana* Bartsch.— Section *Neobankia* Bartsch, 1921. Free margin of the membrane finely denticulate. *B.* (*N.*) *zeteki* Bartsch.—Section *Bankia* s. s. Free margin of the membrane fringed; the lateral tips have long processes. *B.* (*B.*) *bipalmulata* (Lamarck).

Suborder ANOMALODESMATA

Shell often thin, inequivalve and internally nacreous; ligament in most cases with internal cartilage, which often contains a calcareous structure (lithodesma); hinge teeth weak or absent; mantle sinus and siphons more or less developed; gonads as a rule hermaphroditic (Fig. 857).
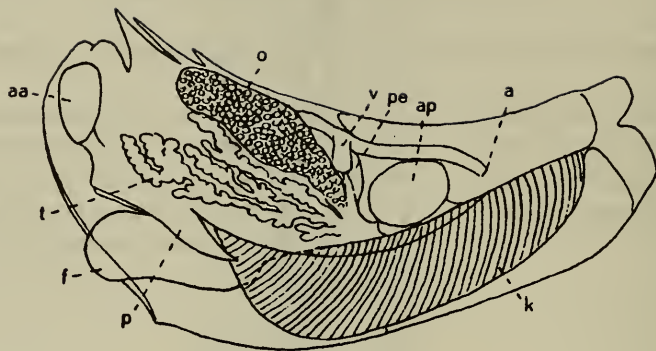
Fig. 857. *Pandora elongata* Carpenter.
a, anus; aa, ap, anterior and posterior adductor muscle; f, foot; k, gill; o, ovary;
p, labial palps; pe, pericardium; t, testis; v, ventricle (after Pelseneer).

1. STIRPS PANDORACEA

Inner gill lamina well developed, folded, the outer one more or less reduced, in most cases forming a narrow, upwardly-directed lamella. Without calcareous tube outside the shell.

1. Family LYONSIIDAE

Shell in most cases thin and somewhat inequivalve, interiorly nacreous, exteriorly with more or less strong periostracum, longish; hinge margin toothless; the internal ligament is attached in a narrow groove near the margin and contains a lithodesma; mantle sinus shallow; siphons short and separate, without separate retractors; foot with byssus; outer gill lamina fairly broad.

Lyonsia Turton, 1822

Synonyms *Magdala* (Leach) T. Brown, 1827; *Hiatella* T. Brown, 1827, non Daudin, 1802; *Tetragonostea* Deshayes, 1830; *Myatella* T. Brown, 1832; *Osteodesma* Deshayes, 1835, non Blainville, 1825; *Pandorina* Scacchi, 1836, non Bory de St. Vincent, 1824.
Characters of the family.
A few species, in various seas.
Subgenus *Lyonsia* s. s. Shell thin; umbo close to the center. Section *Lyonsia* s. s. Surface with fine radial threads and often with attached sand grains. *L.* (*L.*) *norvegica* (Chemnitz).—Section *Allogramma* Dall, 1903.

Shell with radial and sometimes slanting, occasionally somewhat spiny folds. *L.* (*A.*) *formosa* Jeffreys.

Subgenus *Entodesma* Philippi, 1845. Shell more or less irregular; umbo close to the anterior end, with strong periostracum; the animals live in holes, or in sponges, or colonial ascidians. Section *Philippina* Dall, 1901. Shell fairly small, thin, anteriorly short and ventrally gaping, posteriorly compressed. *L.* (*P.*) *beana* Orbigny. Living in sponges or ascidians.—Section *Entodesma* s. s. Shell fairly large and strong, inflated; ligament long, with large lithodesma. *L.* (*E.*) *chilensis* (Philippi).—Section *Agriodesma* Dall, 1909. Shell large and thick, with very strong periostracum, ventrally broadly gaping; lithodesma very large. *L.* (*A.*) *saxicola* Baird. Living in cavities of stones.

Mytilimeria Conrad, 1837

Shell equivalve, thin, in most cases irregularly oval, more or less bulging, with a smooth periostracum, interiorly nacreous; umbo close to the anterior end; ligament fairly long, on either side attached in a furrow close to the margin, with a lithodesma; muscle scars small; mantle sinus shallow. Mantle margins thick; siphons with wide opening; foot and labial palps very small.

M. nuttalli Conrad. Few species, in the Pacific and Atlantic Oceans.

The genus is sometimes placed beside *Lyonsiella*, sometimes beside *Lyonsia*.

2. Family PANDORIDAE

Shell compressed, longish, posteriorly beaked; dorsal margin often concave posterior to the umbones; outer layer consisting of small, irregular prisms; inner side nacreous; left valve as a rule bulging, the right one flat; ligament with a narrow cartilage, which is more or less obliquely posteriorly directed from the scarcely projecting umbones and is affixed in furrows; accessory ridges run from the umbones on the inner side of the shell; mantle line discontinuous, without indentation. Siphons very short; mantle with an anterior opening for the fairly large foot, which has a small byssus groove; outer gill lamina very narrow.

Pandora (Hwass) Chemnitz, 1795

Synonyms *Calopodium* (Bolten) Röding, 1798; *Trutina* T. Brown, 1827; *Pandorella* Conrad, 1863.

Characters of the family.

A few species, in various seas.

Section *Pandora* s. s. Cartilage without lithodesma; right valve with 2 internal ridges; left valve with a weak ridge or without same. *P.* (*P.*) *inaequivalis* (Linné).—Section *Kennerleya* Carpenter, 1864 (*Kennerlia*). Cartilage with lithodesma; internal ridges similar to those in *Pandora* s. s.; right valve with a few radial lines. *P.* (*K.*) *filosa* (Carpenter). —Section *Frenamya* Iredale, 1830 (synonym *Coleodon* Carpenter, 1865, non Audinet-Serville, 1832, nec Lund, 1838). Cartilage without lithodesma; right valve with 3 ridges; left valve with a posterior and an angle-shaped anterior ridge. *P.* (*F.*) *patula* (Tate).—Section *Clidiophora* Carpenter, 1864. Cartilage with lithodesma; right valve with 3 ridges, the posterior of which is very long, the anteriormost in low; left valve with 2 ridges anterior to the cartilage, the anterior of which ends behind the adductor muscle scar, and a long posterior one. *P.* (*C.*) *claviculata* (Carpenter). —Section *Heteroclidus* Dall, 1903. Cartilage with lithodesma; of the ridges, the left posterior one absent and the right posterior one is short; both anterior ridges end anterior to the anterior muscle scar. *P.* (*H.*) *punctata* Conrad.

938

3. Family MYOCHAMIDAE

Shell inequivalve; dorsal margin of the more bulging valve enclosing that of the opposite valve; hinge margin toothless; ligament with 2 lithodesma; mantle sinus small. Mantle with an opening for the foot and a small one anterior to the lower siphon; siphons moderately long, separate; foot small or rudimentary; labial palps large, triangular.

Myodora Gray, 1840

Shell not cemented, compressed, fairly thin; umbo angulate, scarcely projecting, sometimes closer to the center, sometimes to the anterior end, posteriorly truncated, exteriorly with concentric rings and with rodlet-shaped prisms, parallel to the margin, arranged in regular rows; right valve bulging, the left one flat; dorsal margin of the right valve with a furrow corresponding to the margin of the left valve; ligament triangular, situated below the umbones, with sickle-shaped lithodesma; inner side shiny nacreous; anterior adductor muscle scar narrow, the posterior one roundish.

M. brevis (Sowerby). A few species, in the Pacific and Indian Oceans.

Myochama Stutchbury, 1830

Shell highly inequivalve; right valve flat, cemented onto other bivalves; left valve greatly bulging, irregularly ribbed; cartilage affixed in a pit on either side, with a lithodesma; the dorsal margins beside the cartilage may be thickened somewhat tooth-shaped; anterior adductor muscle scar longish, the posterior one roundish; mantle sinus angular.

M. anomioides Stutchbury. Few Australian species.

4. Family CHAMOSTREIDAE

Shell highly inequivalve; right valve greatly deepened and cemented by the anterior half; left valve flat; inner side nacreous-like; outer side with rough growth lines; umbo anteriorly inrolled; ligament on either side affixed in a pit, with large, curved lithodesma; left valve with a cone-shaped tooth anterior to the ligament; right valve with a corresponding pit, but the tooth and pit may be absent; muscle scars large, the anterior one very long, parallel to the anterior margin; mantle line without indentation. Siphons very short; mantle completely closed or with a small opening for the foot and one on the ventral side; foot very small; gill laminae strongly folded; oral lobes narrow.

Chamostrea (Roissy) Blainville, 1825

Synonym *Cleidothaerus* Stutchbury, 1829.
Characters of the family.
C. albida Lamarck. 2 Australian species.

939

5. Family PHOLADOMYIDAE

Shell very thin, equivalve, more or less distinctly radially sculptured; ligament external, affixed on ridges; a weak cartilage below the umbones is often borne on a weak tooth-shaped tubercle of one valve; mantle line and indentation indistinct. Siphons in most cases long, completely united; between the anterior mantle opening and the siphons a very small opening is present; foot small; gills thick and finely folded.

Parilimya Melvill & Standen, 1899

Shell oval, thin, posteriorly only slightly longer than anteriorly, with indistinct radial folds; on the left with a weak tooth and on the right with a triangular pit below the umbones.

P. haddoni (Melvill & Standen), in the Torres Strait, in shallow water.

Pholadomya G.B. Sowerby, 1823

Shell more or less longish; umbones close to the anterior end, fairly inflated, with tuberculate radial folds; posterior end gaping; the anterior margin of the attachment of the cartilage may be somewhat elevated.

P. candida Sowerby. Few species, in the Atlantic and Pacific Oceans, in deep water.

Panacca Dall, 1905

Synonyms *Aporema* Dall, 1903, non Scudder, 1890; *Notomya* Cotton, 1931.

Shell triangular, inflated, anteriorly very short, posteriorly rounded, somewhat depressed below the umbones; surface with a few thread-shaped radial folds; external ligament borne on fairly strong ridges; inner side very shiny.

P. arata (Verrill) (Fig. 858). Few species, in the Atlantic Ocean, and one near Tasmania, in most cases in the deep sea.
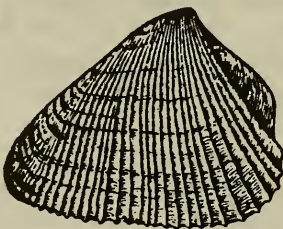
Fig. 858. Shell of *Panacca arata* (Verrill) (after Verrill).

6. Family THRACIIDAE

Shell thin, not nacreous, composed of small, irregular prisms, somewhat inequivalve, without hinge teeth; internal ligament in most cases only slightly sunken; mantle sinus moderately deep. Siphons long, separate; mantle on the ventral side with a small opening; foot small, without byssus; labial palps broadly triangular.

Thracia (Leach) Blainville, 1824

Synonym *Odoncinetus* O. G. Costa 1829 = *Cinetodonta* Herrmannsen, 1847.

Shell more or less longish, anteriorly rounded, posteriorly broadly truncated, in most cases anteriorly and posteriorly somewhat gaping; umbo close to the center; surface concentrically striated or with irregular granulations; external ligament short, internal one borne on an oblique expansion of the dorsal margin which is downwardly in most cases only slightly projecting, with an occasionally weak and fragile lithodesma; mantle sinus broad and more or less deep.

Several species, in various seas.

940   Subgenus *Cyathodonta* Conrad, 1849. Shell with concentric folds; hinge line not interrupted; umbo not perforated; cartilage bearer short, rounded, projecting below; lithodesma thin, semicircle-shaped, vertically attached anterior to the cartilage. *T. (C.) undulata* (Conrad).

Subgenus *Thracia* s. s. Shell concentrically striated and granulose; umbo in most cases perforated due to rubbing against one another; cartilage bearer more or less elongated and ventrally only slightly projecting. Section *Thracia* s. s. Lithodesma short, transverse, lying in a furrow anterior to the cartilage; mantle margin not elongated posteriorly. *T. (T.) pubescens* (Pulteney).—Section *Homoeodesma* P. Fischer, 1887. Lithodesma more or less rudimentary; mantle margin elongated posteriorly and enclosing the base of the two siphons. *T. (H.) conradi* Couthouy.

Subgenus *Phragmorisma* Tate, 1894. Shell fairly large, with concentric folds; right valve flatly bulging, the left one nearly flat; umbo close to the center; cartilage on strong processes below the umbones. *T. (P.) watsoni* E. Smith.

Subgenus *Ixartia* Leach, 1852 (synonyms *Rupicola* Fleuriau de Bellevue, 1802, non Brisson, 1760; ? *Pelopia* H. Adams, 1868). Shell irregular; cartilage bearer short, roundish, projecting freely downward, with lithodesma. *T. (I.) distorta* (Montagu).

? *Tyleria* H. & A. Adams, 1854

Shell thin, oval, posteriorly somewhat truncated and gaping, anteriorly rounded; ligament partly external; pit of the cartilage obliquely posteriorly directed, extending anteriorly from it parallel to the margin is a ridge which is joined to the margin by a few transverse plates; mantle sinus fairly small. Animal unknown.

T. fragilis H. & A. Adams, near Mazatlan. Found in hole of a *Spondylus* shell.

Asthenothaerus Carpenter, 1865

Shell somewhat inequivalve, oval or rounded triangular, anteriorly longer than posteriorly; hinge margin without teeth or processes; cartilage with large lithodesma; mantle sinus deep.

Few American species.

Subgenus *Asthenothaerus* s. s. Shell finely granulose, posteriorly somewhat gaping; external ligament rudimentary; lithodesma X-shaped, lying below the posterior part of umbones. *A.* (*A.*) *villosior* Carpenter.

Subgenus *Bushia* Dall, 1886. Shell not granulose, not gaping; ligament external; umbo interiorly thickened; lithodesma very large, transversely arch-shaped *A.* (*B.*) *elegans* Dall.

? *Parvithracia* Finlay, 1927

Shell small, triangular, finely concentrically striated, white; hinge margin very narrow; right valve with an anterior long and narrow lamella and a triangular tooth anterior to the umbo; left valve with a broad elevated tooth; cartilage fairly long and narrow; mantle sinus deep.

P. suteri Finlay = *Montacuta triquetra* Suter (non Verrill & Bush), near Stewart Island.

Thraciopsis Tate & May, 1900

Synonym *Alicia* Angas, 1867, non Johnson, 1861.

Shell longish, exteriorly microscopically granulose, anteriorly rounded, posteriorly short truncated; hinge margin on the right with a callous thickening corresponding to a depression on the left, and a marginal ridge; cartilage below the umbones, with a triangular lithodesma; mantle sinus deep.

941

T. angustata (Angas). A few Australian species.

Iredale, 1924, proposed a genus *Eximiothracia* for "*Alicia*" *speciosa* Angas, with the statement that it has an external ligament.

7. Family LATERNULIDAE

Shell oval, in most cases exteriorly granulose and interiorly shiny nacreous; hinge margin toothless; cartilage borne on processes, from which an accessory ridge extends obliquely backward; umbo cleft; mantle sinus distinct.

A. Subfamily Periplomatinae

Shell more or less inequivalve; mantle sinus moderately deep; siphons naked; mantle with a small anterior opening for the foot and one below the ventral siphon.

Periploma Schumacher, 1817

Shell distinctly inequivalve, exteriorly granulose, interiorly somewhat shiny nacreous; right valve deeper and largely enlosing the left; posterior end short, truncated, and somewhat gaping; ligament completely internal, on processes, which distinctly project into the interior and are anteriorly directed; between their upper margin and the shell margin lies a half-moon-shaped lithodesma and from their base runs a ridge-like thickening along the posterior margin of the shell to the adductor muscle scar; the mantle line runs close to the margin and forms a triangular indentation posteriorly.

P. inaequivalve Schumacher = *margaritaceum* (Lamarck). Few mainly North American species. Dall, 1904, proposed a section *Halistrepta* for *P. sulcatum* Dall, characterized by irregular wavy concentric folds similar to those in *Cyathodonta*.

Iredale, 1930, erected a genus *Pendaloma* for *P. micans* Hedley, for which only a right valve from Sydney has been described; the shell is very thin, short beaked, finely granulose and with a few concentric folds; umbo cleft; inner side somewhat shiny silver; cartilage bearer small, downwardly directed.

Cochlodesma Couthouy, 1839

Shell compressed, somewhat inequivalve, posteriorly slightly shorter than anteriorly; cartilage bearer downwardly directed; mantle sinus anteriorly rounded.

Few species, in the northern Atlantic Ocean.

Subgenus *Cochlodesma* s. s. Shell exteriorally not granulose; cartilage bearer posteriorly with a callous thickening and a ridge running to the adductor muscle scar; without lithodesma. *C. (C.) leanum* (Conrad).

Subgenus *Bontaea* (Leach) T. Brown, 1844 (synonyms *Ligula* Montagu, 1808, non Bloch, 1782, nec Mus. Calonn., 1797; *Galaxura* Leach, 1852; *Calcaraea* Recluz, 1868). Shell exteriorly granulose; cartilage bearer without callous thickening, with a small sickel-shaped lithodesma. *C. (B.) praetenue* (Pulteney).

Offadesma Iredale, 1930

Shell thin, fairly large; right valve inflated, the left one flatly bulging; umbo situated somewhat posterior to the center; posterior end gaping; outer side finely granulose; cartilage bearer downwardly directed, with posterior accessory ridge; mantle sinus triangular. Siphons naked.

942

O. angasi (Crosse & P. Fischer), near South Australia, Tasmania, and New Zealand.

B. Subfamily Laternulinae

Shell longish, thin, nearly or completely equivalve, ventricose, posteriorly gaping, exteriorly rough, internally shiny nacreous; cartilage bearer downwardly projecting, supported by a descending lamella and a thickening near the margin; mantle sinus large. Siphons moderately long, united, with horny epidermis, at the end of which a ring of tentacles is present, some of which may contain eyes; mantle with a small opening for the foot; labial palps long and pointed; the inner gill laminae are united with one another posterior to the foot.

Laternula (Bolten) Röding, 1798

Synonyms *Auriscalpium* Megerle von Mühlfeld, 1811; *Anatina* (Lamarck) Bosc, 1816; *Butor* Gistel, 1848, non Forster 1827, nec Swainson, 1834; *Butorella* Strand, 1928.

Characters of the subfamily.

L. anatina (Linné). Several species (Fig. 859), in various seas.
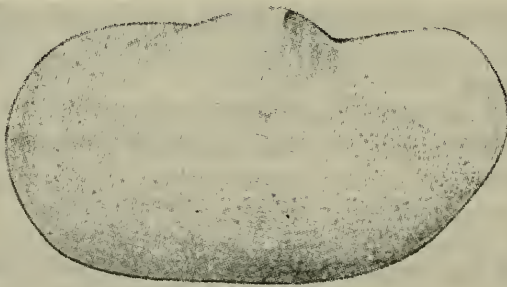
Fig. 859. Shell of *Laternula anatina* (Linné), seen from the left.

II. STIRPS CLAVAGELLACEA

The interiorly nacreous shell remains more or less small and one or both valves are embedded in a calcareous tube, which is sometimes simple, sometimes at the anterior end perforated sieve-like and carrying a number of fine tubules. The mantle has a very small opening for the foot and long, united siphons; foot small, without byssus; gills long and narrow, strongly folded; outer lamina simple, upwardly directed.

Family CLAVAGELLIDAE

Characters of the stirps.

Clavagella Lamarck, 1818

Shell inequivalve, irregular, flattened, finely granulose; left valve fused with the inner side of the tube; right valve free; the hinge margin has a weak projection and an indistinct depression posterior to it; the ligament rests on a small ridge; mantle sinus deep. Tube more or less long, sometimes divided by a longitudinal ridge; anterior end either bored into limestone, corals, or molluscan shells, or free with a small opening; posterior end simple or with wavy folds. Mantle closed except for a small opening for the foot; siphons with a ring of tentacles and the lower one fringed at the end; foot small, finger-shaped, with a short groove; oral lobes triangular; gills posteriorly united and projecting into the ventral siphon.

Few species, in various seas.

943 Section *Dacosta* Gray, 1858. Both ends of the tube simple. *C. (D.) australis* Sowerby.—Section *Bryopa* Gray, 1842. Anterior end simple; posterior end folded. *C. (B.) aperta* Sowerby.—Section *Stirpulina* Stoliczka, 1870. Anterior end with a median cleft and surrounded by branched tubules; posterior end with lamellae. *C. (S.) ramosa* Dunker. —Section *Clavagella* s. s. Anterior end with irregular spiny processes. *C. (C.) echinata* Lamarck †.

Brechites Guettard, 1770

Synonyms *Bunodus* Guettard, 1770; *Penicillus* Bruguière, 1792; *Verpa* (Bolten) Röding, 1798; *Aquaria* Perry, 1811; *Arytene* Oken, 1815; *Aspergillum* Lamarck, 1818.

Shell very small, nearly equivalve, with fine radial striae, completely fused with the outer side of the tube. The latter is long, perforated sieve-like, and often surrounded by a frill of longer, often bifurcated tubules,

posteriorly sometimes with broad wavy margins. Mantle with a small anterior opening for the foot and a small ventral opening; siphons very long; foot very small; gills posteriorly united; adductor muscles rudimentary.

A few species, in warm seas.

Subgenus *Humphreyia* Gray, 1858. Tube attached, quadrangular anteriorly with irregular tubules. *B. (H.) strangei* (Gray).—Section *Foegia* Gray, 1842. Anterior end without frill; posterior end simple. *B. (F) novaezelandiae* (Gray).—Section *Brechites* s. s. (synonym *Clepsydra* Schumacher, 1817). Anterior end with a frill of long tubules; posterior end simple. *B. (B.) javanus* Bruguière (Fig. 860).—Section *Warnea* Gray, 1858. Anterior end with a frill; posterior end with a few folded lamellae. *B. (W.) vaginiferus* (Lamarck).
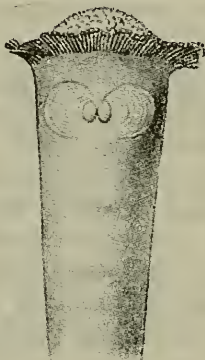
Fig. 860. Anterior part of the tube of *Brechites annulatus* (Deshayes), with the small shell attached within it.

III. STIRPS POROMYACEA

Shell free, nearly or completely equivalve, smooth or beset with small spinules; ligamental cartilage with lithodesma; hinge margin with or without teeth; mantle sinus not or weakly developed; siphons short as a rule; gill laminae narrow, net-shaped or modified into a horizontal septum pierced by minute sieves or rows of perforations; foot without byssus. Inhabitants of the deep sea.

1. Family VERTICORDIIDAE

Shell exteriorly beset with spinules, interiorly nacreous, in most cases roundish, sometimes distinctly ribbed; hinge margin often with a bulging

tooth anterior to the cartilage in the right valve. Mantle with a short anal siphon and a scarcely elongated, but sometimes very wide, incurrent aperture, which is surrounded by tentacles; gill laminae narrow, net-shaped, in most cases enclosed in an incomplete septum; foot small, with a groove; labial palps rudimentary; gonads hermaphroditic.

944   *Lyonsiella* (M. Sars, 1868) G. O. Sars, 1872

Shell roundish or somewhat longish, thin, sometimes inflated; umbo more or less close to anterior end; right valve without hinge tooth, left with a weak thickening of the margin below the umbo; mantle line not indented.

The gill septum and mantle form a sort of valve, which can form or prevent a communication between the upper and lower mantle cavity.

A few species, in all seas.

Subgenus *Thracidora* Iredale, 1924. Shell somewhat compressed, longish; umbo close to the center, scarcely elevated. *L. (T.) arenosa* (Hedley); the South African *L. agulhasensis* Jaeckel & Thiele may also belong here.

Subgenus *Lyonsiella* s. s. Shell greatly bulging, rounded rectangular; umbo close to the anterior end, inflated; inhalent opening moderately large, situated at the posterior end; gill septum united with the visceral sac. *L. (L.) abyssicola* M. Sars (Fig. 861). Iredale, 1930, proposed a genus *Proagorina* for the Australian *L. quadrata* Hedley; however, this species is so similar to *L. abyssicola* that it can hardly be placed in a different group.

Subgenus *Laevicordia* Seguenza, 1876. Shell roundish, in most cases somewhat higher than long; incurrent opening very wide; gill septum not united with the visceral sac. *L. (L.) insculpta* (Jeffreys).

Fig. 861. Outer and inner side of the shell of *Lyonsiella abyssicola* M. Sars (after Sars).

Halicardia Dall, 1895

Shell fairly large, heart-shaped, with radial folds, the largest of which forms an angle at the end, externally granulose; hinge teeth rudimentary; lithodesma asymmetrical, narrow, right limb longer than the left. Mantle with very wide incurrent opening, which bears several large tentacles, and small opening for the foot; labial palps thin, smooth; foot with a small posterior process; the gills are attached only at the posterior part of foot, without outer lamina.

H. flexuosa (Verrill & Smith), in the Atlantic Ocean.

Halicardissa Dall, 1913

Shell similar to that in Halicardia with a few strong folds and small deep lunule; in the right valve with a strong cone-shaped tooth. The gills are largely free, with direct and indirect lamellae; septum thin and incomplete; labial palps and foot having more resemblance with the usual condition, the latter without posterior process.

H. perplicata (Dall), near the Galapagos Islands.

Verticordia (Gray, 1842) J. Sowerby, 1844

Synonyms Hippagus Philippi, 1844, non Lea, 1833; Iphigenia O. G. Costa, 1850, non Schumacher, 1817; Hippella Mörch, 1861.

Shell fairly small, closed, beset with spinules, in most cases roundish and with radial folds; umbo more or less elevated, anteriorly directed; lunule more or less depressed; right valve in most cases with a cone-shaped tooth; left valve in most cases with projecting margin of the lunule; ligament internal, with fairly large lithodesma.

945

Many species, in various seas, often in deep water.

Section Vertisphaera Iredale, 1930. Shell unribbed. V. (V.) cambrica (Iredale).—Section Vertambitus Iredale, 1930. Shell with flat radial folds, uniformly granulose; umbo sharply projecting. V. (V.) vadosa Hedley.—Section Haliris Dall, 1886. Shell with numerous, dense folds; umbo not sharply projecting. V. (H.) fischeriana Dall. Setaliris Iredale, 1930 (setosa Hedley), is scarcely different.—Section Trigonulina Orbigny, 1845. Shell compressed, partly ribbed; hinge tooth longish. V. (T.) ornata Orbigny (Fig. 862).—Section Verticordia s. s. Shell with strong folds, without hinge tooth. V. (V.) verticordia S. Wood.—Section Spinosipella Iredale, 1930. Lunule very small, covered by the umbones, with a tubercular hinge tooth. V. (S.) ericia Hedley = deshayesiana P. Fischer.
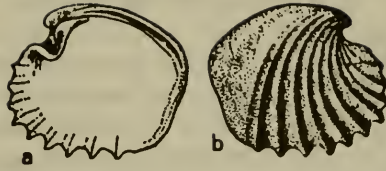
Fig. 862. Right shell/valve of *Verticordia* (*Trigonulina*) *ornata* Orbigny, inner and outer side enlarged (after Verrill).

Euciroa Dall, 1881

Shell fairly large, in most cases oval or roundish, more or less bulging, with numerous spinose radial ribs; umbo close to the center; right valve with a tubercle-shaped tooth, left with projecting margin of the lunule and of the posterior dorsal area; an indentation of the hinge margin corresponds to the right tooth. The mantle has a wide opening for the foot and scarcely elongated siphons, the lower of which is somewhat wider than the dorsal, surrounded by several tentacles; a ventral part of the mantle contains strong muscles; foot well developed, in most cases pointed; labial palps smooth, elongated, in the center with vesicular swellings; the ventrally slightly projecting gills are united exteriorly with the mantle and posterior to the foot with one another and with the siphonal septum.

A few species, mainly in the Indo-Pacific region, in the deep sea.

Section *Euciroa* s. s. Shell roundish or transversely oval. *E.* (*E.*) *elegantissima* (Dall).—Section *Acreuciroa* Thiele, 1931. Shell posteriorly pointed beak-shaped. *E.* (*A.*) *rostrata* Jaeckel & Thiele (Fig. 863).
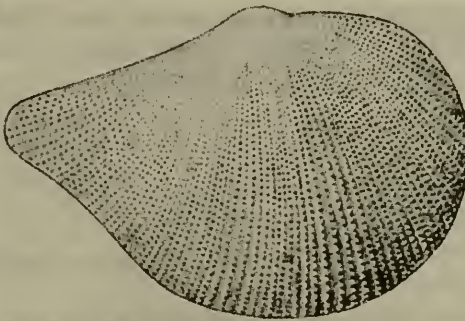
Fig. 863. Right shell valve of *Euciroa* (*Acreuciroa*) *rostrata* Jäckel & Thiele

2. Family POROMYIDAE

Shell fairly small and thin, roundish or oval, interiorly nacreous, often with a hinge tooth of the right valve; cartilage fairly weak, lying just below the exterior ligament. Mantle ventrally widely open; the short siphons surrounded by a ring of tentacles, the lower one has a large valve-like process in the interior; its retractors are in most cases scarcely developed; foot with ventral groove, sometimes with weak byssus; labial palps large, the rudimentary gills on either side forming 2 or 3 small sieves or rows of perforations in most cases muscular septum; gonads hermaphroditic (Fig. 864).
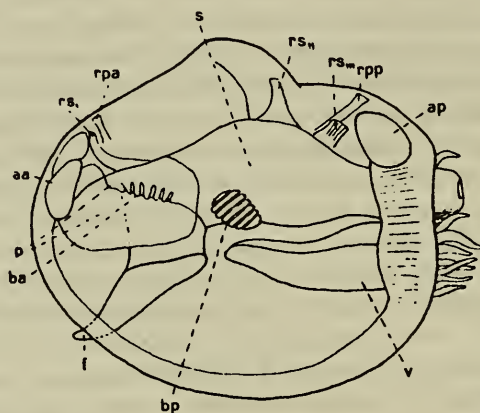
Fig. 864. *Poromya* (*Cetoconcha*) *butoni* Prashad.
Animal seen from the left side, after removal of the left mantle lobe.
aa, ap, anterior and posterior adductor muscle; ba, bp, anterior and posterior gill sieve; f, foot, p, outer and inner labial palp; rpa, rpp, anterior and posterior retractor of the foot; rs, - rs,,,, retractors of the gill septum s; v, valve of the incurrent siphon (after Pelseneer).

The animals inhabit the deep sea.

Poromya Forbes, 1844

Synonyms *Embla* Lovén, 1846; *Thetis* (err. non J. Sowerby, 1826) H. & A. Adams, 1856.
Shell in most cases inflated, roundish, posteriorly somewhat truncated and often with an edge; umbo projecting, close to the center. Gill septum on either side with 2 pore sieves.
A few species, in all seas.

Section *Poromya* s. s. Surface finely spinose; hinge tooth distinctly developed; no mantle sinus. *P. (P.) granulata* (Nyst & Westendorp) (Fig. 865). According to Dall, *Ectorisma* Tate, 1892, belongs to *Poromya*, therefore *E. granulata* Tate was called *P. illevis* by Hedley; Iredale, in contrast, upholds this genus; the latter in 1930 also proposed the genus *Questimya* for *P. undosa* Hedley & Petterd.—Section *Dermatomya* Dall 1889. Surface not spinose. Hinge margin strong; a mantle sinus developed. *P. (D.) mactroides* Dall.—Section *Cetomya* Dall, 1889. Surface spinose; hinge tooth rudimentary; no mantle sinus. *P. (C.) elongata* Dall.

Fig. 865. *Poromya granulata* (Nyst & Westendorp).

Cetoconcha Dall, 1886

Synonym *Silenia* Edg. Smith, 1885, non Mulsant, 1873.
Shell oval, with more or less elevated umbones situated in the center; hinge tooth rudimentary; without mantle sinus. The gill septum on either side contains 3 groups of pores; those in the two anterior rows are transversely, in the posterior row longitudinally directed.
C. bulla (Dall). Few species, in the deep sea.

3. Family CUSPIDARIIDAE

947   Shell posteriorly beaked, smooth or variably sculptured, thin, in most cases inflated, interiorly not nacreous; hinge margin with or without teeth; mantle sinus fairly shallow. Siphons in most cases short; at the base of the lower one on either side with 2 tentacles, its inner end closed by a membrane with a small aperture; above the upper siphon are 3 tentacles; gill septum fairly thick, on either side with a row of 4 or 5 pores; labial palps small or absent; foot in most cases with a groove; sexes separate (Fig. 866).

Cuspidaria Nardo, 1840

Synonym *Neaera* Gray, 1833, non Robineau-Desvoidy, 1830.

Ligament projecting below the hinge margin or ventrally, with small lithodesma; hinge margin sometimes with main or lateral teeth, sometimes toothless.

Numerous species, in the deep sea in all oceans.
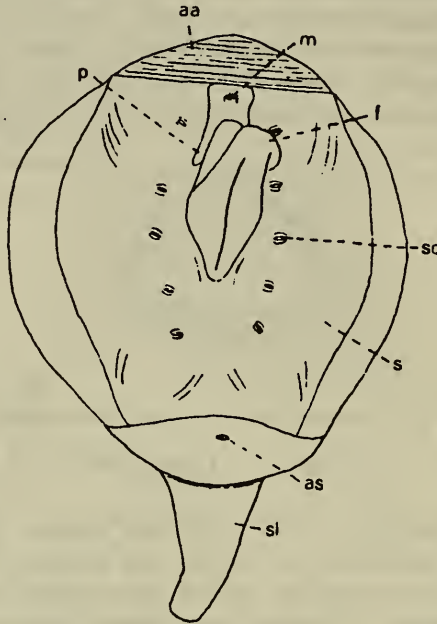
Fig. 866. Ventral view of *Cuspidaria convexa* Prashad, without shell; mantle lobes largely cut away.
aa, anterior adductor muscle; as, internal opening of the current siphon; f, foot; m, mouth opening; p, labial palps; s, gill septum; si, excurrent siphon; so, the median of the 5 pores in the septum (after Pelseneer).

Subgenus *Pseudoneaera* Sturany, 1900. Shell short beaked, concentrically sculptured; hinge margin on the right with 2 diverging teeth, on the left with an indistinct denticle anterior to the short ligamental pit; mantle widely open; ventral siphon long. *C. (P.) thaumasia* (Sturany).

Subgenus *Myonera* Dall & E. Smith, 1886. Shell in most cases short beaked, often with a few radial and concentric folds; hinge margin toothless. *C. (M.) paucistriata* (Dall).

Subgenus *Halonympha* Dall & E. Smith, 1886. Shell fairly short beaked, smooth or concentrically striated; in the right valve with one pointed tooth; ligamental pit short; a half-moon-shaped lamella surrounds the attachment of the posterior adductor muscle. *C. (H.) claviculata* (Dall).

Subgenus *Liomya* A. Adams, 1864 (*Leiomya*). Shell short beaked, smooth or concentrically striated; ligament very oblique; hinge margin on either side with one tooth and on the right with one anterior and posterior lateral lamella. *C. (L.) adunca* (Gould).

Subgenus *Tropidomya* Dall & E. Smith, 1886 (synonym *Tropidophora* Jeffreys, 1881, non Troschel, 1847). Shell similar to *Liomya*; hinge margin on either side with one tooth. *C. (T.) abbreviata* (Forbes).

Subgenus *Luzonia* Dall & E. Smith, 1889. Shell short beaked, concentrically striated; right valve with one tooth below the umbo. *C. (L.) philippinensis* (Hinds).

Subgenus *Plectodon* Carpenter, 1864. Shell rough as in *Poromya*; hinge margin with a tooth-like thickening; ligamental pit posterior to and below the umbones; ends of the siphons protected by a leather-like ring which is broadened on the sides. *C. (P.) scabra* (Carpenter).

948   Subgenus *Rhinoclama* Dall & E. Smith, 1886 (synonym *Rhinomya* A. Adams, 1864, non Robineau-Desvoidy, 1830). Surface concentrically striated, not granulose; hinge margin toothless. *C. (R.) adamsi* nom. nov. = *philippinensis* A. Adams non Hinds.

Subgenus *Vulcanomya* Dall, 1886. Surface concentrically striated; hinge margin on the right with small, fairly thick, anterior and posterior lateral lamellae; on the left only with a similar anterior one; ligamental pit small, situated below the umbones. *C. (V.) smithi* Dall.

Fig. 867. Inner side of the right shell valve of *Cuspidaria cuspidata* (Olivi).

Subgenus *Cuspidaria* s. s. Hinge margin with only one posterior lamella in the right valve; posterior beak variable in length. Section *Cuspidaria* s. s. Shell smooth or concentrically sculptured. *C. (C.) cuspidata* (Olivi) (Fig. 867).—Section *Cardiomya* A. Adams, 1864 (synonym *Spathophora* Jeffreys, 1881). Shell with radial folds. *C. (C.) gouldiana* (Hinds).

Class CEPHALOPODA

The cephalopods are exteriorly symmetrical animals, which seldom possess an external chambered spiral shell, in most cases a calcareous or

horny shell below the dorsal integument; sometimes they have no shell. The foot of the remaining mollusks is here as a rule modified into a funnel-shaped tube, which serves the animals for a swimming mode of life. The large head in most cases contains highly developed eyes and bears strong arms, which are as a rule beset with suckers used for grasping prey. The mantle encloses a ventral space, which contains the two gills (doubled only in *Nautilus*) as well as the anus and the openings of the kidneys and the gonad. The mouth, surrounded by the arms, leads into a strong buccal mass with a dorsal and a ventral jaw and with a radula, which is only very seldom reduced; a pair of salivary glands is nearly always present; in dibranchians also a more or less large, occasionally paired poison gland; below the tongue lies an organ of taste; the intestinal system has a large digestive gland; the rectum is in most cases short and opens into the mantle cavity behind the funnel. The nervous system is bilaterally symmetrical; that of *Nautilus* shows some similarity with that of bivalves, because it has cerebral, pedal, and visceral ganglia, but in addition buccal ganglia are also present; in the remaining cephalopods the pedals are fused with the visceral ganglia; the arms have received a strong nervous system, and a pair of ganglia (stellate ganglia) are developed for innervation of the mantle musculature. The blood vascular system is well developed; the heart lies in a pericardium; it is not traversed by the intestine and has 4 auricles in *Nautilus*, 2 in the remaining cephalopods. The pericardium in *Nautilus* and decapods is considerably widened and forms a body cavity which surrounds the viscera; in octopods, on the other hand, the true pericardium is reduced and the part associated with the gonads forms 2 flask-shaped pouches containing the glandular processes of the gill-hearts and opening into the kidneys through ciliated funnels. Corresponding to the gill vessels, 4 kidneys in *Nautilus*, 2 in the remaining cephalopods are present. The sexes are always separate; the single gonad lies in or beside the body cavity, into which the ripe products first enter and are then discharged through the gonoducts. These often remain paired in the females, whereas in the male one of them is nearly always reduced, the other one has glands which produce spermatophores. This duct opens often with a penis-like process, although the transfer of spermatophores to the female is accomplished by more or less modified arms. The more or less large eggs are yolk-rich; they are laid sometimes in very large quantities and are often attached on the substratum or on seaweed; in *Argonauta* they are kept in a thin calcareous shell.

949

I. Subclass TETRABRANCHIA

Among the primitive cephalopods with an external shell (Ectocochlia Schwarz, 1894; Tomochonia Haeckel, 1896; Protocephalopoda Grimpe, 1922), of which a large number of species populated the seas in earlier times, only the genus *Nautilus* has survived to the present day. The shell is bilaterally symmetrical, spirally coiled, divided by several partitions perforated in the center; these septa are posteriorly bulging and produced into a small funnel-shaped process at the perforation; the inner side is nacreous, the outer side porcellaneous. Half of the body whorl represents the living chamber of the animal, in which its ventral side is outwardly directed; a thin process of the posterior end traverses the entire series of chambers. The mantle forms a dorsal lobe, which adjoins the penultimate shell whorl, ventrally it forms a broad membrane covering the gills and the posterior part of the funnel. The latter consists of 2 large lobes, which are anteriorly and at the sides free and enrolled toward each other, so that they form an anteriorly narrowed tube, open below in which lies a tongue-shaped anteriorly directed valve in front of the center. The large head bears numerous annulated cirri with their sheaths, which are arranged into an outer and an inner system. The sheaths of the dorsal arms are considerably enlarged and fused together to form a thick membranous cephalic hood, which largely covers the shell aperture when the animal is retracted into the shell; the outer system comprises 19 arms on either side, of which 4 smaller ones are the outermost; 8 lie in the central and 7 in the innermost row. The inner system differs in the two sexes; in the female it consists of 2 lateral parts with 12 cirri each and a ventral bilobed part, which on either side forms a lobe with 12–14 cirri and a median indentation with a few lamellae, this ventral part is sunken in a pocket between the buccal mass and the body wall, the outer wall of which forms fine lamellae, to which the spermatophores are attached by the male. In the male the lateral parts of the inner system form a dorsal section with 8 cirri and a ventral one with 4 cirri; the latter, in adult animals, is on one side modified into a copulatory organ (spadix); the ventral part of the inner system is borne in a deep membranous sheath, the ventral side of which has numerous lamellae. An annulated cirrus is present anterior and posterior to the eye. The eyes are in the form of open vesicles without lens and vitreous body. Below the eye a finger-shaped process with 2 pits is present, probably a rhinophore. The
950 strong buccal mass contains powerful jaws and a broad radula, in which each transverse row consists of 13 plates; the central plate has moderately long pointed cutting edges, the 3rd and 5th of the lateral plates have long curved edges, the remaining ones have short cutting edges (Fig. 868); the liver consists of 4 lobes; the intestine forms one loop. In the mantle

cavity on either side lie 2 pinnate gills, attached to the body with only their bases. Corresponding to each gill is a spindle-shaped auricle of the heart and a renal sack; they open into the mantle cavity, the lower pair immediately beside the openings of the pericardial ducts. The pericardium communicates with the wide body cavity, in which the gonad lies, borne on the genital septa. Only the right gonoduct is developed, the left one is modified into an internally closed vesicle. Whereas the oviduct is short and wide, the sperm duct is narrow and coiled, in association with a spermatophore gland, and it opens into the mantle cavity with a penis-like process behind the funnel. The large eggs are attached to the substratum.
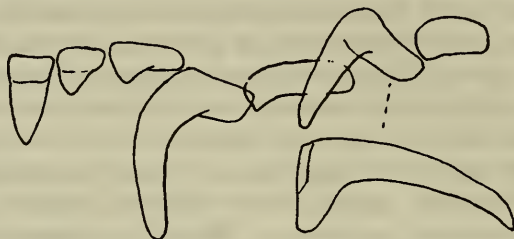
Fig. 868. Half radular row of *Nautilus pompilius* Linné; under it one plate in lateral view.

951   **Family NAUTILIDAE**

Shell coiled in one plane, externally smooth; septa perforated in the center.

Nautilus Linné, 1758

Characters of the family.
N. pompilius Linné (Fig. 869). Few living species, in the Indo-Pacific region.

II. Subclass DIBRANCHIA

Recent cephalopods without external shell (Endocochlia Schwarz, 1894; Gamochonia Haeckel, 1896; Metacephalopoda Grimpe, 1922) have 2 gills as in the bivalves and the zeugobranch snails. The shell is here inside the body, and in most cases lies below the dorsal integument. It is seldom calcified; only in *Spirula* it has a form reminiscent of *Nautilus*, being spiral, cylindrical, distinctly chambered and is pierced by
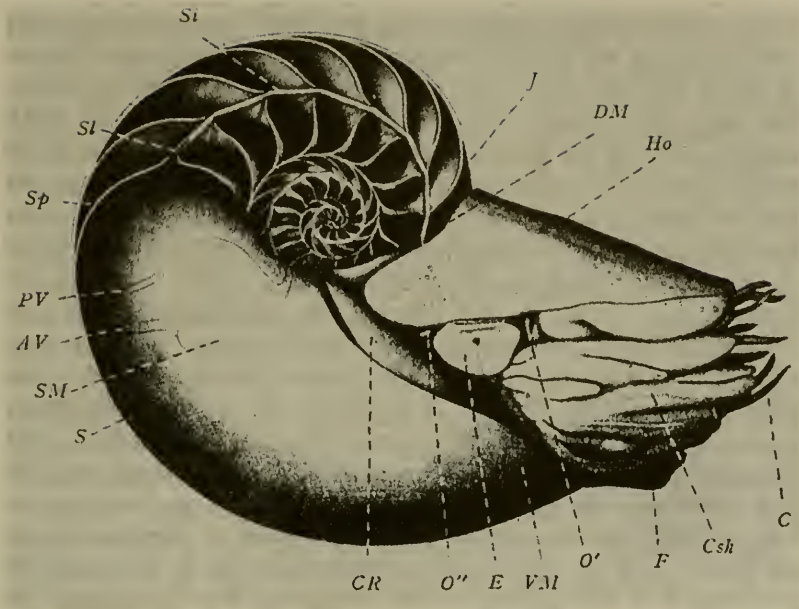
Fig. 869. *Nautilus pompilius* Linné, seen from the right side, the shell sectioned in the center.

AV, anterior muscle band; C, cirri; Csh, sheaths of the cirri; CR, posterior part of the funnel; DM, dorsal part of the mantle; E, eye; F, anterior part of the funnel; Ho, cephalic hood; J, spire of shell; O', O'', tentacles attached anterior and posterior to the eye; PV, posterior muscle band; S, living chamber of the shell; Si, siphuncle; Sl, process of the body running through; SM, attachment of the right shell muscle; Sp, last septum; VM, ventral part of the mantle (after Griffin).

a siphon, but it is small, enclosed in the posterior part of the body, and ventrally coiled, with completely separated whorls. Its form is very different in sepiids, where it forms a dorsal plate with a posterior spine, whose inner side has numerous fine septa. In most cases the shell is a horny, more or less elongated, often plume-shaped plate, sometimes posteriorly with a small cone-shaped chamber or a solid apex. In a few groups the shell has become rudimentary, occasionally completely lost in adult animals. The mantle encloses the posterior half of the body which contains the viscera and is rather variable in form and ventrally surrounds the gills and part of the funnel, with which it is in most cases joined by knob-like cartilaginous elevations, seldom firmly fused. A pair of membranous fins are in most cases developed on the sides of the mantle. The funnel is a closed, anteriorly narrowed tube, whose anterior part is in most cases sunken into a depression of the head and which in the interior as a rule has a valve and glandular bulges. The large head nearly

always contains highly developed eyes and bears 8 more or less strong prehensile arms bearing suckers, to which are added in decapods a pair of longer raptorial arms, which however are reduced in a few genera. The arms often possess more or less extensive membranous webs; unpaired webs on the outer side are known as swimming webs, paired ones on the inner side as protective webs. Such membranous webs are most extensive in a few octopods, where they occupy nearly the entire intervening spaces to the ends of arms. In octopods the suckers developed on the arm side facing the mouth are unstalked, radially organized, and arranged in one or two rows; in decapods they are stalked, in most cases distinctly bilaterally symmetrical, and with denticulate chitinous rings, which are sometimes modified into strong hooks, they are arranged in most cases in 2 or 4 rows. Females of *Argonauta* bear a strong lobe-shaped expansion on the uppermost pair of arms, clasping a thin, spirally coiled, calcareous shell which is not firmly attached to the body and serves mainly as a container for the laid eggs. The male animals as a rule use a more or less modified arm, more seldom a pair, for transfer of spermatophores to the female; such an arm, known as the hectocotylus, is most strikingly

952   developed in a few octopods, where it detaches from the animal. The mouth opening is surrounded by a membrane, which is often supported by spindle-shaped pillars, which are radially directed toward the arms, to which they are joined by attachments; extending from these pillars are delicate membranes, which form pocket-like, sometimes partly closed spaces. Besides chromatophores and glands, the integument of cephalopods sometimes contains light organs. The highly developed eyes are sometimes completely covered by the external integument of the body, sometimes the eye cavity remains open; sometimes the eyes are elevated on more or less long stalks; only extremely seldom they are rudimentary. Statocysts and small pit-shaped olfactory organs are present. The central nervous system forms an esophageal ring, in which the pedal and visceral ganglia are fused with one another, whereas the arm ganglia lie anterior to the pedals; the ganglionated arm nerves are joined with one another by a ring commissure; a pair of ganglia (stellate ganglia) innervate the musculature of the mantle.

The buccal mass contains a pair of horny jaws and a radula, the rows of which as a rule have 7 plates, besides which, mainly in the Octopoda, there is another pair of toothless marginal plates. In most cases the plates have more or less long, pointed, simple cutting edges. Sometimes the central plate has a small accessory cusp on either side, seldom the neighboring plates also bear accessory cusps; in *Gonatus fabricii* there is one less pair of plates and in cirroteuthids and *Spirula* the radula is reduced. The tongue and the subradular organ are surrounded by the

lamellae of a pouch, the free surface of which bears a cuticle beset with thorns. The salivary glands are paired and below the esophagus lies the exit duct of a poison gland, which is sometimes paired. The esophagus leads into the in most cases sack-like main stomach, whereas in most cases single liver and a pancreas open into an accessory stomach; the intestine is short, into its terminal part opens the exit duct of the ink sack, which is most strongly developed in sepiids; in cirroteuthids it has been lost. The two gills are attached to the mantle by a band, which in most cases leaves only its outermost tip free. Corresponding to them, the heart has 2 auricles and between the veins and the gills on either side lies a gill heart. In decapods, the pericardium with the body cavity has an extent similar to that in *Nautilus*; in octopods the pericardium is reduced and the gonadal part is also greatly narrowed. The two kidney sacks are separate in octopods, united in decapods. The oviducts are as a rule paired, seldom only one is developed; on the other hand, the sperm duct is nearly always unpaired; it forms a spermatophore gland, then a so-called finishing gland and a spermatophore sack (Needham's sack), at the end with a muscular or glandular penis-like process.

I. Order DECAPODA

Cephalopods with an internal calcareous or horny shell, seldom rudimentary, with 8 arms and 2 longer tentacles, which however are sometimes reduced; suckers stalked, in most cases bilateral, with an often denticulate horny ring; buccal membrane with 6–8 more or less distinct tips mantle with lateral fins; kidney openings close to the anus.

953

I. STIRPS SEPIACEA

Shell calcareous, horny, or absent; body fairly massive, in most cases without light organs; arms never armed with hooks; eye cavity in most cases closed; buccal membrane without attachments with the arm bases; only one oviduct developed; accessory nidamental glands present.

1. Family SPIRULIDAE

Shell calcareous, enclosed in the posterior part of the animal, cylindrical, spiral, with about 2½ separated whorls, coiled ventralward, with a nearly sphere-shaped initial chamber and many chambers separated by arched septa with a continuous, ventral siphuncle (Fig. 870). Body (Fig. 871) cylinder-shaped, with small, roundish, nearly terminal fins and a posterior annular bulge surrounding a luminous organ; eyes with an
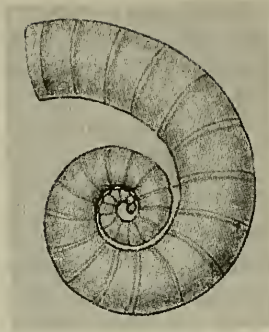
Fig. 870. Shell of *Spirula spirula* (Linné), double size.

Fig. 871. *Spirula spirula* (Linné), in dorsal view
(after Chun).

open lid fold; arms moderately strong, with many, at the base with up to
six rows of small, short-stalked suckers and joined with one another by
broad membranous webs; the two ventral arms in the male are hectocotylized,
without suckers and without connecting web; they are different from each
other; the right one is channel-shaped, spoon-shaped at the end with a pair
of claw-shaped points; the left one cylindrical, at the end with a few
variously formed processes and a few small points (Fig. 872); tentacles
only partly retractile, considerably longer than the arms. The buccal mass
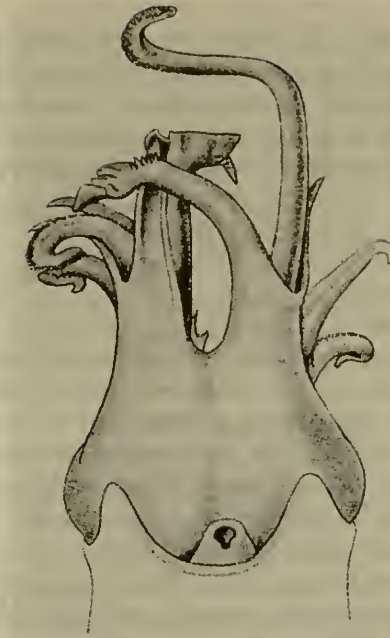
Fig. 872. Ventral view of the head and the arms of the male of *Spirula spirula* (Linné) (after Kerr).

contains no radula; the posterior gland is single; liver lobes separated; the mid-gut traverses the urine sack which is open with 2 papillae; oviduct developed only on the left side; besides the true nidamental glands, accessory glands are also present.

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Spirula Lamarck, 1801

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Synonyms *Lituina* Link, 1806; *Lituus* Gray 1849.——Characters of the family.

S. *spirula* (Linné), in warm seas, living bathypelagically.

954

<div align="center">

2. Family SEPIIDAE

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Shell calcareous, forming a dorsal plate, often with a posterior thorn, on the ventral side with a mass of fine oblique septa supported by small vertical pillars, the last-formed septum forming the anterior part of this bulge, followed by the margins of the remaining septa; a siphuncle is indicated by a flat posterior pit, delimited laterally and sometimes also ventrally by a margin, the so-called fork. Body more or less massive,

somewhat compressed, with lateral fin membranes; eye cavity nearly completely closed; with a secondary lid fold; arms with 2–4 tentacular clubs with 4–8 rows of suckers; tentacles completely retractile into pockets; ventral arms with muscular fin membranes; ink sack very large; left ventral arm hectocotylized. Radular plates without accessory cusps.

Sepia Linné, 1758

Mantle sack without glandular pores.

Numerous species, in various seas.

Section *Crumenasepia* Iredale, 1926. Shell medium-sized, elongated oval, with broad fork covering the posterior end of the bulge and which forms a broad and deep horny pocket. *S. (C.) hulliana* (Iredale).— Section *Solitosepia* Iredale, 1926. Inner pocket well developed; posterior thorn keeled. *S. (S.) liliana* (Iredale).—Section *Mesembrisepia* Iredale, 1926. Shell similar to the preceding; thorn cylindrical. *S. (M.) macandrewi* Iredale.—Section *Ascarosepia* Rochebrune, 1884 (*Ascarosepion*) (synonym *Amplisepia* Iredale, 1926). Shell large, posteriorly narrowed, without thorn; bulge anteriorly swollen, posteriorly depressed; posterior margin elongated and thickened; pocket fairly deep with warts. *S. (A.) verreauxi* Rochebrune.—Section *Lophosepia* Rochebrune, 1884 (*Lophosepion*). Shell without thorn, posteriorly rounded; bulge elevated to form a massive comb. *S. (L.) lefebrei* Orbigny.—Section *Acanthosepia* Rochebrune, 1884 (*Acanthosepion*). Shell with strong, projecting thorn; posterior margin freely projecting downward; fork freely projecting, strong. *S. (A.) aculeata* Hasselt.—Section *Ponderisepia* Iredale, 1926. Shell very large and thick, with very large thorn; bulge strongly swollen. *S. (P.) eclogaria* (Iredale).—Section *Rhombosepia* Rochebrune, 1884 (*Rhombosepion*) (synonym *Parasepia* Naef, 1923). Shell slender oval, with posterior wings; marginal lines of the lamellae of the bulge on the sides with regular angles. *S. (R.) elegans* Orbigny.—Section *Doratosepia* Rochebrune, 1884 (*Doratosepion*) (synonyms *Andreaesepia* Grimpe, 1922; *Arctosepia* Iredale, 1926). Body and shell slender, the latter posteriorly pointed, with strong thorn and small, projecting wings; ends of the arms elongated whip-like. *S. (D.) andreana* Steenstrup.—Section *Platysepia* Naef, 1923. Shell fairly broadly oval, with terminal thorn; ventral margin very blunt closely leaning on the thorn; fork low, in part tipped over. *S. (P.) esculenta* Hoyle.—Section *Sepia* s. s. (synonym *Eusepia* Naef, 1923). Shell broadly oval; fork recurved, spreading over the posterior; indistinctly winged dorsal shield; few suckers of the tentacular club distinctly enlarged. *S. (S.) officinalis* Linné. *Spathidosepia* Rochebrune, 1884 (*Spathidosepion*) is related; shell fairly short oval,

uniformly rounded, without thorn. lateral margins posteriorly very broad. *S. (S.) tuberculata* Lamarck.—Section *Decorisepia* Iredale, 1926. Shell moderately broad, anteriorly pointed with cylindrical thorn; posterior margin broad, weakly calcified, without pocket. *S. (D.) rex* (Iredale).—Section *Glyptosepia* Iredale, 1926. Shell similar to the preceding group; thorn long and strongly keeled. *S. (G.) opipara* (Iredale).—Section *Tenuisepia* Cotton, 1932. Shell small, narrow, with moderate, cylindrical thorn; pocket rudimentary. *S. (T.) mira* (Cotton).—Section *Metasepia* Hoyle, 1885. Shell rhomboid, without thorn; pocket shallow; tentacular club with unequal suckers. *S. (M.) pfefferi* Hoyle. This group was considered as a genus by Grimpe.

<div align="center">

Sepiella Gray, 1849

</div>

Synonym *Diphtherosepion* Rochebrune, 1884.

Shell without thorn, slender oval, posteriorly with a broad margin, without distinct pocket; the posterior end of the shell is overlain by a spacious folded glandular pocket, which opens posteriorly between the fin membranes; tentacular club with 8 regular rows of small suckers.

S. ornata (Rang). Few species, in warm seas.

<div align="center">

Hemisepius Steenstrup, 1875

</div>

Synonym *Hemisepion* Rochebrune, 1884.

Shell weak, calcified only in the posterior half, posteriorly pointed; animal fairly small; mantle short and broad, on either side on the ventral side with a row of about 12 glandular pores; arms short, with 2 rows of suckers; tentacular clubs short, with several small suckers; the hectocotylized arm is broadened; suckers largely reduced, some of them enlarged on the distal part.

H. typicus Steenstrup, near South Africa.

3. Family SEPIADARIIDAE

Mantle margin dorsally fused with the head, with broadly attached fins, without shell; arms with distinct protective membrane, on their distal part with 4 rows of suckers; the left ventral arm hectocotylized.

<div align="center">

Sepioloidea Orbigny, 1845

</div>

Body short; fins nearly as long as the mantle, the margin of which is dorsally fused to the head and laterally fringed, ventrally it has

numerous pores; arms joined by a fairly broad membrane, which is absent only between the ventral ones; the left ventral arm of the *f with transverse channels and conical papillae distally, without suckers.

S. *lineolata* (Quoy & Gaimard), near Australia.

Sepiadarium Steenstrup, 1881

Fins short, attached closer to the posterior end; mantle joined with the funnel by a muscular band; the funnel contains a valve only in the   ; arms proximally with 2, distally with 4 rows of suckers; hectocotylus distally without suckers; clubs of the tentacles with very small suckers.

S. *kochii* Steenstrup. 3 species, near eastern and southern Asia and Australia.

4. Family SEPIOLIDAE

Animals in most cases small; mantle short, rounded, with more or less large, rounded fins attached somewhat above the center; shell rudimentary; inserted in the cornea is a lid fold, which does not enclose the pore; arms without protective webs, with spherical suckers; tentacles retractable into pockets; radular plates without accessory cusps; one or both dorsal arms or one laterodorsal arm hectocotylized.

956

A. Subfamily Rossiinae

Mantle margin dorsally free, with neck cartilage and distinct shell rudiment; fins rounded; the basal parts of the arms joined by a protective membrane; the marginal suckers on the central part of the arms strikingly enlarged; tentacular club more or less broadened, with a swimming web; one or both dorsal arms in the *f hectocotylized; without luminous glands in the mantle cavity; funnel with a valve. Living on the substratum.

Rossia Owen, 1834

Synonym *Epitychusa* Gistel, 1848.
Characters of the subfamily.
Subgenus *Semirossia* Steenstrup, 1881. Arms with 2 rows of suckers; only the left dorsal arm hectocotylized. R: (S) *tenera* (Verrill). A couple of species, along the Atlantic coasts of America.
Subgenus *Allorossia* Grimpe, 1922 (synonym *Franklinia* Norman, 1890, non Jerdon, 1863). Arms with 2 rows of suckers; both dorsal arms hectocotylized. R. (A.) *glaucopis* Lovén (Fig. 873). Few species, in the northern seas.
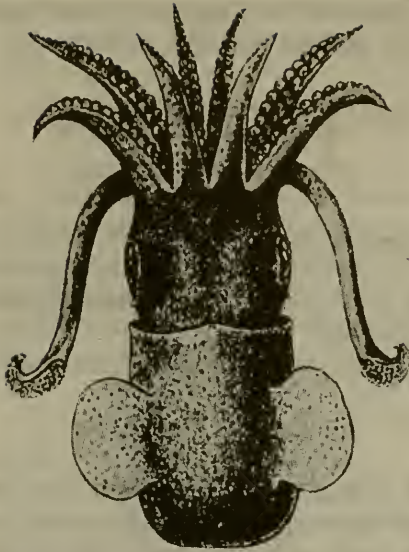
956   Fig. 873. *Rossia (Allorossia) glaucopis* Lovén in dorsal view
(after Sars).

Subgenus *Austrorossia* Berry, 1918. Arms with 2 rows of suckers, in the ♂ a few suckers are enlarged on all arms; tentacular club very long, with very numerous and very small suckers. *R. (A.) australis* Berry. A couple of species, near Australia and East Africa.

Subgenus *Rossia* s. s. Arms with 4 rows of suckers; tentacular club moderately long; suckers variable in size. *R. (R.) palpebrosa* Owen. A few northern species.

B. Subfamily Heteroteuthinae

Mantle margin dorsally free or fused with the head; fins large; arms joined by a fairly broad membrane, the dorsal ones distinctly shorter than the lateroventral ones, with 2 rows of suckers, some of which on the 3rd pair are strongly enlarged; tentacular clubs scarcely broadened, with rudimentary swimming web; massive light glands lie on the ink sack near the center. Living pelagically.

Heteroteuthis Gray, 1849

Synonym *Stephanoteuthis* Berry, 1909.

Body somewhat laterally compressed and posteriorly pointed; mantle margin dorsally free, ventrally largely covering the funnel; eyes without

lid fold; tentacles long and thin, with very small suckers; in the right dorsal arm swollen, and the 3rd arms have 2 or 3 greatly enlarged suckers.

H. dispar (Rüppel). Few species, in warm seas.

Nectoteuthis Verrill, 1883

Animal small; mantle posteriorly rounded, short, below with a large anterior lobe which covers the funnel and head; eyes with round pupils; arms small, on the distal parts with cone-shaped elevated suckers (?♂); tentacles long and slender.

N. pourtalesi Verrill, in the Atlantic Ocean near Barbados.

Iridoteuthis Naef, 1912

Animal small, roundish; head relatively long; mantle short and rounded, with large wing-shaped fins; mantle margin dorsally fused with the head, ventrally produced far forwardly; arms short; tentacles fairly long; light glands weak.

I. iris (Berry), near the Hawaiian Islands.

Stoloteuthis Verrill, 1881

Mantle fairly short, broadly fused with the head, without shell, with large rounded fins attached to the anterior part of the mantle; arms short, with 2 or 3 enlarged suckers on the 2nd pair and in the ♂ with a few larger suckers on the dorsal pair; tentacles moderately long, with very small suckers.

S. leucoptera (Verrill), on the North American east coast.

Sepiolina Naef, 1912

Neck band fairly broad; suckers uniformly small in the ♀, unequal in size in the ♂; both dorsal arms with small suckers without special copulatory organ; light organ disk-shaped.

S. nipponensis (Berry), near Japan.

C. Subfamily Sepiolinae

Mantle margin dorsally fused with the head, without neck cartilage; arms for the most part with 2 rows of suckers; in the ♂ the left dorsal

arm has a peculiar copulatory organ near the base, and on the remaining arms the suckers are enlarged; orbital pores open; light glands may be present.

Euprymna Steenstrup, 1887

Without shell; neck band broad; protective membrane distinct only between the 3rd and 4th arms; suckers at the base and on the point of the arms in 2, otherwise in 4 rows; tentacular club with very small or rudimentary suckers; light glands present.

E. morsei (Verrill), near eastern and southern Asia.

Sepiola Leach, 1817

Synonym *Fidenas* Gray 1849.

A weak shell in most cases present; arms with 2 rows of suckers, only occasionally in 4 rows at the tips of the ventral arms; in the ♂ only the left dorsal arm modified; tentacular club with 8 suckers rows; light glands present.

A few species, in various seas.

958 Section *Sepiola* s. s. (synonym *Eusepiola* Grimpe, 1922). Arms with 2 rows of suckers. *S. (S.) intermedia* Naef.—Section *Heterosepiola* Grimpe, 1922. Tips of the ventral arms with 4 rows of very small suckers. *S. (H.) atlantica* Orbigny.—Section *Hemisepiola* Grimpe, 1922. Buccal funnel 7-partite. *S. (H.) pfefferi* Grimpe.

Rondeletiola Naef, 1921

Synonym *Rondeletia* Naef, 1916, non Goode & Bean, 1894.

Shell reduced; ventral arms with 2 rows of suckers; 2nd arms with a few enlarged suckers of the ventral row; ink sack pear-shaped; light glands in both sexes situated close to the midline.

R. minor (Naef), in the Mediterranean Sea.

Sepietta Naef, 1912

Synonym *Sepidium* Levy, 1912.

Shell rudimentary; arms and tentacles long; ventral arms with 2 rows of suckers; in the ♂ the left dorsal arm broadened and hollowed between the sucker rows; ink sack slender pear-shaped; without light glands.

S. oweniana (Orbigny), in European seas.

Inioteuthis Verrill, 1881

Neck band fairly narrow; suckers uniformly small in the ♀, large and unequal in the ♂; light glands absent.

I. japonica Verrill, near Japan.

5. Family IDIOSEPIIDAE

Body without shell, moderately long; fins fairly small, attached near the rounded or pointed posterior end; dorsal mantle margin free, without cartilaginous support; arms short and strong, with 2 rows of suckers; tentacles fairly small, with 2 or 4 rows of suckers; eyes without lid fold; in the ♂ the two ventral arms are hectocotylized in different ways; both oviducts are present, although only the left one is in use.

Idiosepius Steenstrup, 1881

Synonyms *Microteuthis* Ortmann, 1888; *Naefidium* Grimpe, 1920. Characters of the family.

I. pygmaeus Steenstrup. Few species, near eastern Asia and Australia.

By the body form and the two ventral hectocotylized arms, the species show similarity with *Spirula*, but have no shell.

II. STIRPS LOLIGINACEA

Shell horny; mantle with large, as a rule terminal fins and with free margin; arms and tentacles with suckers; tentacles not retractable into pouches; cornea with an anterior pore.

1. Family LOLIGINIDAE

Shell feather-shaped; fins roundish and terminal or extending farther anteriorly; buccal membrane as a rule with 7 tips and in most cases with a few small suckers; the 3 median radular plates with a point on the outer corner of the base; in most cases the left ventral arm is hectocotylized.

959

Loliolopsis Berry, 1929

Mantle more slender in the ♀ than in the ♂, with terminal roundish fin; buccal membrane with 7 short tips and few suckers; shell very thin, anteriorly narrow, then distinctly broadened and posteriorly pointed; ♂ with longer arms, both ventral ones hectocotylized, the left one with a

lobe on the inner margin, the right one greatly elongated, with few basal suckers and with a comb-shaped row of small points on the distal part; tentacles fairly short.

L. *chiroctes* Berry, near California.

Loliolus Steenstrup, 1856

Animal fairly small and delicate; mantle short, rounded; fin anteriorly rounded; gladius with broad vane; funnel without externally visible adductors; suckers without fringed membrane; left ventral arm hectocotylized throughout its length, with a cuspidate comb, without suckers; tentacles fairly long and thin.

L. *typus* Steenstrup. Few species, in the Indian and Pacific Oceans.

Lolliguncula Steenstrup, 1881

Animal fairly small and strong; fin elliptical, fleshy, occupying about half the mantle length; buccal membrane with suckers; the spermatophores are attached in the mantle cavity in the vicinity of the left gill.

L. *brevis* (Blainville), on the American coast.

Loligo Lamarck, 1798

Mantle fairly slender, about six times as long as broad; fin rhomboid, occupying over half the mantle length; arms short; buccal membrane with 7 tips which bear 2 rows of suckers; shell with curved lateral margins.

L. *vulgaris* Lamarck. A few species, in various seas.

Sepioteuthis Blainville, 1824

Synonym *Chondrosepia* Rüppell & F.S. Leuckart, 1828.

Fin occupying nearly the entire length of the mantle; dorsal mantle margin obtusely angled; shell with curved lateral margins; buccal membrane in most cases with, occasionally without suckers.

S. *sepioidea* Blainville. A few species, in warmer seas.

Doryteuthis Naef, 1912

Mantle very slender, about eight times as long as broad; fin rhomboid, occupying about half the mantle length; shell broadest near

the short stalk, and then with straight margins, posteriorly pointed; buccal membrane with suckers on the 7 tips.

D. plei (Blainville). Few species, in warm seas.

Alloteuthis (Naef) Wülker, 1920

Synonyms *Teuthis* Gray, 1849, non Linné, 1758; *Acroteuthis* Berry, 1913, non Stolley, 1911; ? *Acruroteuthis* Berry, 1920; *Acrololigo* Grimpe, 1921.

960 Posterior end of the adult animal produced into a more or less long point, which contains the more or less cone-like enrolled tip of the shell and is bordered by the ends of the fins; buccal membrane without distinct tips and suckers.

A. media (Linné). 2 European species and one from the Sunda Islands.

? Family LEPIDOTEUTHIDAE

Mantle long, with a polygonal segmentation of the integument, posteriorly pointed, with large circular fin not reaching the posterior end; shell with narrow vane which is constricted in the center and forms a long terminal cone; head and anatomy unknown.

Lepidoteuthis Joubin, 1895

Characters of the family.
L. grimaldii Joubin, in the northern Atlantic Ocean.

? Family PROMACHOTEUTHIDAE

Body short, posteriorly rounded, with large, broad, posteriorly united fins; mantle margin free, transversely truncated; shell ?; head small, with a pore anterior to each eye; arms fairly long, the ventral ones the shortest, with 2 rows of suckers, tentacles strong, not retractile; buccal membrane with 7 weak tips, without suckers.

Promachoteuthis Hoyle, 1885

Characters of the family.
P. megaptera Hoyle, near Japan.

III. STIRPS ARCHITEUTHACEA

Shell (gladius) horny, feather-shaped; anterior eye cavity open; integument often with light organs; female gonoducts paired, accessory nidamental glands absent. Buccal membrane in most cases with 7, more seldom 8 or 6 tips and attachments; a hectocotylus is in most cases unknown.

1. Family LYCOTEUTHIDAE

Animal fairly small; mantle moderately long, posteriorly pointed, with large triangular fins on the posterior part; eyes large, flatly bulging, with light organs on their ventral side; arms with 2 rows of suckers; tentacles moderately long, with a few luminous organs and with 4 rows of suckers on the club; lower side of the body with luminous organs inside the mantle; buccal membrane with 8 pillars, tips, and attachments; radula with simple points without accessory cusps. Hectocotylus?

961

A. Subfamily Lycoteuthinae

Gladius narrow, distinctly concave, constricted behind the center, spoon-shaped at the end; below each eye with 5 light organs with 2 on each tentacle, and with 8 of these in the mantle cavity.

Lycoteuthis Pfeffer, 1900

Synonym *Thaumatolampas* Chun, 1903.
Arms not strikingly different in length.
L. diadema Chun (Fig. 874), in the Atlantic Ocean.

Nematolampas Berry, 1913

Lateroventral arms greatly elongated, thick in the proximal part, with suckers, thread-shaped in the distal part, without suckers, but with several light organs.
N. regalis Berry, near the Kermadek Islands.

? *Leptodontoteuthis* Robson, 1926

Only one head with the arms known. Arms with suckers; buccal membrane with 8 pillars; eyes surrounded by light organs; radular plates with long simple cusps.
L. inermis Robson, near South Africa.
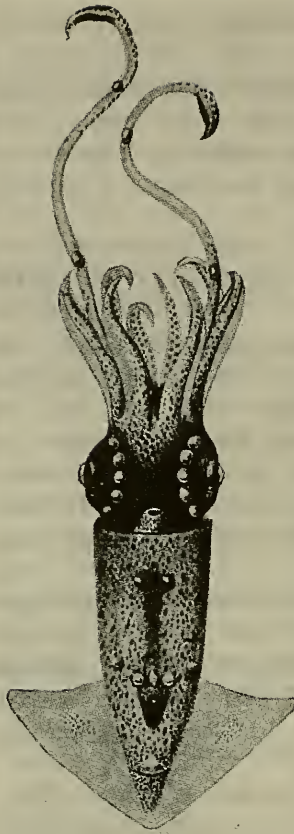
Fig. 874. *Lycoteuthis diadema* Chun, in ventral view
(after Chun).

B. Subfamily Lampadioteuthinae

Gladius with an obtusely angled vane, which occupies almost two-thirds of its length, without distinct terminal cone; 5 light organs in the mantle cavity, 3 below the eye on either side and one on the eye lid, as well as 5 on each tentacle.

Lampadioteuthis Berry, 1916

Characters of the subfamily.
L. megaleia Berry, near the Kermadek Islands.

2. Family ENOPLOTEUTHIDAE

Animals fairly small; mantle in most cases pointed, with large, nearly or completely terminal fins; gladius feather-shaped with distinctly developed vane, on either side with a ridge-shaped thickening near the margin; rachis groove-shaped, posteriorly with somewhat elevated median rib; terminal cone flatly spoon- to slender cone-shaped; arms in most cases with strong protective membranes; all or most of the suckers are modified into hooks; carpal part of the tentacular club with 2 rows of suckers and adhesive knobs; buccal membrane with 8 pillars, tips and attachments; light organs in most cases present, sometimes below the eyes, sometimes as numerous small organs in the external integument, sometimes inside the mantle cavity; one ventral arm is hectocotylized.

A. Subfamily Abraliinae

Numerous small light organs on the ventral side of the mantle, the head, and the ventral arms, and a few larger ones on the lower side of eyes; fins extending to the posterior point; tentacular club with one row of hooks; radular plates without accessory cusps.

962 *Abralia* Gray, 1849

Fins triangular, posteriorly narrowed; arms with 2 rows of hooks, the ventral ones with pointed ends, the left one hectocotylized, with moderate protective membranes and glandular swellings behind the tip. Light organs on the mantle closely aggregated, on the eyes 5–7 on either side, the marginal ones more or less large; gladius with more or less broad vane and small terminal cone (Fig. 875).

A few species, in various seas.

Section *Stenabralia* Grimpe, 1931. Mantle slender, with fairly small fins; gladius with narrow vane. *A. (S.) renschi* Grimpe.—Section *Abralia* s. s. Mantle moderately long, with large fins. *A. (A.) armata* (Quoy & Gaimard). *Asteroteuthis* Pfeffer, 1909, is scarcely different. *A. veranyi* Rüppell.

Abraliopsis Joubin, 1896

Form similar to that of *Abralia* with large fins; arms with 2 rows of hooks, the ventral ones produced into 3 knob-shaped swellings, the left one with greatly broadened ventral protective membrane, without glandular swellings; light organs densely aggregated on the ventral side, 5 on either side on the eyes.
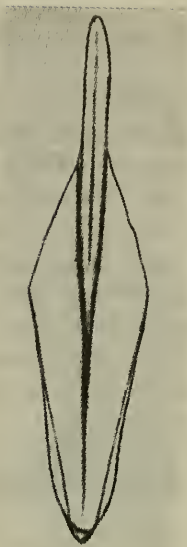
Fig. 875. Gladius of *Abralia veranyi* Rüppell
(after Pfeffer).

A. morisii (Verany), in the Atlantic Ocean and Mediterranean Sea.

The names *Nepioteuthion* and *Prodromoteuthis* Pfeffer, 1912, *Compsoteuthis* and *Micrabralia* Pfeffer, 1900, were based on juvenile forms; to which genera *Enoploion* and *Asthenoteuthion* Pfeffer, 1912, belong is uncertain.

Watasenia Ishikawa, 1914

Synonym *Watasea* Ishikawa, 1913, non Jordan & Snyder, 1901.

Mantle fairly slender; the fins occupying about half of its length; mantle with innumerable closely aggregated light organs, 5 small ones on the eyes and 3 large ones on the ends of the ventral arms; neck on either side with 4 longitudinal folds; right ventral arm hectocotylized, with hooks and 2 half-moon-shaped membranes, although without suckers; tentacular clubs with 4 rows of suckers and few large hooks.

W. scintillans (Berry), near Japan.

B. Subfamily Enoploteuthinae

Lower side of the body with many small, more or less distinct light organs arranged in longitudinal bands and one row of 8–10 small organs

below the eyes; fins not extending completely to the posterior point; tentacular clubs with 2 rows of hooks; the 3 median radular plates with points on the outer corners; right ventral arm hectocotylized.

Enoploteuthis Orbigny, 1839

Characters of the subfamily.
E. leptura (Leach), near West Africa and one species near Japan.

C. Subfamily Ancistrochirinae

Light organs on the lower side of the mantle large, in small number and more regular arrangement, flat or knob-shaped; tentacular club with 2 rows of hooks.

963

Ancistrochirus Gray, 1849

Fins large, extending nearly to the anterior mantle margin, surpassed by the posterior end; light organs in moderate number present on the lower side of the mantle; tentacular clubs with one row of larger and one row of smaller hooks.
A. lesueurii (Férussac & Orbigny), in the Indian and Atlantic Oceans.

Thelidioteuthis Pfeffer, 1900

Fins occupying about two-thirds of the mantle length, posteriorly forming a small point; light organs in small number on the mantle, head, and tentacular stalk; ventral arms shorter than the others; tentacular clubs with 2 rows of numerous hooks.
T. alessandrinii (Verany), in warmer seas.
According to Sasaki, this (?) species has a buccal membrane with 7 pillars and attachments.

D. Subfamily Pyroteuthinae

Buccal membrane in juveniles free, with 8 pillars, in adult animals free only in the ventral half, dorsally fused with the protective membranes of the arm bases of form a velum; posterior end pointed, surpassing the fins; light organs in the mantle cavity and on the lower side of the eyes.

Pyroteuthis Hoyle, 1904

Synonym *Charybditeuthis* Vivanti, 1914.

Arms with 2 rows of hooks, with suckers on the tips of the 3 upper pairs of arms; on the hand part of the club a small number of suckers of the ventral middle row are modified into hooks; right ventral arm hectocotylized, with a broad glandular lobe on the ventral surface of the distal part, the 2 rows of hooks are developed throughout the length.

P. margaritifera (Rüppell). A couple of species in the Mediterranean Sea and Atlantic Ocean.

Pterygioteuthis H. Fischer, 1896

A small number of the median suckers on the arms modified into hooks; tentacular club beset only with suckers; left ventral arm hectocotylized, without hooks or suckers, with a massive swimming membrane and 2 strong glandular pads opening in the middle of the arm.

P. giardi H. Fischer. A couple of species, in warmer seas.

Pfeffer, 1912, proposed the names *Pterygonepion* and *Ioteuthion* for young animals of this subfamily.

3. Family OCTOPODOTEUTHIDAE

Buccal membrane free, in most cases with 6 pillars and attachments; light organs may be developed; the tentacles present in juveniles are reduced in adult animals.

Octopodoteuthis Rüppell, 1844

Synonym *Verania* Krohn, 1847.

Body partly gelatinous; mantle cone-shaped, posteriorly with rounded point; fins large, somewhat rounded; light organs may be developed at the ends of the ventral arms, in one species one pair on the lower side of the head and 2 pairs below the mantle; eyes large; arms somewhat 964 swollen at the ends, with 2 rows of densely placed narrow hooks; gladius with a small flat cone.

O. sicula Rüppell, in various seas and a second species near the Bermudas.

Taningia Joubin, 1931

Mantle with very large, roundly, triangular fins; arms with 2 rows of suckers with hooks; the dorsolateral arms on the ends with a large

light organ; tentacles very small, with 6 rudimentary and 2 somewhat larger suckers; buccal membrane with 7 pillars.

T. danae Joubin, near the Cape Verde Islands.

Octopodoteuthopsis Pfeffer, 1912

Fin large, posteriorly leaving a small part of the pointed mantle end free; arms with pointed ends and 2 rows of not very densely placed, short hooks; tentacles absent.

O. megaptera (Verrill), on the east coast of North America. A doubtful genus.

Cucioteuthis Steenstrup, 1882

Animal large, fleshy; fins large, as long as the mantle; arms thick, pointed, with fairly densely placed strong hooks in 2 rows buccal membrane with 6 tips and attachments.

C. molinae (Orbigny). The species is insufficiently known, according to earlier reports in the Pacific Ocean, according to Joubin in the Atlantic Ocean.

4. Family NEOTEUTHIDAE

Body slender, posteriorly pointed; fins occupying about two-thirds of the mantle length, moderately broad; arms fairly short, with stalked roundish suckers in 2 rows; tentacular clubs with 4 rows; gladius with pointed terminal cone.

Neoteuthis Naef, 1921

Characters of the family.

N. thielei Naef, in the southern Atlantic Ocean (known only from juvenile animals).

5. Family ONYCHOTEUTHIDAE

Mantle more or less slender, posteriorly pointed; fins large, triangular, terminal; gladius feather-shaped, with more or less broad vane, roof-shaped in the posterior part, with strong median keel, posteriorly flatly spoon-shaped with a solid chitinous or cartilaginous terminal point; funnel cartilage simple, narrow; mantle cartilage longer; neck with a transverse fold and on either side 3 longitudinal folds, often also with

neck folds; buccal membrane in most cases with 7 tips and attachments and 6 pores; arms with 2 rows of small suckers with smooth or weakly denticulate rings; tentacles fairly long, on the carpal part with a roundish group of densely placed small suckers and adhesive knobs; hand part in juveniles with rows of suckers, of which the median ones are later in most cases modified into hooks, whereas the outer ones are reduced or persist as suckers or hooks; a hectocotylus is not known; light organs in most cases absent, occasionally these are developed in the mantle cavity. The central plates and the adjacent plates of the radula have small outer cusps.

965   *Cycloteuthis* Joubin, 1919

Animal fairly small, with long posterior point and large rhombic fin which does not extend to the point; integument smooth and thick; buccal membrane with 7 pillars; gladius weakly broadened in the anterior third; the posterior expansion forms a large spoon and ends in a sharp, anteriorly curved point; the end of the rachis is flattened; tentacles strong, at the base of the hand part with 5 small suckers and 3 knobs, anterior to which with 4 rows of larger, at the end smaller suckers which have a semicircle of denticles; central plate of the radula with outer cusps; between the gills lies a large light organ and on the eyes there seems to be a ring of small yellow luminous organs.

C. sirventi Joubin, near Madeira.

Joubin wanted to place this genus beside *Lycoteuthis*; Naef erected the subfamily Lycoteuthinae for it, which he included under the onychoteuthids.

Tetronychoteuthis Pfeffer, 1900

Body, fleshy, slender, pointed; integument of young animals with star-shaped minute chitinous warts; fin transversely rhombic, of less than half the mantle length; funnel depression anteriorly roundish; with neck folds; gladius with very narrow vane and narrow, flat spoon; median rib strong; terminal point thread-shaped; arms strong, exteriorly with deep longitudinal furrows; tentacles with scattered carpal suckers; hand part with 4 longitudinal and many transverse rows of suckers; no light organs.

T. dussumieri (Orbigny), in the Indian Ocean; whether the Atlantic *T. massyae* Pfeffer is a separate species seems uncertain.

Onychia Lesueur, 1821 (*Onykia*)

Synonyms *Steenstrupiola* Pfeffer, 1884; *Teleoteuthis* Verrill, 1885.

Animal fleshy, with smooth, soft, strongly pigmented integument, moderately slender, with short point; fins of less than half the body length; without folds; funnel depression anteriorly roundish; gladius with short free rachis and broadly lanceolate vane; the chitinous terminal point lies obliquely on the spoon; carpal group of the tentacles only on the sides webbed by a membranous fold; hand part in the adults with 2 rows of hooks and 2 marginal rows of suckers, some of which are occasionally lost.

O. caribaea Lesueur. Few species, in various seas.

Onychoteuthis Lichtenstein, 1818

Synonym *Teleonychoteuthis* Pfeffer, 1900.

Animal fleshy, with soft, strongly pigmented integument, slender, with long posterior point; fin large, transversely rhombic, with produced posterior point, in the adult animal longer than half the mantle length; with neck folds; funnel depression anteriorly pointed; cartilaginous ridge of the mantle at least twice as long as the funnel cartilage; gladius with moderately long free rachis and in the median third with lanceolate vane which is greatly narrowed posteriorly and is inflected downward, whereby the short, flat spoon appears separated; the median rib on the posterior part forms a high, sharp keel, which becomes lower toward the spoon; the chitinous terminal point is slender triangular, obliquely attached; carpal group of the tentacles surrounded by a membranous web; hand part in the adults with 2 rows of hooks, without marginal rows; in the mantle cavity lie 2 light organs, the anterior one on the liver capsule, the posterior larger one on the ink sac.

966

A single species *O. banksii* (Leach) (Fig. 876), distributed throughout nearly all seas.

Chaunteuthis Appellöf, 1880

Body gelatinous-cartilaginous, flaccid, with very soft, strongly pigmented integument, slender, with long posterior point; fin large, transversely rhombic, with only slightly produced posterior point, longer than half the mantle length; neck with folds; funnel depression anteriorly pointed; cartilaginous ridge of the mantle twice as long as the funnel cartilage; gladius similar to that in *Onychoteuthis*, although the vane is present only in the posterior half and the terminal point is shorter; arms short; tentacles were torn off; no light organs.

C. mollis Appellöf, in the Mediterranean Sea and Atlantic Ocean.

Fig. 876 *Onychoteuthis banksii* (Leach) in ventral view
(after Pfeffer).

Ancistroteuthis Gray, 1849

Body fleshy, with soft, smooth integument, slender with very long point; fin rhombic, with long drawn-out posterior point, longer than half the mantle length; neck with folds; funnel depression anteriorly pointed; gladius only with narrow vane in the posterior third; spoon narrow and fairly deep with long and slender chitinous terminal point; carpal group of the tentacles surrounded by a membranous web; hand part with 2 rows of hooks, without marginal rows; no light organs.

A. lichtensteinii (Férussac & Orbigny), in the Mediterranean Sea.

Moroteuthis Verrill, 1881

Animal large, fleshy, with long posterior point, sometimes with flat tubercles of the lower integument, without distinct neck folds; funnel

depression anteriorly roundish; gladius with broad lanceolate vane occupying nearly the entire length, posteriorly passing into the spoon, which nears a large, slender, cartilaginous terminal cone; carpal group of the tentacles surrounded by a membranous web; hand part with 2 rows of hooks, without marginal suckers; no light organs.

Subgenus *Moroteuthis* s. s. Gladius without dorsal median furrow; terminal cone with roundish cross-section. *M.* (*M.*) *robusta* (Verrill). 2 species in the northern Pacific Ocean.

Subgenus *Moroteuthopsis* Pfeffer, 1908. Gladius with dorsal median furrow, posteriorly roof-shaped; terminal cone with triangular cross-section. *M.* (*M.*) *ingens* (Edg. Smith), near Patagonia. According to Grimpe, *M. aequatorialis* Thiele, from the equatorial part of the Atlantic Ocean, perhaps does not belong here.

967 ## ? *Mesonychoteuthis* Robson, 1925

Animal large (insufficiently known); gladius? Mouth without lobes; lips with long thorns; arms with 4–9 pairs of large hooks between 2 rows of suckers at the end of the proximal quarter, their terminal quarter naked and greatly thinned; tentacles small, on the hand part only with hooks which can be rotated; shaft with a dense row of suckers and knobs besides the carpal·ones; central plate and its adjacent plates with outer cusps.

M. hamiltoni Robson, near the South Shetland Islands.

6. Family GONATIDAE

Body medium-sized; mantle fairly slender, posteriorly pointed with terminal rhombic or roundish fin; gladius with relatively large pointed terminal cone, which does not extend to the posterior end of the mantle; neck with annular and 3 longitudinal folds; funnel cartilage narrow, with simple longitudinal groove; mantle cartilage thread-shaped; buccal membrane with 7 attachments; arms with 4 rows of suckers, of which the two inner rows on the 1st to 3rd pairs of arms in older animals are transformed into hooks; also on the hand part of the tentacles a few suckers may be modified into hooks; no light organs. Hectocotylus development does not seem to take place. Central plate of the radula and the adjacent plate (which is reduced in *Gonatus* s. s.) with outer cusps.

Gonatus Gray, 1849

Synonyms *Lestoteuthis* + *Cheloteuthis* Verrill, 1881.
Tentacles are developed.

Subgenus *Berryiteuthis* Naef, 1921 (*Berryteuthis*) (synonym *Pfefferiopsis* M. Ishikawa, 1924). Tentacular club also in older animals beset only with suckers; radula with 7 longitudinal rows of plates. *G. (B.) magister* Berry, in the northern Pacific Ocean.

Subgenus *Gonatus* s. s. Proximal part of the tentacular club broadened; in addition to suckers with a longitudinal row of variably-sized hooks; radula with 5 longitudinal rows of plates. *G. (G.) fabricii* (Lichtenstein), distributed in northern and southern seas.

Gonatopsis Sasaki, 1920

Tentacles are reduced; 1st to 3rd arms with 2 rows of hooks and marginal suckers, the ends thin, with 10 or more rows of long-stalked suckers; radular rows with 7 plates.

G. octopedata Sasaki. 2 species, in the northern Pacific Ocean.

7. Family PSYCHROTEUTHIDAE

Body fairly large, elongate, posteriorly pointed, with large triangular fins which do not completely reach the posterior end; gladius long, feather-shaped, keeled; vane fairly large, not reaching the anterior end, posteriorly gradually narrowed and forming a small pocket at the end, without solid terminal cone, not extending to the posterior end of the mantle; buccal membrane with 7 pillars, tips, and attachments; dorsal and ventral interlocking cartilages large, with flat furrows; arms fairly strong, moderately long, with 2 rows of smooth-ringed suckers, the 3rd pair with darkly colored membranous webs at the end, whose inner side 968 shows several alternately placed transverse bulges; tentacles long, with strong, slightly broadened club which bears 4 longitudinal rows of suckers with denticulate chitinous rings; behind the club with a row of small suckers and adhesive knobs; hectocotylus?; radular plates without outer cusps. No light organs.

Psychroteuthis Thiele, 1920

Characters of the family.
P. glacialis Thiele, in the Antarctic Ocean.

8. Family ARCHITEUTHIDAE

Animals gigantic; mantle slender, posteriorly pointed, with terminal, elongated oval, posteriorly pointed fin; gladius posteriorly pointed; vane

flat in the anterior part, in the posterior part inrolled into a small terminal cone, in most cases with 2 stronger ribs diverging anteriorly from the posterior end of the rachis and several weaker ribs, ending far anterior to the posterior end of the mantle; neck with transverse and longitudinal folds; funnel and mantle cartilages longish, simple; arms long and strong, with 2 rows of suckers with denticulated rings; tentacles very long; club with 4 rows of suckers with denticulated rings; shaft with longitudinal rows of small suckers and adhesive knobs; buccal membrane with 7 tips and attachments; hectocotylus?; central plate of the radula and adjacent teeth with outer cusps.

Architeuthus Steenstrup, 1857

Synonyms *Megaloteuthis* Kent, 1874; *Dinoteuthis* More, 1875; *Mouchezia* Vélain, 1877; *Megateuthis* Hilgendorf, 1880; *Plectoteuthis* Owen, 1881; *Steenstrupia* Kirk, 1882 (non Forbes, 1846); ? *Dubioteuthis* Joubin, 1900.

Characters of the family.

A. dux Steenstrup. It is still not established whether all described giant squids belong in the same genus.

9. Family HISTIOTEUTHIDAE

Mantle small in comparison to the head with the arms, short cone-shaped, posteriorly more or less pointed, with rounded fins of moderate size attached on the dorsum; left eye more or less enlarged; numerous light organs mainly on the lower side of the mantle, the head, and the arms; neck without folds and funnel depression; funnel cartilage moderately broad, with a longitudinal furrow; mantle cartilage short, ridge-shaped; gladius feather-shaped, without terminal cone; arms with 2 rows of suckers, the stalks of which are laterally attached, in *Histioteuthis* with a large velum; tentacles long, club in most cases with 4–7 rows of suckers, on the shaft with one row of suckers and adhesive knobs; buccal membrane in most cases with 7 pillars, points, and attachments; as a rule both dorsal arms are hectocotylized.

Stigmatoteuthis Pfeffer, 1900

Mantle pointed or somewhat rounded with terminal, posteriorly indented fin; light organs not very numerous, on the ventral arms in 3 longitudinal rows, on the remaining arms in one ventral row and one row of smaller organs on the dorsal side; arms without distinct web; the

969

suckers on the arms and tentacles with denticulate horny rings; radular plates without lateral cusps.

S. hoylei (Goodrich). A few species, some of which are doubtful, mainly in the Indian and Pacific Oceans, probably also in the Atlantic Ocean.

Calliteuthis Verrill, 1880

Animal similar to *Stigmatoteuthis*; fin posteriorly distinctly indented; light organs not very numerous, on the arms as in the preceding genus; the 3 upper pairs of arms joined by a narrow velum; the larger suckers on the arms with smooth, the smaller ones with denticulate, horny rings, those on the tentacles with accessory thickenings.

C. meneghinii (Verany), in the Mediterranean Sea and the neighboring Atlantic Ocean.

Meleagroteuthis Pfeffer, 1900

Light organs on the ventral side of the mantle and head, as well as on the ventral arms very densely placed, on the remaining arms in 1–5 rows; fin terminal; posteriorly indented; the 3 upper pairs of arms have a narrow velar membrane at the base; the suckers on the arms and tentacles are denticulate.

M. hoylei Pfeffer on the west coast of Central America, one species (*asteroessa* Chun) near the Cape Verde Islands, and one (*separata* Sasaki) near Japan.

Histioteuthis Orbigny, 1839

Fin roundish, posteriorly somewhat indented; light organs on the lower side of the mantle and head not very densely placed; ventral arms with 3 longitudinal rows, the remaining arms with one dorsal row of large and one ventral row of small light organs, although large organs also lie ventrally at the base of the 3rd pair; buccal membrane in juveniles with seven parts, in older ones with 6 parts; the 3 dorsal pairs of arms are joined together by a broad velum; whereas the ventral pair is connected with the velum by its ventral protective membranes and the tentacles remain free; suckers on the arms and tentacles with denticulate rings.

H. bonelliana (Férussac) (Fig. 877), mainly in the Mediterranean Sea and Atlantic Ocean, although also in the Indian Ocean. *Histiopsis* Hoyle, 1885 (*atlantica* Hoyle) is a juvenile form.
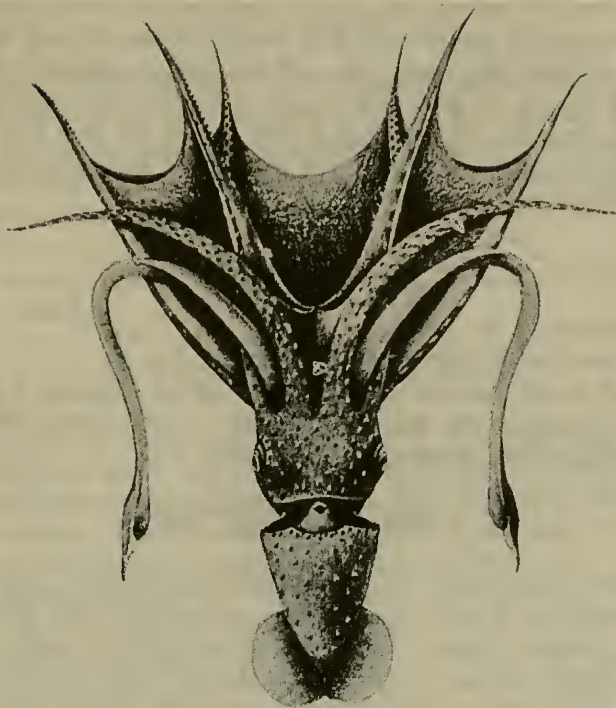
Fig. 877. *Histioteuthis bonelliana* (Férussac), in ventral view (about 1/6 nat. size) (after Pfeffer).

970   ? *Histiochromius* Pfeffer, 1912

The genus is based on a young animal described by Chun as *Brachioteuthis*; mantle calyx-shaped, distinctly longer than broad, posteriorly rounded, with terminal fin; head with large (different?) eyes; club of the tentacles with many suckers in several (up to 9) rows; without light organs.

H. chuni Pfeffer, in the Indian Ocean.

10. Family ALLUROTEUTHIDAE

Animal small; mantle fairly long, cylindrical, posteriorly with short papilla-shaped tip below the thin fin, which is posteriorly deeply indented and far surpasses the end of the body; head broader than the mantle, with large eyes; gladius anteriorly with narrow, free rachis; vane broad and thin, its posterior end downwardly inflected and forming a hole at the end; buccal membrane with 7 parts; funnel cartilage longish,

simple; arms fairly strong, with 2 rows of suckers with distally denticulate chitinous rings, the ventral arms with smaller suckers and near this with one row of small light organs, also with swimming membranes; tentacles short and thin, on the shaft with 2 rows of small suckers, on the carpal part with a quantity of very small suckers and on the club with 2 rows of large ones and on either side with one row of small suckers; radular plates without accessory cusps.

Alluroteuthis N. Odhner, 1923

Characters of the family.
A. antarctica N. Odhner, in the Antarctic Sea.
Based on the structure of the radula, Odhner considers it possible that the juvenile form described by me in 1921 under the name *Parateuthis tunicata* belongs to *Alluroteuthis*.

11. Family BATHYTEUTHIDAE

Animal small; mantle fairly short, with separated fins; gladius with broad, posteriorly roundish vane on the posterior half; eyes large; neck without distinct folds; funnel cartilage simple. with narrow groove; mantle cartilage longer, thread-shaped; arms short, with 2–4 rows of very small suckers; tentacular club with very numerous and small suckers.

Bathyteuthis Hoyle, 1885

Synonym *Benthoteuthis* Verrill, 1885.
Fin small, attached just before the posterior end of the mantle, with continuous musculature; head with enormously bulging eyes; arms attached externally far upward, the 3 upper pairs with strong supports of the protective membranes; ventral arms dorsally attached; the 3 upper pairs of arms each have a light organ on the basal part of their outer surface.
B. abyssicola Hoyle, in various seas.
Robson, 1921, described a small animal from the Indian Ocean, with a sack-shaped mantle, large eyes, and long thin tentacles, under the name *Chunoteuthis minima*, and placed it in this family; Grimpe in 1922 changed the genus name to *Indoteuthis* and considered the animal with doubt as a young *Bathyteuthis*.

Ctenopteryx Appellöf, 1889

Mantle dorsally flattened, with laterally attached fins, which in young animals occupy only the posterior part, in older animals the entire length, and are supported by comb-shaped muscle bundles; eyes only slightly bulging, laterally directed; arms externally not attached; protective membranes without supports; ventral arms ventrally attached; no light organs.

C. sicula (Verany), in the Mediterranean Sea and the neighboring Atlantic Ocean.

12. Family BRACHIOTEUTHIDAE

Mantle slender, posteriorly sharply pointed, with fairly large terminal fin; gladius with short vane, which posteriorly forms a pointed terminal cone; light organs seem to be absent; eyes large; neck folds weak; funnel cartilage simple, longish, with broad depression and narrow margins; mantle cartilage longer, ridge-shaped; buccal membrane with 7 supports, points, and attachments; arms with 2 sucker rows and with swimming and protective membranes, the 2 lateral pairs much stronger than the others; rings of the suckers in the distal half with broad, blunt teeth; tentacles strong, fairly long; club in distal half with 5 or 6 rows of larger suckers with pointed teeth, in the proximal half with very numerous and small suckers; an attachment apparatus absent.

Brachioteuthis Verrill, 1881

Synonyms *Tracheloteuthis* Steenstrup, 1882; *Verrilliola* Pfeffer, 1884; *Entomopsis* Rochebrune, 1884.

Characters of the family.

B. beanii Verrill. Few species, some of which are doubtful, in the Atlantic Ocean.

13. Family VALBYTEUTHIDAE

Mantle elongated calyx-shaped, posteriorly very pointed, with large roundish, nearly terminal fin; head with large, obliquely directed eyes; funnel large, interiorly with 3 strong glandular bulges; cartilaginous cusps elongated oval; no light organs; arms weak, the dorsal pair the shortest, with small suckers, the two lateral pairs largely with 2 rows of variably-sized suckers, the ventral pair soft, colorless, almost without musculature, on the proximal part with a row of 12 suckers becoming

gradually smaller; tentacles in the basal part with a pointed, proximally directed process, from which a brown chitinous longitudinal strip extends to the club, the weakly broadened club bears 4 rows of small, scarcely stalked suckers with large, dark, smooth rings, whereas the suckers on the arms are spherical, stalked, and furnished with denticulate rings.

Valbyteuthis Joubin, 1931

Characters of the family.
V. danae Joubin, in the Gulf of Panama.

14. Family OMMATOSTREPHIDAE

972
Mantle long and slender, posteriorly pointed, with large, in most cases triangular fins; gladius very thin; vane rudimentary, only at the posterior end forming a short cone; funnel depression in most cases with a system of folds which are longitudinally directed in the anterior part, this part (foveola) is posteriorly delimited by a half-moon-shaped transverse fold and there may be additional folds in the corners; funnel cartilage triangular; the furrow posteriorly broadened and separated from the posterior transverse furrow by a pair of strong tubercles; mantle cartilage T-shaped; eyes not projecting; neck with strong folds; buccal membrane with 7 points, in most cases separated from the arms by a ring-shaped space, joined with the tentacles by a membranous bridge; arms fairly strong, with 2 rows of suckers; tentacular club in the center with larger, in the terminal part with smaller suckers, on the carpal part in most cases with an attachment apparatus consisting of suckers and knobs; one ventral arm or both hectocotylized; the 3 median radular plates with outer cusps (Fig. 878); in young animals (*Rhynchoteuthis* Chun, 1903, non Orbigny, 1847 = *Rhynchoteuthion* Pfeffer, 1908) the tentacles are fused together to form a hollow proboscis; light organs developed only in *Hyaloteuthis* and one *Ommatostrephes* and one *Symplectoteuthis* species.
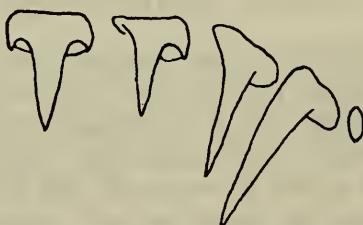
Fig. 878. A half radular row of *Illex coindeti* (Vérany)
(after Naef).

A. Subfamily Illicinae

Folds in the funnel depression indistinct; furrow of the funnel cartilage and longitudinal ridge of the mantle cartilage straight; an open pore between the buccal membrane and the attachment of the 2nd arms; attachment apparatus of the tentacles indistinctly developed; gladius weak, brownish yellow.

Illex Steenstrup, 1880

Distal part of the tentacular club with 8 rows of suckers; large rings of the lateral arms distally with crenellated teeth, proximally with a high ridge, in the ♂ the suckers are enlarged; right or left ventral arm hectocotylized; the large median suckers of the tentacular club with rings having entire margins or ringed with crenelle-like incisions.

I. illecebrosus (Lesueur), in the Mediterranean Sea and Atlantic Ocean. Pfeffer does not consider *I. coindeti* (Verany) as a separate species.

Todaropsis Girard, 1890

Distal part of the tentacular club with 4 rows of suckers; large rings of the lateral arms with pointed teeth distally, proximally with a low major ridge; both ventral arms hectocotylized; the large median suckers of the tentacular club ringed with pointed teeth which are separated from one another.

T. eblanae (Ball), in the Mediterranean Sea and Atlantic Ocean.

B. Subfamily Ommatostrephinae

Funnel depression with foveola, half-moon-shaped pocket, and longitudinal folds, without lateral pockets; cartilage similar to that in Illicinae; buccal membrane joined with the base of the 2nd arms by a thin membrane, without pore; attachment apparatus of the tentaacles incomplete, with denticulate small suckers; large suckers of the club without cross-teeth.

973

Nototodarus Pfeffer, 1912

Large suckers of the lateral arms with pointed triangular teeth distally, high edge of the proximal side with few broad crenellated teeth.

N. insignis (Gould), near New Zealand.

Ommatostrephes Orbigny, 1839 (*Ommastrephes*)

Synonyms *Todarodes* Steenstrup, 1880; *Martialia* Rochebrune & Mabille, 1889.

Large suckers of the lateral arms with slender cone-shaped teeth distally, proximally with smooth margin which is outwardly reflected; large suckers on the median part of the tentacular club ringed with slender teeth separated from one another, between which low crenellated teeth may be present.

O. sagittatus (Lamarck). Few species, in the Atlantic and Pacific Oceans.

Okada, 1927, erected the genus *Ornithoteuthis* for *O. volatilis* Sasaki, which has an elliptical light organ on the rectum; it may be considered as a subgenus or section of *Ommatostrephes*.

C. Subfamily Sthenoteuthinae

Funnel depression also with lateral pockets; buccal membrane as in Ommatostrephinae; depression of the funnel cartilage anteriorly buckled; rings of the largest suckers on the lateral arms denticulated all-around, the farther distally-situated suckers smooth on the proximal side, outwardly reflected; large suckers of the tentacular club with 4 larger teeth arranged crosswise; attachment apparatus well developed, with smooth-ringed suckers and knobs; right ventral arm hectocotylized.

Hyaloteuthis Gray, 1849

On the ventral side of the mantle are 19 regularly arranged, roundish light organs situated in pits and one pair on the lower side of the head; funnel and mantle cartilages not fused with one another, similar to those in Illicinae, 2nd arms with 1 or 2 considerably enlarged suckers somewhat below the center; the rings of the arm suckers with alternately large and small teeth on the distal side; rings of the largest tentacular suckers smooth, a few smaller suckers with unequal teeth; carpal part with a single adhesive knob.

H. pelagica (Bosc), in the Atlantic and Pacific Oceans.

Sthenoteuthis Verrill, 1880

Locking cartilages of the funnel and mantle not fused with one another; arms not elongated whip-shaped, with about 50 pairs of suckers;

ventral protective membrane of the 3rd pair of arms very broad; supports of the protective membranes not free lobe- or palp-shaped.

S. pteropus (Steenstrup) = *megaptera* (Verrill). Few species, in the Atlantic Ocean and Mediterranean Sea.

Dosidicus Steenstrup, 1857

Animal very large. Locking cartilages not fused with one another; ends of the arms elongated whip-shaped, with over 200 pairs of small suckers; ventral protective membrane of the 3rd pair of arms about as broad as the arm; supports of the remaining protective membranes in the proximal half in most cases produced into free, lobe- or palp-shaped tips.

974   *D. eschrichti* Steenstrup, probably *gigas* (Orbigny), in the southern Pacific Ocean.

Symplectoteuthis Pfeffer, 1900

Locking cartilages of the funnel and mantle firmly fused with one another at the boundary of the longitudinal and transverse furrow; arms not elongated whip-shaped; ventral protective membrane of the 3rd arms as broad as the arm; left ventral arm hectocotylized; carpal part of the tentacles with 2–4 adhesive knobs.

S. oualaniensis (Lesson). 2 species, in the Pacific and Indian Oceans.

S. luminosa Sasaki has pale bands on the lower side of the mantle, the head, and the ventral arms, which Okada considered as light organs without pigment; Berry, 1916, erected the genus *Eucleoteuthis* for this species.

15. Family THYSANOTEUTHIDAE

Mantle long and moderately broad, with long lateral fins which are obtusely angled anterior to the center; gladius posteriorly pointed, without terminal cone; vane anteriorly gradually broadened and anteriorly produced wing-shaped; free rachis short; funnel depression without folds; neck with transverse and longitudinal folds; buccal membrane with 7 points; longitudinal furrow of the funnel cartilage in the center strongly broadened unilaterally; mantle cartilage with a thick transverse ridge; arms with broad protective membranes having thread-shaped muscular supports and with 2 rows of small denticulate suckers; left ventral arm hectocotylized; tentacular club with 4 sucker rows, behind which there are 2 rows of alternating suckers and knobs; no light organs.

Thysanoteuthis Troschel, 1857

Characters of the family.

T. rhombus Troschel, in the Mediterranean Sea and northern Pacific Ocean. According to Sasaki, *T. nuchalis* Pfeffer is not different from *rhombus*.

? *Cirrobrachium* Hoyle, 1904

From one animal only the head with the arms is known; these have smooth-margined suckers in 2 rows and more or less long threads, which probably represent muscular supports of protective membranes.

C. filiferum Hoyle, in the equatorial Pacific Ocean.

16. Family CHIROTEUTHIDAE

Mantle slender calyx-shaped, posteriorly more or less greatly elongated and sometimes far surpassing the roundish fin; gladius narrow; vane weak, forming a long terminal cone; light organs are often developed; eyes large, more or less projecting; an olfactory tubercle present on either side; neck without folds; funnel cartilage oval or ear-shaped, sometimes with 1 or 2 strong tubercles; mantle cartilage nose-shaped; arms fairly long, with 2 sucker rows, the ventral pair the largest; tentacles long, without attachment organ, on the outer side with a few luminous glandular knobs; club with 4, 8, or many sucker rows.

A. Subfamily Chiroteuthinae

Tentacular club with 4–8 sucker rows; light organs on the eyes, on the ink sack, and in one row on the ventral arms.

975   *Chiroteuthis* Orbigny, 1839

Characters of the family.

Pfeffer has recognized a number of groups as subgenera, some of them known only from juvenile forms, whose relationships to mature forms are uncertain.

Doratopsis Rochebrune, 1884 (synonyms *Hyaloteuthis* Pfeffer, 1884, non Gray, 1849; *Toroteuthis* Tomlin, 1931). Eyes circular, without ventral process; tentacular club with a proximal part with small suckers increasingly differentiated from a distal part with larger rings. *C. (D.) vermicularis* (Rüppell).—*Planctoteuthis* Pfeffer, 1912. Eyes in most

976 cases oval, with a ventral process; suckers of the tentacular club not distinctly different. *C. (P.) exophthalmica* (Chun).—*Tankaia* Sasaki, 1929. Mantle posteriorly with thread-shaped process, attached to which is kidney-shaped fin; anterior part of body long; eyes roundish, without process; tentacular club with many (about 150) small suckers in several rows. *C. (T.) borealis* Sasaki, near Japan. ? *Diaphanoteuthis* Tomlin, 1931 (synonym *Leptoteuthis* Verrill, 1884, non H.V. Meyer, 1834). Fin leaf-shaped, longer than broad; anterior part of body half as long as the mantle; tentacular club with about 4 rows of small suckers. *C. (D.) diaphana* (Verrill), in the northern Atlantic Ocean.—*Chiridioteuthis* Pfeffer, 1912. Mantle posteriorly stalk-shaped with oval fin; rings of the arm suckers distally with high, proximally with low teeth; suckers of the tentacular club with thin stalks, distally with high teeth, proximally smooth. *C. (C.) pellucida* Goodrich, in the Indian Ocean.

Subgenus *Chiroteuthis* s. s. Mantle end posteriorly thin, without spindle-shaped swelling; ventral arms very large; stalks of the suckers of the tentacular club with a broad basal pillar, the latter at the end with a thickened or fluted knob from which a thin stalk arises; about 100 suckers on each club; arm suckers distally with crenellated teeth, proximally smooth. *C. (C.) veranyi* (Férussac) (Fig. 879), in the Mediterranean Sea and Atlantic Ocean.

Subgenus *Chirothauma* Chun, 1910. Mantle end posteriorly swollen spindle-shaped, with a narrow membrane which is not continuous with the roundish fin; stalks of the tentacular suckers at the base somewhat thickened or with a triangular process in the center; about 300 suckers on each club; arm suckers similar to those in *Chiroteuthis* s. s. or distally with pointed, proximally with blunt teeth. *C. (C.) imperator* Chun. Few species, in the Pacific and Indian Oceans.

? *Chirosoma* Joubin, 1912

Arms and tentacles with 4 rows of small suckers. So far insufficiently described. According to Joubin, it has to be placed in a separate subfamily.

C. regnardi Joubin, in the Atlantic deep sea (4000 m).

? *Chiroteuthoides* Berry, 1920

Mantle posteriorly produced thread-shaped, with posteriorly indented fin, probably also with a posterior membrane; arms with 2 sucker rows, the ventral ones the largest, the third very short; tentacular club unknown; no light organs.

C. hastula Berry, in the northern Atlantic Ocean.
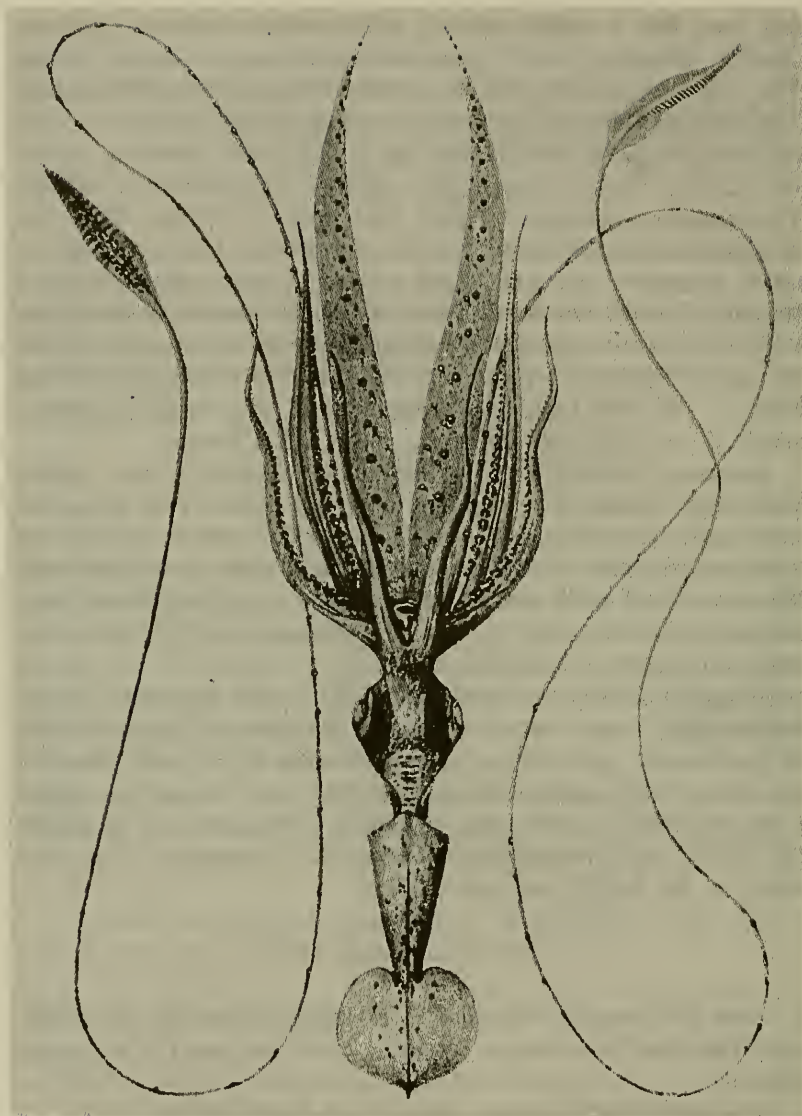
Fig. 879. *Chiroteuthis veranyi* (Férussac), in dorsal view
(after Pfeffer).

B. Subfamily Mastigoteuthinae

Tentacular club with numerous sucker rows; distinctly developed light organs absent.

Mastigoteuthis Verrill, 1881

Synonyms *Chiroteuthopsis* Pfeffer, 1900; *Idioteuthis* Sasaki, 1916 = *Iridioteuthis* Sasaki, 1929.

Mantle more or less elongated pointed, with large roundish or rhombic fin; head broad; eyes large, anteriorly indented; olfactory tubercles short-stalked; tentacular suckers small, in 10–30 rows.

M. agassizii Verrill. A few species, in the northern Atlantic and Pacific Oceans.

Grimpe, 1922, erected a subgenus *Mastigopsis* for *M. hjorti* Chun.

977

? *Valdemaria* Joubin, 1931

Mantle very slender cylindrical, posteriorly pointed and produced into a long thread; the roundish fin attached at the end of the mantle and the beginning of the thread; head narrow, with roundish projecting eyes; arms long, the ventral ones the shortest, the 2nd the longest; suckers small, long-stalked, distally with pointed teeth, on the ventral arms in 1–2 rows, on the 3rd arms in 6, on the remaining ones in 4 rows; tentacles thin; club with several (6–8) rows of very small suckers.

V. danae Joubin, in the northern Atlantic Ocean.

C. Subfamily Grimalditeuthinae

Mantle slender, posteriorly greatly produced, with a fin-like membranous web posterior to the transversely oval fin; gladius in the region of the fin steeply arched roof-like, with a narrow, unclosed terminal cone; funnel very large, without locking cartilage, but fused with the mantle; neck without folds; arms fairly large, with 2 sucker rows; the ventral arms small; tentacles reduced.

Grimalditeuthis Joubin, 1898

Characters of the subfamily.

G. bonplandi (Verany), in the northern Atlantic Ocean.

According to Grimpe, *Enoptroteuthis* Berry, 1920 (*spinicauda* Berry),

is perhaps a juvenile form of *Grimalditeuthis*; the eyes are stalked, the mouth part is elongated; tentacles with a small club which bears few suckers in 2 rows.

17. Family JOUBINITEUTHIDAE

Mantle broader than the head, at the end with a roundish fin; without light organs; head fairly long and narrow; arms thin, with very small stalked suckers, which in the center of the arms are arranged in 6 rows; the ventral arms are about as long as the mantle, the others considerably longer, up to four times as long.

Joubiniteuthis Berry, 1920

Characters of the family.
J. portieri (Joubin), in the northern Atlantic Ocean.

18. Family CRANCHIIDAE

Mantle dorsally fused with the dorsum and ventrally with the funnel in 3 bands; the musculus depressor infundibuli expands into a thin lamella, which approaches the sides of the mantle and the ventral margin of the musculus collaris and divides the mantle cavity into 3 chambers; mantle in most cases transparent, gelatinous or membranous, slender or swollen, often produced into a pointed tip; fins short and roundish or long and narrow; the gladius anteriorly forms a small plate, posteriorly a lanceola, which is either directed straight posteriorly or is curved ventrally; eyes sessile or stalked, with light organs on the ventral side of the eye ball; funnel large, without valve; buccal membrane with 7 pillars and attachments; arms in most cases short and weak, with 2 rows of suckers; one ventral arm hectocotylized; tentacles in most cases strong, with weak club, sometimes reduced; some of the suckers only in *Galiteuthis* modified into hooks.

978

A. Subfamily Cranchiinae

A row of light organs on the ventral margin of the eye ball, sometimes a few also close to the pupillary margin; mantle beset with star-shaped tubercles or proceeding from the points of fusion, with one or more cartilaginous ridges with a row of small warts.

Leachia Lesueur, 1821

Synonyms *Perothis* Rathke, 1833; *Dyctydiopsis* Rochebrune, 1884.
Mantle ventrally on either side with a cartilaginous ridge with small star-shaped warts; fins terminal; anterior and posterior half of the lanceola slender and produced into a greatly pointed tip, with straight axis; eyes large, projecting vesicle-like; head short and thick, between the ventral row of light organs and the pupillary margin also with one or more light organs; tentacles torn off.

L. cyclura Lesueur. Few species, in various seas.

Pyrgopsis Rochebrune, 1884

Synonyms *Zygaenopsis* Rochebrune, 1884, non Felder, 1874; *Zygocranchia* Hoyle, 1909; *Euzygaena* Chun, 1910.
Eyes small, long-stalked; head long and slender, with only one ventral row of light organs beside the ridge-shaped margin of the eye ball; median suckers of the tentacular club larger than the marginal suckers, their rings ringed with pointed denticles; the other characters as in *Leachia*—perhaps a juvenile form.

P. rhynchophora Rochebrune, probably = *zygaena* (Verany). Few species, in various seas.

Drechselia Joubin, 1931

Mantle slender cone-shaped, posteriorly gradually pointed, anteriorly with 2 ventral cartilaginous ridges, posteriorly with large transversely oval fin; funnel in ♀ larger than in ♂, internally with a strong mucous gland; head short and thick; eyes large, externally flattened, lens and margin projecting, on the bulging lower side with a group of 6 light organs, on the margin and between it and the lens with another group of 6 organs, in addition another row of very small yellow organs lying above the lens; gladius narrow, strong, anteriorly and posteriorly only slightly broadened; terminal cone very long and pointed; arms strong, the 3rd pair in the ♀ considerably longer than the dorsal and ventral ones, with 2 rows of roundish short-stalked suckers, whose horny rings distally have 3 teeth, the central of which in the ♀ is much larger than the other 2; in the ♂ the right ventral arm is hectocotylized, it forms a peculiarly twisted expansion; tentacles in the ♂ distinctly thickened at the base, thereafter thin, in the ♀ as broad as the arms without proximal thickening; club narrow, with a few shallow pits, although without suckers.

D. danae Joubin, in the Pacific Ocean near Panama.

Liocranchia Pfeffer, 1884

Mantle with small fins which freely surpass the posterior end of lanceola, anterior half of the lanceola long and pointed, posterior half greatly shortened; the dorsal axis of the mantle continues into the median axis of the fin, whereas the posterior end of the mantle and ʒ⸲ lius is curved ventrally; head short and thick, eyes spherical, sessile, with 4 equally-large light organs; mantle with 4 ventral cartilaginous ridges.

L. reinhardti (Steenstrup). Few species, in various seas.

Cranchia Leach, 1817

Mantle and dorsal surface of the fins with densely placed star-shaped tubercles; eyes with 12 light organs below the pupil and 2 above it; otherwise similar to *Liocranchia*.

C. scabra Leach (Fig. 880), in various seas.

Fig. 880. *Cranchia scabra* Leach, in dorsal view
(after Chun).

Liguriella Issel, 1908

Mantle with a dorsal row of sawtooth-shaped tubercles on a ridge, although without ventral cartilaginous ridges; lanceola short rhombic with greatly shortened anterior and posterior halves; the mantle posterior to the end of the lanceola continues considerably toward the posterior in form of an obtuse bulge, so that the small fins are separated from one another, attaching infraterminally; cephalic pillars distinct; eyes stalked.

L. podophthalma Issel, in the northern Atlantic Ocean.

B. Subfamily Taoniinae

On the ventral side of the eye ball with only one round or 1 half-moon-shaped light organs concentrically embracing each other; mantle without cartilaginous ridges, which at the most may be indicated at the points of fusion; anterior and posterior halves of the lanceola slender and pointed in mature animals; dorsal axis of the mantle coinciding with that of the visceral sack and of the fin.

Phasmatopsis Rochebrune, 1884

Mantle membranous, slender, cone-shaped, gradually narrowing into a long, sharp tip; fin long, broadly lanceolate with greatly elongate point, terminal, attached completely at the sides of the mantle; vane of the gladius as long as the fin; head broad; eyes on thick, short barrel-shaped stalks; larger rings of the arm suckers with crenellated teeth; tentacles torn off.

P. cymoctopus Rochebrune, in the Atlantic Ocean near Madeira.

Toxeuma Chun, 1906

Fins long and narrow, anteriorly considerably surpassing the greatest width of the lanceola, posteriorly not reaching the needle-shaped pointed tip; head long and slender; eyes cone-shaped with broad, moderately long stalks; arms small; tentacles with swimming membrane and narrow club; suckers differing only slightly.

T. belone Chun, in the Indian Ocean (probably a juvenile stage).

Anomalocranchia Robson, 1924

Mantle muscular, without fins and cartilaginous ridges; the gladius only slightly surpassing the posterior end; eyes large, on short, thick

stalks; arm suckers toothless, some of those on the tentacles denticulate, some smooth; funnel very large.

A. impennis Robson, near South Africa.

Taonius Steenstrup, 1861

Synonym *Desmoteuthis* Verrill, 1881.

Body gelatinous, strongly colored, with a tail thread; fin anteriorly extending beyond the greatest breadth of the lanceola; head short and thick, with very large, nearly spherical, bulging eyes; funnel fairly large; gladius with narrow rachis and broad, lanceolate vane, whose posterior half is inrolled and forms a long, slender terminal cone; arms short, with variably-sized, in most cases weakly denticulate suckers; tentacles torn off.

T. pavo (Lesueur), in the Atlantic and Pacific Oceans.

Verrilliteuthis Berry, 1916

Mantle membranous, spindle-shaped, very gradually narrowed posteriorly; fins long, attached on the lateral edges of the mantle; lanceola anteriorly and posteriorly elongated pointed, very broad; eyes very large, nearly spherical, unstalked; suckers on the distal half of the two lateral pairs of arms especially large, with smooth or somewhat incised rings; tentacles with thick shaft and distinct club, with 4 rows of suckers, whose rings all around have pointed teeth; carpal part and distal half of the shaft with small denticulate suckers and knobs.

V. hyperborea (Steenstrup), in the northwestern Atlantic Ocean.

Megalocranchia Pfeffer, 1884

Mantle calyx-shaped, posteriorly thinning fairly rapidly and forming a narrow, pointed cone; fin fairly large, oval, terminal, attached on the dorsum; lanceola posteriorly slender, anteriorly with a very short rhombic expansion; eyes very large, unstalked; arms with very strong protective membranes supported by cross bridges and 2 rows of suckers, the rings of which have blunt teeth; tentacles moderately strong; club with distinct protective membranes and a swimming membrane and with 4 rows of suckers, the rings of which have pointed denticles, proximally they merge into 2 rows of small suckers.

M. maxima Pfeffer. Few species, in various seas.

Leucocranchia Joubin, 1912

Body large, with strong tubercles between the fins; below each eye with a very large light organ.

L. pfefferi Joubin, in the Atlantic deep sea (4000 m). So far insufficiently described.

Taonidium Pfeffer, 1900

Mantle calyx-shaped, posteriorly with short, very slender tip; fin terminating at the posterior end of the mantle or slightly surpassed by it; head slender; eyes stalked; no light organ on the ink-sack; tentacular club with 4 rows of suckers, the median of which are larger than the marginals.

T. suhmii (Hoyle). Few, more or less doubtful species from various seas.

? *Phasmatoteuthion* Pfeffer, 1912

Body gelatinous; mantle slender; gladius with very long and slender cone-vane; head slender; eyes with thick stalks and vesicle-shaped light organ; median suckers of the tentacular club many times larger than the marginals, on the distal part of the stalk with few pairs of small suckers.

981   *P. richardi* (Joubin), near Europe insufficiently known, presumably juvenile form.

Galiteuthis Joubin, 1898

Mantle slender, half-spindle-shaped, produced into an elongated tip, which projects beyond the large, broad lanceolate fin; head short, with large eyes; arms short, with membranes; suckers with smooth rings; tentacles strong; shaft distally with 2 rows of numerous alternating suckers and adhesive knobs, which form a small group on the carpal part; club in juveniles with 4 rows of suckers, the lateral of which later disappear, whereas the suckers of the 2 median rows are modified into hooks.

G. armata Joubin (Fig. 881), in the Mediterranean Sea and Atlantic Ocean, as well as in the northern Pacific Ocean.

Crystalloteuthis Chun, 1906

Mantle spindle-shaped, posteriorly pointed, with a few branched tubercles at the points of fusion; fins small, terminal; eyes on thick stalks, with 2 ventral half-moon-shaped light organs; arms small, with 2 rows of suckers; tentacles strong, on the shaft with 2, on the club with 4 rows of suckers.
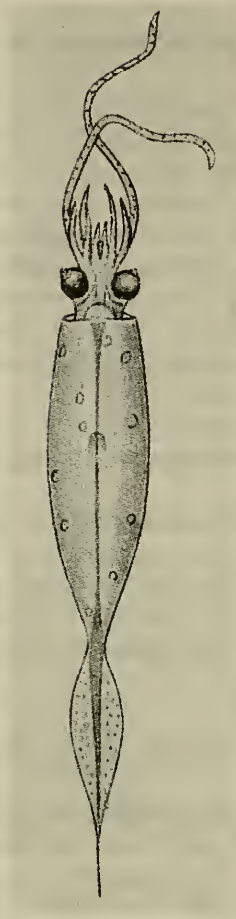
Fig. 881. *Galiteuthis armata* Joubin, in dorsal view, 2/3 nat. size (after Chun).

C. glacialis Chun, in the Antarctic Ocean and one species (*behringiana* Sasaki) in the northern Pacific Ocean.

Corynomma Chun, 1906

Mantle elongated calyx-shaped, in the adult condition probably long and produced into a tip with moderately large fin; head broad, anteriorly thinned pyramid-shaped, with fairly long pillar and long, slender eye stalks; eye small with a large ventral light organ; 2 ventral light organs on the ink-sack; rings of the arm suckers scarcely denticulate; tentacles long and strong; club with swimming membrane, median suckers larger than the marginals, distally with denticles.

C. speculator Chun, in warm seas (Atlantic and Indian Oceans).

Hensenioteuthis Pfeffer, 1900

Mantle membranous, calyx- or cylinder-shaped, in most cases posteriorly gradually pointed; extreme tip ventral to the fin more or less distinctly deflected from the long axis of the dorsal surface of the mantle; fin small, terminal; cephalic pillars in most cases short and broad; eyes stalked, with a round light organ; funnel very large; arms short; tentacles with only slightly broadened club.

Subgenus *Teuthowenia* Chun, 1910 (synonym *Owenia* Prosch, 1847, non Chiaje, 1844). Fins very small, spatula-shaped, attached at the posterior end of the midline of the mantle dorsum; beak-shaped process of the eye moderately large, with large light organ extending to the margin of the iris. *H. (T.) megalops* (Prosch). Few species, in various seas.

982   Subgenus *Hensenioteuthis* s. s. Differing from *Teuthowenia* in having larger arms and stronger tentacles; process of the eye stronger; gladius broader. *H. (H.) joubini* (Pfeffer), in the Atlantic Ocean.

Subgenus *Helioocranchia* Massy, 1907. Fin larger than in *Teuthowenia*, somewhat quadrangular, attached with the inner anterior corner of the lanceola, extending beyond its posterior end, here attached in the midline by a connecting line; mantle posteriorly very gradually thinned, without its tip curving ventrally; process of the eye large; arms well developed, the 3rd the longest; tentacles long and strong. *H. (H.) pfefferi* (Massy), in the northern Atlantic Ocean.

Subgenus *Ascoteuthis* Berry, 1920. Fins larger, nearly half-circle-shaped; mantle thick spindle-shaped, posteriorly with sharp tip which somewhat surpasses the fins; head with thick snout; eyes with thick stalks; the 2 ventral arm pairs larger than the 2 dorsal pairs, with small suckers; tentacles long; club with 4 rows of very small suckers. *H. (A.) corona* (Berry), in the western Atlantic Ocean. Beak-shaped processes of the eyes have neither been figured nor described; the group may have the rank of a genus.

Sandalops Chun, 1906

Mantle more or less calyx-shaped, posteriorly pointed; fins small, not completely terminal, in most cases distinctly separated from one another; eyes with long stalks and large, ventrally directed, beak-shaped processes, each bearing a small light organ; arms small; tentacles long; club scarcely broadened, with 4 rows of suckers; shaft with 2 rows, which extend to the center or to the base.

S. melancholica Chun. Few species, some of which are doubtful, in the Atlantic Ocean.

Bathothauma Chun, 1906

Mantle long, bell-shaped, posteriorly rounded, with roundish short-stalked fins widely separated from one another, close to the posterior end; gladius consisting of a narrow longitudinal band and a posterior transverse buckle situated between the fins bases, which are joined by a connective tissue band; funnel broad and short; cephalic pillars long and thin; eyes with very long stalks; with a large light organ below a short lobe; arms small and weak, the 3rd pair the longest; tentacles long and moderately strong; club scarcely broadened, triangular in cross-section, with 4 rows of stalked, bowl-shaped suckers; shaft with 2 rows of suckers.

B. lyromma Chun (Fig. 882), in the Atlantic Ocean.

983   Because of the peculiar gladius, Grimpe assumed a separate family for this genus.

Joubin, 1920, described a young animal under the name *Fusocranchia alpha*, which according to him may belong to *Bathothauma*.

II. Order OCTOPODA

Body more or less short, sack-shaped, with or without fins; internal shell rudimentary or completely reduced; light organs are seldom developed; mantle at the dorsum nearly always fused with the body; the head bears 8 arms, in most cases differing only slightly in length, which are connected with one another by a more or less broad membrane; tentacles absent; suckers in most cases unstalked, radially organized, almost always arranged in 1 or 2 longitudinal rows; funnel in most cases without valve; often a third arm is hectocotylized; body cavity narrowed and pericardium reduced, in most cases 2 oviducts are developed; penis with a blind sack.

Suborder CIRRATA

Mantle in most cases with one pair, seldom with 2 pairs of fins; a shell rudiment is retained as a variably-formed fin support; arms more or less large, only slightly different in length, with very extensive velar membrane, each with a row of fairly weak suckers and in addition 2 rows of cirri, without distinct hectocotylus; radula often reduced; a right oviduct, an ink sack, and an intestinal sinus absent.

Fig. 882. *Bathothauma lyromma* Chun, in dorsal view, about 2/3 nat. size (after Chun).

I. STIRPS VAMPYROTEUTHACEA

Mantle with wide ventral opening, sometimes with a locking appa-ratus similar to that in decapods, with one or 2 pairs of fins; arms with one row of suckers and in addition paired cirri, sometimes between the 1st and 2nd arms with a thread-shaped contractile process in a depression of the velar membrane; funnel with a valve; radula well developed. Inhabitants of the deep sea.

1. Family VAMPYROTEUTHIDAE

Body fairly small; suckers developed only on the distal part of the arms; cirri distinct; central plate of the radula with one point (Fig. 883).

983   Fig. 883. Radular row of *Vampyroteuthis infernalis* Chun.
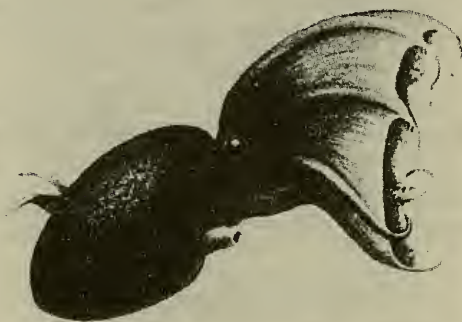
Fig. 884 *Vampyroteuthis infernalis* Chun (the narrow posterior fins are not shown here) (after Chun).

Vampyroteuthis Chun, 1903

Mantle with 2 pairs of narrow fins, which are close to the posterior end 984   and the dorsum; one pair of light organs at the base of the fins; gladius thin and transparent, in the form of a fairly narrow lamella, anteriorly shortly pointed, posteriorly gradually narrowed; arms with few small suckers on the distal part; a thread-shaped process on the velum absent.
V. infernalis Chun (Fig. 884), in the Atlantic Ocean.

Melanoteuthis Joubin, 1912

Mantle broad and short, with a pair of fairly large fins; a thread-shaped process between the 1st and 2nd arms; light organs on the head and one pair at the bases of the fins; without distinct constriction anterior to the base of the mantle; the gladius appears to be a saddle-shaped

plate, broader than long; radular plates with short, fairly broad bases and sharp tips; funnel without locking apparatus; the suckers begin in most cases at the velar margin, the cirri in about the center between it and the mouth.

M. lucens Joubin.   A few species, in warm seas.

Danateuthis Joubin, 1929

Similar to *Melanoteuthis* with a pair of fins and a thread-shaped process; small scattered light organs (?) and a pair of groups of densely aggregated white granulations; funnel with locking apparatus and valve; arm suckers stalked, the cirri extending beyond two-thirds of the distance of the velar margin from the mouth.

D. schmidti Joubin, in the Gulf of Mexico.

Retroteuthis Joubin, 1929

The arms are directed not anteriorly but toward the dorsum; funnel very large, with locking apparatus and triangular valve; mantle with one pair of fins; posterior to the bases is a pair of light organs; suckers in part sessile, in part stalked; small thread-shaped processes present.

R. pacifica Joubin, in the Gulf of Panama.

Hansenoteuthis Joubin, 1929

Mantle with 2 pairs of narrow fins; one pair of light organs at the bases of the posterior pair; one pair of fairly short processes between the 1st and 2nd arms; funnel with locking appartus.

H. lucens Joubin, near the West Indian islands.

Watasella Sasaki, 1920

Mantle with 2 pairs of fins, without light organs; one pair of thread-shaped processes present; eyes only slightly projecting; funnel with small half-moon-shaped valve, without locking appartus; arm suckers stalked.

W. nigra Sasaki, near Japan.

Hymenoteuthis Thiele, 1916

Mantle with one pair of large, fairly narrow fins, which are attached somewhat laterally; gladius more or less saddle-shaped; light organs absent; thread-shaped processes on the very broad velum and a locking

apparatus on the funnel also absent; cirri from the mouth to the arm tips; central plate of the radula distinctly smaller than the neighboring plates, the outer ones with long and narrow points; a small scale-shaped marginal plate present; eyes greatly projecting, the left one larger; funnel largely fused with the head, without valve (?).

H. macrope (Berry), near California.

2. Family LAETMOTEUTHIDAE

Arms with suckers to the mouth, although without (?) cirri; radula very large; central plate large, tricuspid; body large, posteriorly rounded, on either side with a small fin; arms fairly long, with broad velum.

Laetmoteuthis Berry, 1913

Characters of the family.

L. lugubris Berry, in the Pacific Ocean, near the Hawaiian Islands. So far insufficiently known.

II. STIRPS CIRROTEUTHACEA

Mantle with narrow ventral opening, sometimes even fused with the funnel, with one pair of fins; without thread-shaped processes on the velum, without light organs and without ink sack; the radula is reduced; shell rudiment cartilaginous, saddle or buckle-shaped.

1. Family STAUROTEUTHIDAE

Arms moderately long, in most cases with simple velum; shell cartilage buckle-shaped.

Cirroctopus Naef, 1923

Synonym *Grimpoteuthis* Robson, 1932.

Velum simple; cirri only slightly longer than the diameter of the largest suckers; fins in most cases shorter than the width of the head.

C. mawsoni (Berry). A few species, in various seas.

Stauroteuthis Verrill, 1879

Arms joined with the velum by secondary membranes; shell cartilage V-shaped; body long; fins small, attached in the center; cirri large.

S. syrtensis Verrill, in the western Atlantic Ocean.

Chunioteuthis Grimpe, 1916

Body broad and short; mantle margin fused with the funnel; arms with secondary velar membranes; cirri at least twice as long as the width of the suckers; fins about half as long as the width of the head.

C. ebersbachii Grimpe, in the northerwestern Atlantic Ocean, and one species [*gilchristi* (Robson)] near South Africa.

2. Family CIRROTEUTHIDAE

Arms long, with secondary velar membranes; cirri in most cases longer than the diameter of the suckers; body longish'; fins in most cases longer than the width of the head; shell cartilage saddle-shaped; fore-gut crop-shaped.

Cirroteuthis Eschricht, 1938

Synonym *Epulo* Gistel, 1949.
Characters of the family.
C. mulleri Eschricht. A few species, in various seas.
Subgenus *Cirroteuthopsis* Grimpe, 1920, differs in having the cirri placed not between but beside the suckers. *C. (C.) massyae* Grimpe.

986

? *Froekenia* Hoyle, 1904

Arms very long, without velum (?); shell cartilage nearly half-circle-shaped; body oval; fins somewhat longer than the width of the mantle.
F. clara Hoyle, near Panama.

? *Cirrothauma* Chun, 1911

Body gelatinous, posteriorly pointed, with large fins attached fairly far forward; arms long and strong, with broad velum; suckers peculiarly spindle-shaped; eyes reduced.
C. murrayi Chun (Fig. 885), in the northern Atlantic Ocean.

987

3. Family OPISTHOTEUTHIDAE

Posterior body developed only as a fairly flat hump with a pair of small fins; mantle opening small, surrounding the funnel; shell cartilage
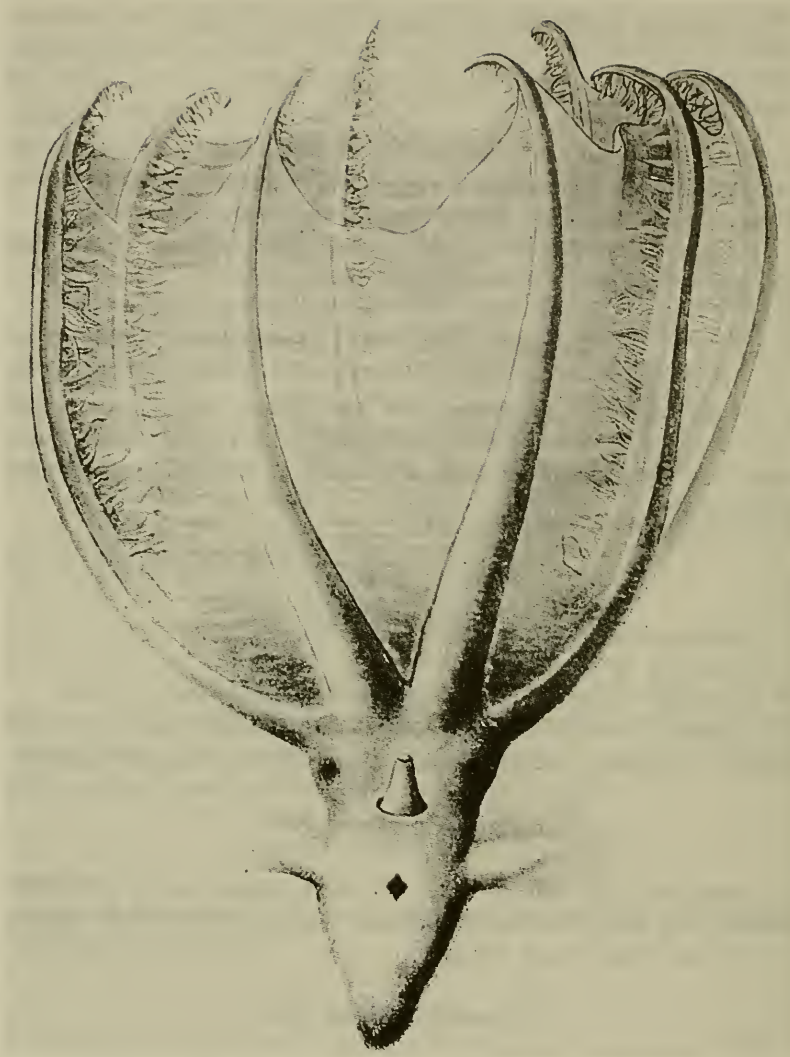
Fig. 885. *Cirrothauma murrayi* Chun, in ventral view
(after Chun).

buckle-shaped, slightly curved; arms largely connected by the large velum; a radula absent.

Opisthoteuthis Verrill, 1883

Characters of the family.

O. agassizii Verrill. A few species, in various seas (Fig. 886).

The named species is stated to differ from the remaining in that the shell cartilage consists of 2 halves (?); for this reason Berry, 1918, has separated the other species as subgenus *Teuthidiscus*. (*O.* (*T.*) *pluto* Berry).
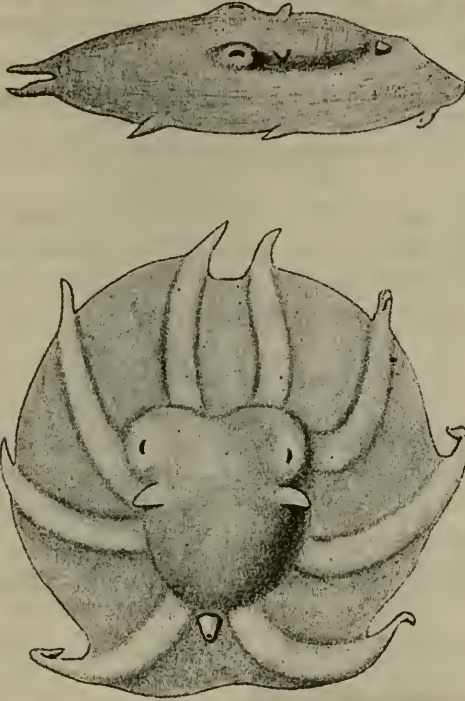
Fig. 886. *Opisthoteuthis depressa* Ijima & Ikeda, in lateral and dorsal view, about 3/5 nat. size (after Ijima & Ikeda and after Meyer).

Suborder INCIRRATA

Mantle without fins, as a rule without shell rudiment; arms more or less long, in most cases with 1 or 2 rows of suckers, without cirri; one arm in most cases hectocotylized in the ♂; funnel without valve; radula well developed; both oviducts retained.

I. STIRPS BOLITAENACEA

Body very soft and gelatinous, without distinct cartilage; arms differing in length, with thin, more or less broad velar membrane, and with one row of suckers; jaw soft; radular plates as a rule with greatly broadened bases (Fig. 887); eye cavity open.

Fig. 887. Left half of a radular row of *Bolitaena* (*Eledonella*) *pygmaea* Verrill.

1. Family BOLITAENIDAE

Arms fairly short, with moderately broad velum; eyes roundish, laterally directed; mantle widely open, not fused with the funnel; funnel organ Λ-shaped; central plate of the radula on either side with 2 or 3 accessory cusps, the 2 intermediate plate pairs in most cases with 4 teeth.

Japetella Hoyle, 1885

Synonyms *Chunella* Sasaki, 1920, noon Kükenthal, 1902; *Bolitaenella* Grimps, 1922.

Optic nerves not greatly elongated; hectocotylized arm with a few enlarged suckers.

J. prismatica Hoyle. Few species, in various seas.

Bolitaena Steenstrup, 1859

Optic nerves elongated.

Few species, in various seas.

Subgenus *Bolitaena* s.s. The ganglion pedunculatum is close to the ganglion opticum. *B.* (*B.*) *microcotyla* Hoyle.

Subgenus *Eledonella* Verrill, 1884. Ganglion pedunculatum farther from the ganglion opticum; right 3rd arm in the ♂ with few enlarged suckers. *B.* (*E.*) *pygmaea* (Verrill) (Fig. 888).

2. Family AMPHITRETIDAE

Arms long, with broad velum; eyes cone-shaped, dorsally close to one another; funnel fused with the mantle in the center, so that on either side this has a small opening; hectocotylized arm distally flattened with 2 rows of small knobs and thickened proximal to it and broadened with an angulate furrow; funnel organ w-shaped; radula similar to that in Bolitaenidae.

Fig. 888. *Bolitaena* (*Eledonella*) *pygmaea* (Verrill)
(after Chun).

Amphitretus Hoyle, 1885

Characters of the family.
A. pelagicus Hoyle. Few species, in most cases doubtful, in various seas.

3. Family VITRELEDONELLIDAE

Arms in most cases long, at the base joined by a thin velar membrane; eyes moderately large, laterally directed; mantle broad and short, not fused with the funnel, funnel organ w-shaped; radula very small; central plate on either side with 2 lateral denticles; inner intermediate plate with one pointed and one low denticle, outer intermediate plate with only one denticle on the moderately broad base; all viscera and the gills strikingly small. Robson has included this family in the following stirps.

989

Vitreledonella Joubin, 1918

Characters of the family.

V. richardi Joubin. Few species, in the Atlantic Ocean.

V. translucida Robson seems to be considerably different; the funnel organ is a very obtusely angled band; the left 3rd arm is hectocotylized.

II. STIRPS OCTOPODACEA

Mantle without fins; arms more or less long, with 1 or 2 rows of sometimes fairly large suckers, without cirri; velar membrane in most cases narrow; shell completely rudimentary; central plate of the radula well developed, sometimes with accessory cusps; inner intermediate plate small, the outer one with broad base, a scale-shaped marginal plate present (Fig. 889); one 3rd arm—in most cases the right on—hectocotylized, with a sperm groove, which in most cases ends in a cone-shaped papilla (calamus), and a spoon-like terminal part (ligula), often with transverse furrows, otherwise the sexes are not strikingly different.

Fig. 889. Half radular row of *Octopus vulgaris* Lamarck (after Naef).

1. Family OCTOPODIDAE

An ink sack present; gills with inner and outer lamelae; a crop in most cases well developed.

A. Subfamily Ozaeninae

Arms with one row of suckers; eggs large. Living in most cases in the vicinity of the shore.

Ozaena Rafinesque, 1814 (*Ozoena*)

Synonym *Eledone* Leach, 1817, non *Eledona* Latreille, 1796; *Heledone* L. Agassiz, 1846; *Epistrophea* Gistel, 1848; *Hallia* Rochebrune, 1884; *Hoylea* Rochebrune, 1885; *Moschites* (Schneider, 1784) Hoyle, 1901.

Distal suckers of the arms modified in the ♂; calamus and ligula are indistinct on the hectocotylus.

O. moschata (Lamarck). A couple of species, in the northern Atlantic Ocean.

Pareledone Robson, 1932

Differing from the preceding genus by distinct development of the calamus and ligula; oviducts short; vagina and spermatophores large.

P. charcoti (Joubin). A few species, in the southern seas.

Velodona Chun, 1915

Arms large, with broad ventral membranes; hectocotylus with distinct calamus; the funnel organ consists of 2 symmetrical, anteriorly indented plates; central plate of the radula without accessory cusps; inner intermediate plate with fairly thick point; outer intermediate plate with strong point and short base; lateral plates short and thick.

990

V. togata Chun, near East Africa.

B. Subfamily Octopodinae

An ink sack present as a rule; eggs small. In most cases living in warmer seas near the shore.

Octopus Lamarck, 1798

Synonym *Polypus* (Schneider, 1784) Hoyle, 1901.

Arms with moderately broad, as a rule symmetrical velar membrane; right 3rd arm hectocotylized; mantle opening wide; penis diverticulum simple.

Subgenus *Octopus* s. s. Arms not strikingly different in length, as a rule with 2 rows of suckers, which are not modified in the ♀; gill lamellae seldom more than 11; penis diverticulum short. *O. (O.) vulgaris* Lamarck. Several species, in various seas. P. Fischer, 1882, erected a genus *Amphioctopus* for *O. membranaceus* Quoy & Gaimard, because this species is said to have a membrane on both sides, although it is not considered as characteristic.

Subgenus *Macrotritopus* Grimpe, 1922. The 3rd arms significantly longer than the remaining. *O. (M.) equivocus* Robson. Few species.

Subgenus *Tritaxeopus* Owen, 1881. Arms with 3 rows of suckers. *O. (T.) cornutus* (Owen).

Subgenus *Macroctopus* Robson, 1928. Body long and slender; distal suckers on the arms in the ♀ modified into papillae; hectocotylus long; gills long, on either side with 13 or 14 lamellae. *O. (M.) maorum* Hutton. 2 species, near New Zealand.

Subgenus *Enteroctopus* Rochebrune & Mabille, 1889. Similar to *Octopus* s. s., although with long, thin penis diverticulum. *O. (E.) membranaceus* (Rochbrune & Mabille). A couple of species, near Tierra del Fuego and the Falkland Islands.

According to Robson, the typical species of *Eledonenta* Rochebrune, 1884 (*filholiana* Rochebrune) belongs to *Octopus*.

Cistopus Gray, 1849

The velar membrane has 8 pockets between the arms, the openings of which lie on the oral side at about the 3rd suckers; hectocotylus without calamus and ligula.

C. indicus (Orbigny), in the Indian Ocean.

? *Pinnoctopus* Orbigny, 1845

Mantle with a broad lateral lamella similar to that in *Sepia*.

P. cordiformis (Quoy & Gaimard), near New Zealand. Robson considers it possible that this is *Octopus maorum* with a membranous web.

Joubinia Robson, 1929

Velar membrane between the arms equally broad and continued only slightly on these; arms equally long; mantle opening partly closed; ligula of the hectocotylus with broad margin; penis diverticulum long, with a roundish process at the base.

J. fontaniana (Orbigny), in the southern Pacific and Indian Oceans, as well as one species [*campbelli* (E. Smith)], near New Zealand.

Scaeurgus Troschel, 1857

991

Arms and velar membrane equal; 3rd left arm hectocotylized, with projecting calamus and large ligula with inrolled margins; penis diverticulum long.

S. unicirrhus (Orbigny), in various seas.

Paroctopus Naef, 1923

Synonym *Pseudoctopus* Grimpe, 1925.

Arms in most cases fairly short; hectocotylus on the 3rd right arm long and narrow; eyes fairly large.

P. digueti (Perrier & Rochebrune). A few species, mainly in the northern Pacific Ocean.

Macrochlaena Robson, 1929

Mantle and head long and narrow; arms very short with fairly broad velar membrane; funnel without freely projecting part; funnel organ paired; outer intermediate plate of the radula with a median point; ♂ organs without appendage.

M. winckworthi (Robson), near India.

Pteroctopus P. Fischer, 1882

Arms with small suckers and broad velar membrane; hectocotylus on the 3rd left arm, simple, with small calamus; funnel organ paired; ink sack not or only slightly sunken into the liver.

P. tetracirrhus (Delle Chiaje), in the Mediterranean Sea and Atlantic Ocean.

Hapalochlaena Robson, 1929

Arms short with broad velar membrane; integument with pigment rings; ink sack very small.

H. lunulata (Quoy & Gaimard). A couple of species, near Australia.

? *Haptochlaena* Grimpe, 1922

This genus was erected for the insufficiently known *H. chuni* Grimpe and the juvenile *H. alberti* Joubin, and is doubtful according to Robson.

C. Subfamily Bathypolypodinae

Without ink sack; mantle opening more or less narrow; arms in most cases short, with 1 or 2 rows of suckers; crop small or absent; eggs and spermatophores large. Living in the deep sea and in most cases in cold seas.

Benthoctopus Grimpe, 1921

Arms with 2 rows of suckers; mantle opening more or less narrow; radula normal. Living in most cases in deep water.

B. piscatorum (Verrill). A few species, in various seas.

According to Robson, *Atlantoctopus* Grimpe, 1921 (*pseudonymus* Grimpe), is not separable from *Benthoctopus*.

Teretoctopus Robson, 1929

Integument smooth; arms short with 2 rows of suckers and broad velar membrane; funnel organ quadripartite; radula normal; crop distinctly developed; posterior salivary glands weak.

T. indicus Robson. 2 species, near India.

992

Grimpella Robson, 1928

Integument with small warts; hectocotylized arm very short, with strikingly deep and long calamus, the remaining arms long; funnel organ bipartite; inner intermediate plate of the radula very weak, without point; sperematophores loop-shaped.

G. thaumastocheir Robson, near South Australia.

Bathypolypus Grimpe, 1921

Arms medium-sized, with 2 rows of suckers, hectocotylus normal; velar membrane moderately broad; funnel organ bipartite; central plate of the radula with a long point without accessory cusp, the remaining plates normal; oviduct gland in most cases large.

B. arcticus (Prosch). Few species, mainly in the Atlantic Ocean (Fig. 890), one in the northern Pacific Ocean.

Graneledone Joubin, 1918

Integument dorsally warty; arms medium-sized, with one row of suckers; hectocotylus small; central plate of the radula with fairly broad, triangular cutting edge and small lateral cusps; inner intermediate plate well developed; cutting edges of the outer intermediate plate and of the lateral plate strong; gill very small; penis with large, sack-shaped diverticulum.

G. verrucosa (Verrill). A couple of species, in various seas.
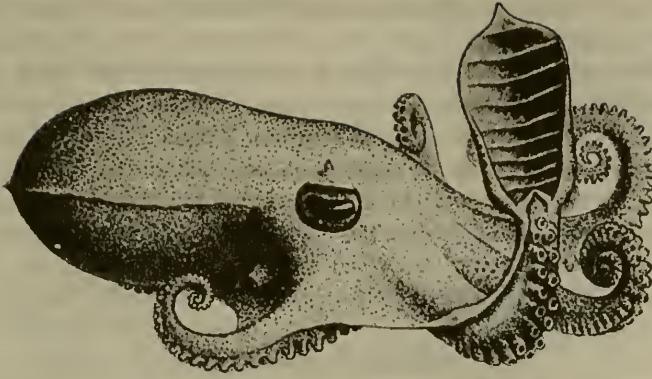
Fig. 890. *Bathypolypus lentus* (Verrill)
(after Verrill).

Bentheledone Robson, 1932

Arms strong, more or less long, with one row of suckers; velar membrane fairly broad; funnel organ [in *B*. ? *albida* (Berry)] simple, broadly V-shaped; central plate of the radula broad, with simple point; innter intermediate plate small and weak; outer intermediate plate with a short triangular point; lateral plate and marginal plate with projecting points; oviduct completely separate; vagina very short and wide; gill small.

B. rotunda (Hoyle), in the southern seas off Kerguelen, Australia, and ? Chile.

It seems uncertain whether "*Moschites*" *albida* Berry belongs here.

Thaumeledone Robson, 1930

Body short and thick; arms short, with fairly broad velar membrane and one row of suckers; funnel organ bipartite; gills small, with 5 or 6 lamellae; radula with strong central plates of similar form to those in *Bathypolypus*; all other plates rudimentary.

993

T. brevis (Hoyle), near Montevideo; a 2nd species (*T. gunteri* Robson), near Sourth Georgia.

III. STRIPS ARGONAUTACEA

Sexes more or less different; arms as a rule with 2 rows of suckers; the hectocotylized arm long, in mature condition detached from the body; eggs small and numerous.

1. Family ALLOPOSIDAE

Body soft, ♀ large, ♂ smaller; arms fairly short, with broad, strong velar membrane; suckers occasionally not very numerous and partly uniseriate; mantle dorsally fused with the body, ventrally with broad opening; funnel short; funnel organ w-shaped; central plate of the radula with distinct lateral cusps on the broad base; inner intermediate plate with distinct point; outer intermediate plate strong; 3rd right arm hectocotylized, with 2 lobed membranes; a seminal vesicle and a penis-like process, it develops in a cavity anterior to the right eye.

Alloposus Verrill, 1880

Characters of the family.
A. mollis Verrill (Fig. 891). Few species, in various seas.

Fig. 891. *Alloposus mollis* Verrill
(after Verrill).

Haliphron Steenstrup, 1859, may refer to this genus, but is insufficiently described. *Alloposina* Grimpe, 1922 (*albatrossi* Robson) = *Bolitaena microcotyla* Hoyle, 1904, non 1886, may be based on a young specimen of an *Alloposus* species, as also is *Heptapus* Joubin, 1929 (*danai* Joubin).

2. Family TREMOCTOPODIDAE

Mantle dorsally fused with the head by a membrane perforated by 2 large holes; an integumental pore is also developed at the base of the ventral arms; dorsal arms of the ♀ much longer than the remaining, they are joined with one another and with the 2nd arms by a large velar membrane, the other two pairs of arms not joined; funnel short; funnel organ formed of a few ridges; a locking apparatus consists of a fairly long and deep mantle portion and a weak triangular or roundish head portion;

central plate of the radula with fairly large lateral cusps; both intermediate plates with one point; hectocotylus long, with 2 rows of suckers, attached to which in the proximal half is a row of thin processes, in the distal part is a thin "penis" and at the end an oval seminal vesicle with terminal opening is present; the hectocotylus develops in a sack attached between the funnel and the eye.

994 *Tremoctopus* Delle Chiaje, 1829

Synonym *Philonexis* Orbigny, 1835.
Characters of the family.
T. violaceus Delle Chiaje, in various seas.

3. Family OCYTHOIDAE

Head with one pair of ventral integumental pores; arms slender, without distinct velar membrane; suckers projecting, the distal ones in 2 rows; funnel large; funnel organ formed of a large Λ-shaped and 2 longish parts; locking apparatus on the funnel formed of a strong curved cartilaginous process with a deep pit; central plate and inner intermediate plate of the radula with distinct lateral cusps; ♀ large, ventrally with stiff warts connected by ridges; water canals paired; oviduct with a short, thick proximal part, and a long, thin, coiled, terminally-widened distal part; ♂ small, 3rd right arm hectocotylized, with long flagellum, and numerous flat suckers in 2 rows, it develops in a stalked sack and then separates from the animal (Fig. 892).

Fig. 892. Hectocotylus of *Ocythoe tuberculata* Rafinesque (after Jatta).

Ocythoe Rafinesque, 1814

Synonym *Parasira* Steenstrup, 1861.
Characters of the family.
O. tuberculata Rafinesque, in the Mediterranean Sea, Atlantic and Pacific Oceans.

4. Family ARGONAUTIDAE

Female with a thin, unchambered, transversely wrinkled spiral shell, which is not firmly fused with the animal but is produced and held by large lobe-shaped expansions of the dorsal arms, it serves partly for the protection of the animal, partly as broad space; arms without velum, with 2 rows of suckers; cartilaginuous locking apparatus on the funnel knob-shaped, deepened in the center, funnel organ similar to that in *Ocythoe*; water canals rudimentary; oviduct very long and coiled, at the end with spherical, closely spaced thickenings; 3rd left arm of the small hectocotylized, very long, its distal part whip-shaped.

Argonauta Linné, 1758

Characters of the family.

A. argo Linné (Fig. 893). A few species, some of them doubtful, in various seas.
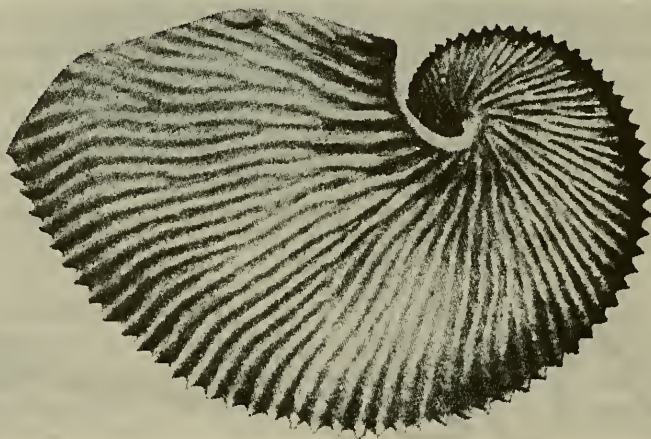
Fig. 893. Shell of *Argonauta argo* Linné
(diameter 16 cm).

EDITORS' NOTE:

"Additions and Corrections to Parts 1 and 2" on these pages have been incorporated as footnotes to appropriate text throughout this translation.

Alphabetic Index of Genera, Subgenera and Sections mentioned in Part III

New names are spaced (in **bold** face in this translation); synonyms printed in *italics*.

1013

PART 4

Comparative Morphology/Phylogeny
Geographical Distribution

Fundamentals of the Natural System of the Mollusks

The task of the natural system is to give expression, as far as possible, to the inter-relationships of the animals. These relationships can be determined only on the basis of comparative morphology and anatomy; however there are innumerable species which are known only from their shells, and with these we must try to determine their position in the system by a comparison of their shells alone. This will, in many cases, provide the correct result, when the shells show sufficient characters by which they can be related to the known species, whose systematic position has been established. Of course at various times, species have been described, which are so isolated that they were placed in separate genera, and whose relationships have not been recognized. A similar case exists with fossils, which also, by a comparison with shells of living species can, with more or less certainty, be allocated in the system; as a rule, the uncertainty increases with geological age.

The shell thus is an exceptionally important, but not the only, character for the system of the mollusks. Phylogenetically the shell is also of great importance, because the molluscan type has originated through its acquisition. In conjunction with the shell, the musculature could strengthen and give the body the characteristic thick-set form, through which the mollusks differentiate themselves from the worms. In the long evolutionary series of snails and cephalopods whenever the shell has become reduced—in most cases as a result of being overgrown by the mantle margins—it remains almost always demonstrable in the ontogenetic development.

The shell of the loricates is essentially different from that of all other mollusks. The immediately recognizable character is its division into 8 parts lying one behind the other and joined with one another by musculature. It must further be emphasized that the shell as a whole directly overlies not only the visceral mass, but also the head, without forming a mantle margin. Also very remarkable is the permeation of the shell by strand-shaped continuations of the epithelium lying under the shell and along its margin; these "aesthetes" provided with conchiolin caps on the surface, are most probably equivalent with the epithelial packets of the perinotum, and are derived from the latter with the formation of the calcified shell, on which the scales have become reduced. Accordingly, the formation of aesthetes is a basis for the assumption that the shell of loricates has originated by calcification of the dorsal culticula impregnated with calcareous scales, which, like the aesthetes is absent in other mollusks. One can assume that, initially at the insertions of the muscles thin calcareous platelets were formed,

1024 which fused together in the center of the dorsum forming transverse bands, while the two end pieces became rounded. For the attachment of the gradually strengthened connecting muscles, at the anterior margins of the 2nd–8th pieces, the apophyses developed, which is *Lepidopleurus* are still small and fairly wide apart from one another; although already in *Hanleya* and *Hemiarthrum* they are considerably enlarged and laterally extend to the posterior corners. Correspondingly, the musculature here has already become considerably strengthened, and one can conclude that this is not the basis for the development of incisions at the margins, but, rather that they result from a different arrangement of the aesthetes. In *Lepidopleurus*, these permeate the median part between the apophyses and a lateral part. In *Hanleya*, the latter is fairly narrow and lies in front of the posterior reflection. In *Tonicella* and *Lepidochiton*, this field is divided into a posterior band situated in front of the reflection, and an anterior band, and the intervening unpermeated field forms a process at the margin, which accordingly is separated from the anterior apophysis by an incision. The margins of the two end pieces have similarly acquired incisions.

In the loricate series, the insertion margins show great diversity, both in their size and in the number of incisions. The anterior margin of the 1st piece is smooth in *Hanleya* and *Hemiarthrum*, but has a variable number of incisions in several groups; in other groups their number is constant, there being 8 in mopaliids, 5 in acanthochitonines, and 3 in *Cryptoplax*. On the middle pieces only one incision is in most cases developed on either side, but in various groups (Callochitoninae, *Stenoradsia*, *Ischnoradsia*, *Anisoradsia*, *Stenochiton*, *Rhombochiton*, *Radsia*) there are 2 to 4 incisions on either side. In some groups the posteriormost shell part has undergone a shortening of the posterior part, along with a narrowing of the posterior insertion margin and a reduction of the incisions, occasionally with the formation of a sinus; these groups belong to various families (Mopaliidae, Acanthochitoninae, Ischnochitonidae, and Chitonidae), therefore this character is not a sign of relationship.

The insertion margins sometimes show radial furrows on the upper side, to which there can be corresponding small nicks at the margin; this condition is in most cases considered as the principal character of the family Chitonidae, although the margins are also furrowed in some acanthochitonines, and especially in *Eudoxochiton*, as well as in some ischnochitonids such as *Chaetopleura fulva* (Wood), *Ischnochiton nigrovirens* (Blainville), *Lepidozona*, *Lorica*, and *Loricella*.

The apophyses on the anterior margins of the 7 posterior shell parts, which are originally small and separated by a broad interspace, occasionally

extend up to the middle, where they collide, as in *Nuttalochiton* and callochitonines. Frequently the connecting margin is only narrow, and is occasionally separated from the apophysis on either side by an incision, in some groups also with several incisions, as in *Lepidozona*, in *Chiton*, *Enoplochiton*, *Mesotomura*, and *Tonicia*; on the other hand, such incisions are lacking in *Squamopleura* and *Acanthopleura*. In *Schizochiton*, in part there are incisions on the individual pieces, in part they are missing. The pores of the median area between the apophyses, in most cases distinct in primitive loricates, can disappear when the apophyses are united; 1025 when the connecting part has incisions, these as a rule correspond to rows of pores, similar to the case of lateral incisions; sometimes the rows of pores corresponding to the latter are also overlain by an internal deposition.

Whereas the insertion margins are still undeveloped in *Lepidopleurus*, they have reached enormous extension especially in *Katharina*, *Amicula*, *Cryptoconchus*, *Choriplax*, and *Cryptochiton*, however, the tegumentum has become increasingly small and become finally completely reduced, so that in *Cryptochiton* the aesthetes have also disappeared.

It was natural to compare the structure of the loricate shell with that of other mollusks, then the tegmentum would correspond to the "ostracum" which likewise grows only at the margins and is covered by a periostracum, while the hypostracum of the snails and bivalves would be homologized not only with the hypostracum but also with the articulamentum, because it has probably originated from the hypostracum. Nevertheless, not only in lepidopleurids but also in higher forms, the layers are not so sharply separated, and in addition, the entire structure is so different that one cannot assume a definite homology. Whereas in *Cryptochiton* the completely covered shell consists only of the articulamentum and the hypostracum, the new shell of certain snails, such as Lamellariinae, Philinidae, Pleurobranchinae, has retained the ostracum along with the periostracum; moreover, the ostracum is never surpassed by the hypostracum.

The external sculpture of the loricate shell originally consists of minute warts, which correspond to aesthetes and which often form radial rows on the end pieces and the lateral areas and parallel longitudinal rows on the median areas. Such warts are sometimes becoming so weak that the surface appears smooth, often there are various secondary sculptures, such as ridges or furrows or larger warts, which in most cases have little effect on the arrangement of the aesthetes, although occasionally these can be aggregated on the projecting places and can be reduced between them. In *Lepidozona* the median areas have longitudinal rows of small tubercles with the intervening spaces having minute pits, and

under the ribs of the lateral areas canal-like spaces with lateral openings can be visible; in *Lorica*, on the outer side of the small folds on the median areas, there can be one row of perforations each and below the lateral areas there are fine canals, which open at the anterior and lateral margins.

The shell of the remaining mollusks (concha) is laid down in one piece, as a dermis without any indication of scales or needles corresponding to those of loricates. It is highly variable in form, but is nearly always composed of the ostracum, the outer layer, covered by a more or less strong periostracum, and the inner hypostracum, which, along the margin, is always surpassed by the ostracum. The primitive concha has nacreous structure. Its phyletically first anlage must be visualized as a flat cap, directly overlying the visceral mass but leaving the head free. Its anterior and lateral margins do not overlie the body mass, but project freely, borne by a membranous expansion which is posteriorly produced into two symmetrical points, between which opens the rectum. The shell of Conchifera can be derived from such a primitive concha.

1026   In snails, the shell very early became considerably deep and at the same time spirally coiled. Along with the enclosed visceral mass it acquired such a weight and such a form that in its original condition it could no longer be carried by the crawling animal, and hence had to be turned around so that. the opening was displaced forward.

In this way a shell form arose similar to that found in the still-living pleurotomariids, although already this group has given rise on the one hand to disk-shaped and on the other hand to high-turreted shells. In addition, the slit could close itself at the end, thus forming a hole or a series of holes. By a rapid expansion of the whorls, the shell acquired a very wide aperture, such as that found in haliotids; the series of holes is similar to that in the fossil genus *Polytremaria*. Proceeding further in a similar direction, the bilaterally symmetrical shells of fissurellids and docoglossans arose.

A reduction of the shell slit could take place mainly as a result of flattening the gill chamber or reduction of the right gill; the sinuses or indentations of the apertural margin, developed in some higher groups of snails (*Janthina*, Turridae, *Terebra*), are not homologous with the slit of pleurotomariids.

The embryonic shell, frequently sculptured differently from the subsequent whorls, is in most cases retained, but is occasionally cast off, sometimes along with a part of the subsequent whorls, especially in high-turreted shells, in which the visceral sack is withdrawn from the initial whorls, whereupon the shell is sealed by a newly formed wall.

The whorls of the shell are very rarely separated from one another, and such forms, like *Blaesospira* (Fig. 110), *Balambania*, Vermetidae, Caecidae, *Scala* species, *Lyocyclus*, *Camptoceras*, are not primitive but are derived from normal groups with contiguous whorls; sometimes only a part of the last whorl has become separated. In such shells, the free part must naturally have a continuous apertural margin, whereas that part of the apertural margin which adjoins the penultimate whorl often does not project freely, but is in most cases indicated only by a callous deposition. Umbilicate shells are in most cases probably more primitive than nonumbilicate ones. The form of the aperture is originally roundish or ovate, in higher groups it occasionally becomes long and narrow, the whorls largely or completely surrounding each another. On the columellar side, and sometimes also on the outer apertural margin, the aperture can be narrowed by folds or teeth, which are developed in various groups. Whereas the shells of opisthobranchs and pulmonates in most cases do not show very striking sculpture, many prosobranchs, besides ribs and rings, also possess more or less large spines and bulges; such forms of scultpure partly serve for strengthening the external wall and partly for protection, and have developed in various groups. The expanded apertural margin of species of *Strombus* and its processes in *Pterocera* are related to the peculiar type of locomotion. The aperture of primitive snails does not have a sinus at the columellar end and lacks a more less long groove-shaped process. Nevertheless its presence alone does not indicate relationship; it has arisen independently in several series, such as in certain melaniids and cerithiids, in aporrhaids and strombids, in cypraeaceans and doliaceans, as well as in the stenoglossans, where it is sometimes very long, for which reason the siphonostomatous snails cannot be put together as a homogeneous group.

1027 　In contrast to the very high-turreted shells, the spire may be elevated only slightly or not at all, as is the case in some prosobranchs (cypraeaceans and certain marginellids), but especially in several Cephalaspidea. In other groups, the spire has become so greatly reduced that a cap or bowl-shaped shell with very wide aperture has developed; this form of shell has also always developed secondarily from a spiral shell.

Among the prosobranchs a complete reduction of the shell has taken place only in *Titiscania,* in which it has been lost without leaving any trace, and the pterotracheids, which are close to the carinariids, which still possess a thin shell. The lamellariids show all stages of the mantle edge overgrowing the very wide-apertured, spiral or cap-shaped shell, giving rise to a mantle edge which has some similarity with the perinotum of loricates, although without being homologous with the

latter. A similar event has taken place in some Cephalaspidea, as in Cryptophthalminae, runcinids, aplysiids, and pleurobranchids, in which the shell eventually completely disappeared. This has happeneed similarly in the groups of oncidiids and soleoliferans, as well as in the philomycids and *Cystopelta*, whereas in other slugs a more or less distinct shell rudiment has persisted below the skin (Athoracophoridae, Arionidae Limacidae, Trigonochlamydidae, and Aperidae). Also completely shell-less are the Philinoglossidae, the Pterota (gymnosomatous pteropods), several sacoglossans, as well as the long series of nudibranchs.

The operculum, present in many prosobranchs, is attached on the posterior part of the dorsum of the foot, hence *behind the shell*. Its original form is that of a spiral with several narrow whorls, with a central nucleus and circular outline, corresponding to the nearly circular shell aperture. This type of operculum is present in the pleurotomariids, scissurellids, and trochids, also of most cyclophorids, of valvatids, turritellids, and potamidids. When the form of the shell aperture undergoes change and becomes ovate or even longer and narrower, the nucleus of the operculum becomes more or less eccentric and growth either takes place spirally with a few, rapidly enlarging whorls, or concentrically. In some families the operculum shows considerable variation; in cyclophorids it is sometimes cartilaginous or calcified, in pomatiasids in most cases with an external calcareous layer, and sometimes has many whorls, sometimes only a few, or only the last whorl is recognizable; among naticids only the genus *Natica* has a calcareous operculum. Among the turbinids, the Liotiinae have opercula with several narrow whorls, which have in *Liotia* a row of calcareous granulations, in *Mölleria* and *Leptothyra* a continuous calcareous layer; in Turbininae and Phasianellinae the calcareous operculum is relatively thick, externally in most cases without indication of the whorls that are visible on the inner side. In neritids the operculum is calcified, spiral with rapidly enlarging whorls, and an internal process at the nucleus, similar to that in hydrocenids, in contrast, it is very peculiar in neritopsids (Fig. 55). The operculum of the helicinids is rather variable, it is horny only in *Pseudhelicina*, otherwise it has a more or less strong calcareous deposition; the roundish operculum of *Ceratodiscus* has nonspiral growth.

In general, the higher prosobranchs in most cases have opercula with terminal or marginal nuclei, from which the direction of growth proceeds mainly straight or only slightly curved. In several groups the operculum has completely disappeared, mainly in shells with very wide apertures, into which the animals cannot retract with incurved foot, but also in shells with narrow apertures, such as the cypraeaceans and the marginellids. Among opisthobranchs, the operculum is still retained only in the

1028

actaeonids and spiratellids, and among pulmonates only in the amphibolids, in all others it is lost.

The shell of bivalves has evolved from the primitive concha in a manner completely different from the snails. The bipartition, indicated in the zeugobranchs by the slit, has in bivalves proceeded to a division into 2 valves joined only by the ligament. An elevation of the shell has never happened, the median line is, on the contrary, straight or only moderately curved. With the bipartition, each half acquired its own center of growth. In order to enable growth along the long median line, at which the two valves were originally united, the two centers had to move apart from one another, giving rise to hinge plates, the margins of which bear the hinge teeth and on the underside of which the foot muscles attach. On both sides, the mantle lobes and the shell valves are considerably broadened, so that they completely enclosed the animal along with the likewise broadened gills.

Because the division of the shell into two halves is to be considered as a secondary process, the hinge margins correspondingly differ from the remaining margins of the bivalve shell and their teeth are not homologous with the marginal teeth.

Originally the shell may have been rather broad and low, with straight hinge margins, which were joined together by numerous minute teeth fitting into pits on the opposite side; the ligament was situated over the hinge plates and between the umbones, extending more or less far posteriorly and anteriorly. However, the bivalve shell is in most cases more compressed and in lateral view it is rounded, the dorsum and the hinge margins narrow. This has already happened in the series of the taxodonts; in limopsids, the number of hinge teeth decreases and in the genera *Hochstetterina*, *Adacnarca*, and *Philobrya*, the hinge margin shows only fine transverse grooves, but not teeth. These are as a rule small animals, the small mytilids *Idasola* and *Dacrydium* also show such finely grooved hinge margins. The anisomyarians do not possess any equivalent at all of the taxodont teeth, their hinge margin is in most cases toothless, occasionally secondary tooth developments have arisen, of which those of *Plicatula* and *Spondylus* are the most strongly developed. The hinge margin is straight, occasionally of considerable length (cf. Figs. 799 and 800), often only short. The ligament is amphidetic when the umbones are situated near the middle; it is opisthodetic when the umbones have moved toward the anterior end. Several cartilagenous thickenings are developed in *Crenatula* and *Pedalion*, in most other cases only one, as in the pectinaceans and ostreaceans. The embryonic shell along the hinge margin shows fine transverse grooves the phyletic significance of which seems doubtful.

In comparing the hinge of the trigoniids with that of taxodonts, one will hardly be inclined to homologize the large grooved teeth with the single small teeth of the latter, but will see them as secondary thickenings of the hinge margin. The homology of the teeth of *Iridina* with those of taxodonts is completely out of the question, they have arisen secondarily after the schizodont teeth were reduced.

1029   Although in some taxodonts, the anteriormost and posteriormost denticles can be very obliquely positioned, so that they are directed almost or completely parallel to the margin, they cannot be homologized with the lamelliform lateral teeth of heterodonts, but should be considered as secondary structures, which are occasionally provided with transverse grooves. The main teeth can be rather similar to the median teeth of taxodonts, but of these too it can be assumed that they have arisen secondarily as arch-shaped lamellae alternating in the two valves around a central tooth of the right valve; from these have developed the anterior and posterior main teeth; the central tooth is often reduced. In general, the hinge margin of the heterodonts increasingly undergoes a shortening, the lateral lamellae are frequently reduced. The ligament always lies posterior to the umbones and often sinks between the teeth, occasionally causing a reduction of certain posterior teeth. In the Adapedonta the reduction of the hinge margin has proceeded still further; the main teeth have a tendency toward reduction, whereas lateral lamellae are entirely lacking. Finally, in the Adesmacea not only the hinge margin but also the ligament have become completely reduced, so that the two valves are joined together only by the musculture.

In a similar fashion as in bivalves, the shell of scaphopods can be derived from the primitive concha, but without bipartition; as in some bivalves, the mantle margins are ventrally fused with each other and with the ventral margins of the shell, so that it became an anteriorly and posteriorly open tube, which was at first only moderately long, and then extended itself into a long, more or less thin structure. The shell is thus to be considered not as turreted but as elongated.

On the other hand, the shell of primitive cephalopods has become turreted in a similar fashion as in snails, but with the retention of bilateral symmetry, which became possible by a shift to the swimming mode of life. A characteristic feature is the formation of septa, which are as a rule pierced by a more or less wide siphuncle. The endoceratids—elongated cylindrical forms with a large siphon divided by funnel-shaped diaphragms—were placed by Spath at the beginning; from these on the one hand the Nautiloidea are said to be descended, on the other hand orthoceratits, and from the latter the Belemnoidea and further the Recent dibranchiates. The large group with an external shell has become extinct,

with the exception of the few *Nautilus* species, their shell is spiral, with simple, anteriorly concave septa and rather thin siphuncle. Among the dibranchiates, only the shell of *Spirula*, with its calcareous nature and the regular septa-pierced by a siphuncle, shows similarity with that of nautilids, but significantly differs by its small size, its enclosure within the posterior part of the body, and its ventral inward coil. The shell of the sepiids seems to be very different, which is still calcified, but has acquired a completely different form due to the special displacement of the thin septa. In the majority of decapods, wherever the shell has not been lost, such as the sepiadriids and idiosepiids, it is uncalcified, elastic, and without trace of septa; this "gladius" can hardly be considered an equivalent of the original calcareous shell, but as secondary proostracum, 1030 whereas the chambered cavity (phragmocone), situated at the posterior end, has disappeared. Among the cirrate octopods, only *Vampyroteuthis* has a thin leaf-shaped shell rudiment, which presents some similarity with the gladius of decapods, otherwise it in most cases forms a saddle— or brace-shaped fin support. In the Incirrata, a shell rudiment is hardly detectable; the shell in the females of *Argonauta* species is a secondary structure, which is not fused with the body and is by no means equivalent to the shell of *Nautilus* and ammonites.

Like the form of the shells, its structure must also be taken into consideration for systematic purposes, but this must be done with caution. Böggild, for instance, states that among anisomyarian Bivalvia the shells in some families are quite uniform, whereas in others they are so variable that the structures have no systematic value. Among the nuculaceans, Böggild considers the condition in *Leda* and *Yoldia* species to be the most primitive, which presents no nacreous layer but where the shell is homogeneous or very indistinctly prismatic; in one species of *Nucula* (*Lionucula*) from the Eocene, the entire shell (?ostracum) consists of very fine crossed lamellae; quite special in *Nucula* s. s. is the formation of radial trabeculae. In arcids the shell largely consists of crossed lamellae. The structure of the schizodont shells is very uniform, whose ostracum consists of an outer prismatic layer and an inner nacreous layer. In mytilids, an external, often very thin, calcitic, homogeneous or indistinctly prismatic layer and an inner, in most cases nacreous, aragonitic layer are differentiated. The Pteriacea have an ostracum consisting entirely of prisms and a nacreous hypostracum. A differentiation in the structure of the two valves is noticeable in some species of *Propeamussium* and *Anomia*. In the shells of heterodonts crossed lamellae are in most cases recognizable.

The shells of the primitive snails (pleurotomariids, haliotids, and trochids) have distinct nacreous structure, but already the fissurellids and

docoglossans have a different structure, and also among the trochaceans we find smaller or larger groups (*Fossarina*, Skeneinae, Cyclostrematidae, and most Phasianellinae) without nacre. The neritaceans and all higher snails have differently formed shells, often with crossed lamellae.

The shell of *Nautilus* is nacreous like that in *Pleurotomaria*, the septa forming the major part of the hypostracum; the shell of *Spirula* consists of fairly regular prisms, the septa of nacre.

The mantle of conchaceans, which is lacking in the loricates, should in its origins be regarded as a fold on the lower side of the shell margins; which anteriorly and laterally is narrow, posteriorly on either side expanded lobe-shaped, and is not fused with the head; the two posterior lobes are separated by the anus, so that between them lies a cleft corresponding to a slit of the shell. In snails, the mantle and the shell are twisted to the right and the cleft is displaced anteriorly. The lobes then lie over the anterior part of the body and form a cavity which is anteriorly open. By fusing of the lobes with each other, the cleft is then closed. In some groups of higher snails the mantle is produced anteriorly to form a shorter or longer groove-shaped process. The two mantle lobes of bivalves are originally completely separated from one another, although in various groups a more or less extensive fusion of the margins takes place along with the formation of sometimes short, sometimes very long, tubes for the in-current and out-current of water. In anisomyarians, arcids, and trigoniids, also in some unionaceans, the mantle has remained open, also in some nucluaceans, whereas most genera of the malletiids and ledids have formed siphons, and in *Solenomya* the ventral margins are fused with one another. The mantle of bivalves encloses a space which contains the entire animal, especially the foot and the gills. This is similar to the condition in the scaphopods, in which the mantle cavity is open anteriorly and posteriorly, whereas in the cephalopods it forms a posteriorly closed sack, which encloses the gills and covers most of the funnel-shaped foot.

The mantle edges in snails are rarely beset with tentacles (Patellacea), but more frequently in bivalves, among the siphoniates they are mainly developed at the current siphon; eye-like organs of various structure are developed in some arcaceans and pectinids as well as on the siphons of a few cardiids.

In some groups of snails with ear- or bowl-shaped shells, the mantle edge extends more or less widely over the surface of the shell, as in the subgenus *Emarginella* and in *Fissurellidea,* lamellariids, and cypraeids, in pirulids, and marginellids, among the opisthobranchs in *Phanerophthalmus, Philine, Gastropteron*, aplysiids, and pleurobranchids; in some of these groups the shell is completely enclosed, and can then

tend toward reduction; this is similar also in some pulmonate groups, among which the oncidiaceans, soleoliferans, and philomycids have completely lost the shell. Among bivalves, it is only in galeommatines and chlamydoconchins as well as in some montacutids that the shell is partly or completely covered by the mantle.

Among the dibranchiate cephalopods, it was probably in the belemnites or similar forms that the shell was first overgrown, grasped, and later completely enclosed by the mantle lobes; it thereby first acquired the function of an internal skeleton, but in animals with short and massive body forms it was completely lost.

If one compares such a form as *Lamellaria* with loricates such as *Cryptochiton*, at a cursory glance the mantle of the former can appear to be a homologue of the body edge of the latter, but a closer inspection reveals the impossibility of such a homologization.

The mantle of the snails has the task of bringing about growth of the shell whereas the perinotum of loricates has nothing to do with shell growth, because this takes place only from a small edge at the dorsal beginning of the perinotum, whereas true mantle is absent. A very important difference exists in the fact that the perinotum attaches anteriorly at the sides of the head, whereas the mantle of the snails covers the gill cavity and often also the head dorsally, without being fused with it. If such characteristically differentiated forms as *Lamellaria* and *Cryptochiton* are compared with one another, without taking into consideration forms which are intermediate between them, one can get completely wrong results.

The perinotum is a more or less strong ring-fold filled with musculature, and is covered by a strong cuticula and variously formed calcareous bodies; by an edge the upper side is separated from the lower side and the inner boundary of the latter forms a more or less distinct fold at which the cuticula ends. The calcareous bodies on the upper and lower sides are originally not very different, they are mainly minute scales, which on the upper side are often ribbed, where scattered among them are small cylindrical bodies in most cases in small groups; similar structures are located at the edge.

The mopallids and cryptoplacids, on the upper side there are in most cases rather small needle- or club-shaped bodies and bristles with a small terminal spine or bundles of longer needles, the scales on the lower side are strikingly enlarged in *Craspedochiton*. In *Ischnochiton* and *Chiton* more or less large scales of the upper side are placed so densely, that the club-like bodies are restricted to the margin, whereas the lower side bears minute scales in radial rows. Most highly differentiated are the spines of *Acanthopleura* and *Mesotomura*, as well as the strong reduction of the calcareous structures in *Tonicina* and *Tonicia*.

It is to be assumed that the cuticula with the minute calcareous bodies was originally a purely dorsal structure, and that the marginal fold, therefore, represented the lateral margin of the probably rather flat animal. It might have been interrupted anteriorly at the head and perhaps also posteriorly. With a strengthening of the ventral musculature and a concentration of the digestive organs, the dorsum bulged higher and the lateral margins sloped downward. The musculature in the latter was strengthened and an edge was developed, which then formed a secondary margin; anteriorly and posteriorly the margins united to form a closed ring. Due to the development of the edge, the impetus was given for differentiation of calcareous bodies on the lower side, the edge, and the upper side.

The most primitive snails possess an epipodium, i.e. a fold beginning at the sides of the head and continuing posteriorly at the sides of the body between the mantle and foot; in *Haliotis*, where it is most strongly developed, at the margin it bears numerous tentacles and irregularly formed processes, mainly on the lower side small sensory hills and under its attachment runs a strong blood vessel. It could be that such a shell shape as in *Pleurotomaria* and trochids was less suitable for the retention of an epipodium than the ear-shaped shell of *Haliotis*, and that for this reason the epipodium in the former is not so well developed; in fissurellids the folds have become reduced, whereas a row of tentacles along with sensory hills has been retained.

The position of the epipodial folds in *Haliotis* corresponds to that of the perinotum, both border the sides of the head and of the body. It must be considered that the loricates lack mantle folds and, if expansions corresponding to them are to be visualized along the shell margin, these, in terms of their position in relation to the perinotum, would completely correspond to the condition in *Haliotis*. *In the same way as the marginal fold of the perinotum, the epipodium corresponds to the lateral margin of the ancestral forms*; however, the former lacks tentacles, so that it must be assumed that these first developed in the conchiferans, and the fold is not interrupted at the head as in the epipodium; this condition can be explained by the fact that with the development of the lateral edge, the two lateral folds have only secondarily united anteriorly and posteriorly.

It cannot be stated with certainty as to what extent an epipodium has been retained in the higher snails. Some *Cocculina* species possess a pair of tentacle-like processes on the posterior part of the foot. The opercular lobes of *Lacuna* on their posterior part have a process on either side, whereas in *Litiopa*, in addition to one pair of similar processes, on either side are 3 cirri. The lateral folds of *Janthina*, which resemble an

epipodium, are in *Recluzia* not clearly delimited, they do not have a blood vessel at the base, and are lacking in the scalids, hence they should not be considered as a true epipodium.

Whereas the bivalves and scaphopods lack an epipodium, one can assume that the arms of the nautilids along with their sheaths, have arisen from such; the external system is dorsally interrupted by the cephalic hood and ventrally by the funnel depression, so that it consists of 2 lateral parts, similar to the anterior part of the epipodiium, whereas its posterior part has been lost as a result of its envelopment by the mantle and the shell.

The **molluscan foot** is originally the ventral, sole-like flattened part of the body provided with a strong musculature, situated behind the head, and serving for attachment to the substratum and for creeping, it is attached to the shell by bundles of muscles. Its form has undergone several modifications in the molluscan series. Corresponding to the body form, in the loricates it is more or less elongated, occasionally greatly narrowed, and without special glandular structures. It has a similar form in the primitive snails, but in littoral forms, such as the haliotids, fissurellids, docoglossans, which move very little, it may assume the form of a powerful sucker. In the sessile vermetids the creeping sole has become reduced, as also in the strombids which have assumed a special type of locomotion. It has undergone greater modification in the swimming heteropods, where the sole is only indicated as a small sucker on the laterally compressed fin. Remarkable also is the foot of naticids, which is distensible and has a propodium, the posterior margin of which covers the head. In some olivids the foot is broad, with a crescent-shaped propodium, its lateral lobes adjoin the shell, but can also be sometimes used for swimming. Similar lateral lobes, which serve wing-like swimming organs, are developed in some opisthobranchs (Atyidae, *Acera*, *Gastropteron*) and most characteristically in the pteropods; on the other hand the foot of nudibranchs is as a rule rather long and narrow, without strong musculature and without retractor muscles, in phyllirrhoids it is rudimentary or completely lost. The foot of scaphopods is protrusible and serves exclusively for burrowing. It functions similarly in many bivalves, although its form is variable, often hatchet- or finger-shaped, in some groups, in which the shell is cemented to the substratum, the foot is rudimentary. As in some snails, the foot of the primitive cephalopods has become broadened to form a pair of large lobes, which enroll against one another to form a tube, in *Nautilus* they are still separated from one another, in others they are fused together to form the funnel.

The foot is often provided with special glands. At the anterior margin a groove is developed, which in most cases gives off posteriorly

a more or less deep median blind sack and is surrounded by mucus gland cells. The glandular cells which open into the sole, in higher prosobranchs, have drawn together around a sometimes rather small, sometimes larger cavity, which is frequently (always ?) used for the production of egg capsules; in janthinids this sole gland also produces the farm-float, which is 'attached to the longitudinal folds of the posterior part of the sole. Similar glands are also present in many bivalves; the sole gland secretes the structure known as byssus in most cases hornlike, in *Anomia* calcified, by which the animal attaches itself to stones, etc. In animals living on sand or muddy substratum, the byssus gland becomes rudimentary. On the funnel of the cephalopods, corresponding glands are recognizable as bulges of variable form.

1034

The condition of the **respiratory organs** is of great importance for the systematics of the mollusks. In the loricates, at the sides of the foot, in the groove formed by the perinotum, on either side are a few bipectinate gills, which are attached at the bottom of the groove by their bases. Their number varies greatly, some lepidopleurids have 6 or 7 on either side, the acanthopleurids between 70 and 80 gills. The restriction of the gills to the posterior half is called the merobranchial type, while in the holobranchial type they extend to the anterior margin of the foot. The largest gills are situated near the kidney opening: when with these the series ends posteriorly, they are called abanal, on the other hand, when a few small ones are also present between these and the anus, they are called adanal.

Accordinlgy, the merobranchial adanal type (lepidopleurids) is to be considered as the most primitive, the merobranchial abanal type is found in lepidochitonines, in *Amicula*, *Cryptoconchus*, *Acanthochiton*, and *Cryptoplax*, whereas the remaining groups, including some fairly primitive ones, such as *Nuttalochiton* and *Callochiton*, have assumed the holobranchial type; hence, this character cannot be indicative of closer relationship, especially because some species, like *Callochiton* (*Icoplax*) *puniceus* (Gould) and *Ischnochiton keili* Plate are still called merobranchial. *Schizochiton*, with merobranchial gills, is highly advanced, but has a specially modified form in some respects.

The primitive form of the conchiferans had a pair of bipectinate gills, which were located below the posterior mantle lobes at the base of which they were attached laterally to the nephridia. Although these gills show some similarity with those of the loricates, they cannot be considered as homologous structures, because they differ in their position, number and innervation. They are called **ctenidia**. It is from these that the development of the respiratory organs has taken place in snails, bivalves, and cephalopods, whereas they are lacking in all scaphopods.

In snails, the gills are displaced anteriorly, so that they lie over the dorsum with their apices directed forward. Among the zeugobranchs, the groups with a spiral shell possess an asymmetrically placed gill chamber and the two gills are largely attached to the margin containing the efferent vessel, they are free on the opposite margin which is somewhat surpassed by the gill leaflets. In fissurellids, the gills have assumed a symmetrical position and, to a variable extent, they are attached to the mantle, partly also on the side of the afferent vessel. The trochaceans have lost the right gill; the left gill is largely attached to the mantle by both margins, and the lamellae of the upper side are gradually reduced in the posterior part, whereas the rachis approaches the mantle and finally fuses with it, so that the lamellae of the lower side, which show wavy folds, arise directly from the mantle. This process has proceeded farther in the higher prosobranchs, so that all their gill lamellae hang on the underside of the mantle. The adeorbids and valvatids, however, possess a bipectinate and protrusible gill, of which it is doubtful whether it should be considered as a new structure.

1035

In the stirps of the docoglossans, which follow the zeugobranchs, both ctenidia are reduced and can be represented by a pair of wart-like elevations, whereas in patellids, instead of ctenidia, on the underside of the mantle a circlet of lamellae has developed, which is sometimes anteriorly interrupted. Such a circlet of gills is also present in *Lottia*, but in addition there is a bipectinate gill, attached only at the base, which could have developed from a lamella arising from the mantle anterior to the heart. The small lepetids lack gills. The condition in the cocculinaceans is similar to that of the docoglossans; the cocculinids possess a pleated lamella attached in the neck, similar to *Bathysciadium pacificum* Dall, whereas the very small *B. costulatum* (Locard), as well as *Cocculinella*, are without gill. In *Lepetella*, anteriorly on the right side, a few gill lamellae have developed on the underside of the mantle, and in *Addisonia* such have developed on the entire right side with considerable increase in number and size (cf. Fig. 73). Among the neritaceans, the neritids, neritopsids, phenacolepadids, and titiscaniids have a bipectinate nuchal gill attached, similar to that in acmaeids, only at the base; on the other hand, the terrestrial hydrocenids and helicinids lack gills. Also gill-less are the terrestrial cyclophorids, pomatiasids, acmids, assimineids, and the genus *Geomelania*, but also the marine, in most cases very small, pyramidellids. Very special are the respiratory organs of the ampullariids, in which a septum divides the mantle cavity into a right half containing the gill, and a left half which serves as the lung.

Among the opisthobranchs, the actaeonids possess a gill consisting of a single lamella, with its apex directed anteriorly, which can be

considered either as a completely new development in contrast to the ctenidium of most of the prosobranchs or as a homologue of only a single lamella. In other cephalaspideans this gill develops further, wherein it shifts more to the right and toward the posterior, and it can become similar to a ctenidium, at the same time the mantle cavity flattens, so that in pleurobranchids it hardly appears like a cavity.

The pteropods in most cases do not possess gills and, when they are present, as in *Cavolinia*, *Peracle*, and some pterotans, they seem to be new structures. Also the gill of oxynoids, consisting of several narrow leaflets on the underside of the mantle, is undoubtedly a special structure; some of the shell-less sacoglossans possess leaf- or club-shaped dorsal appendages, in part gills are lacking completely. A similar condition is present in the nudibranchs, several of which (*Doridoxa*, *Heterodoris*, *Doridoides*, the hedylids, phyllirrhoids, goniaeolidids, pseudovermids, and rhodopids) are without gills, whereas others show variously formed processes which attach to the sides of the dorsum or in the anal region. In the scyllaeids, small gill tufts are developed on the lobe-like processes. Similar to the condition in patellids, the gills of phyllidiids and arminines are made of numerous lamellae leaflets on the underside of the mantle.

The pulmonates are originally and predominantly gill-less. In the littoral siphonariids alone, in the spacious mantle cavity, several triangular gill leaflets are developed on the mantle, which are lacking in the related gadiniids. In planorbids and ancylids a gill has developed in a different way, by expansion of a ventral mantle lobe situated outside the lung cavity. In some oncidiids there are tuft-shaped gills on the upper side of the mantle.

The gill-less mantle cavity of the above-mentioned groups serves as the lung, with the development of a more or less strong network of blood vessels in the mantle. A very special condition is shown only in the athoracophorids, in which the mantle cavity sends out numerous branched tubes, which lie in a wide blood sinus. In the ancylids the lung cavity is more or less reduced, soleoliferans completely lost.

Whereas, in accordance to what has been said, in various groups of snails the ctenidia have been lost and are sometimes replaced by new structures, they are retained throughout the bivalves, in which they have become rudimentary only in a few poromyaceans. The most primitive form of gills is displayed by the nuculaceans: on either side there is a gill consisting of an axis and two rows of short lamellae; these are in most cases directed downward, in solenomyids they are directed laterally. In contrast to these groups, which are known as Protobranchia, in the Filibranchia the two rows of lamellae are produced into long threads,

which hang down from the rachis on the sides of the foot and which are as a rule, sharply bent with their terminal parts so that each thread forms an inner and outer limb, and together form 2 leaflets on either side. Originally the consecutive threads are joined with one another only by brush-like, and each contains a septum so that the blood flows in it to-and-fro throughout its full length (arcaceans).

Similar are the mytilids, also the trigoniids, in which the threads are fused with one another only at the margin. As a result of such a fusion at the free ends, an efferent blood vessel is formed. The gills in other anisomyarians also consist of threads, which can be identical (Vulsellidae, Plicatulinae, Amussiinae, Anomiidae) or their longitudinal rows form folds, the inner marginal filaments of which are distinctly enlarged (Pteriidae, Pinnidae, Pectininae, Spondylinae, Limidae, Ostreidae). Rarely the threads lack the ascending limb. In the series of eulamellibranchiates, the successive threads are fused to form leaflets, which are pierced by clefts, and there are also connections between the two limbs of the threads. The leaflets thus formed may fuse with their free upper margins on the inner side with the visceral sack and on the outer side with the mantle, as a result of which the mantle cavity is divided into a lower and an upper chamber. The outer gill lamella is sometimes more weakly developed than the inner or can even disappear completely. In the verticordiids the gills are narrow, net-shaped, enclosed in a in most cases incomplete septum, in poromyids they only form 2 or 3 small sieves or rows of holes and in cuspidariids on either side there are 4 or 5 separate holes in the septum, so that true gills are here absent.

In bivalves, accessory gills are rarely developed in addition to the ctenidia, such as small folds above the upper margin of the outer lamella in some mytilids and in *Panopaea*, in some cardiids as folds of the septum stretched out between the gills posterior to the foot, and in few lucinids as folds on the inner side of the mantle.

1037

The ctenidia are always present in the cephalopods. Very remarkable is its duplication in *Nautilus*; this is probably explainable by the fact that the anterior ones were originally processes of the posterior ones, which subsequently become more independent, wherein the rachis became detached from the body and formed a free process; accordingly, the two pairs of gills are attached to the body with only their bases lateral to the kidneys, and throughout their length lie freely in the mantle cavity. The afferent vessels are situated on the sides, facing each other on the posterior and anterior ones, and in the basal part form thick bands, whereas the efferent vessels run on the opposite sides. The gill leaflets are irregularly triangular with parallel folds and two rows of tubercles.

All other cephalopods possess only one pair of gills, lying symmetrically in the mantle cavity, their bases are attached to the body, their apices are directed forward and the outer sides are joined to the mantle by a band. The form and number of the leaflets is variable. On the ventral side runs the efferent blood vessel, above which is the afferent. Between them, the gill as a rule is traversed by a canal formed by an incomplete fusion of the leaflets with the rachis. Lying in the suspensory band is the "gill spleen," consisting of cells with large nuclei.

The anteriormost part of the trunk, which contains the oral opening, often bears the **eyes** and **tentacles**. However, originally the tentacles were not yet developed, whereas this is uncertain with respect to the eyes. The loricates have only a narrow sensory fold at the anterior margin of the head; the adult animals lack eyes, but they have been found in juvenile animals. In *Haliotis* a transverse fold is visible between 2 short eye-bearing processes and, beside the eye-bearers and on the anterior tips of the epipodium is a pair of longer tentacles, the structure of which is completely identical with those at the margin of the epipodium and hence morphologically belong to the epipodium. It can be assumed that this head-fold is homologous with that of the loricates, perhaps the eyes also correspond with those of the loricate larvae, whereas the tentacles on the head and on the epipodial margin are new structures. In the trochaceans the head-fold varies, it is sometimes lobed or fringed, sometimes divided into 2 longer, in most cases branched processes, sometimes reduced (*Angaria*, Skeneinae); it is also lacking in the fissurellids, docoglossans, neritaceans, as well as in all higher snails. The processes which bear the eyes are also often completely lost and the eyes are situated lateral to the tentacles in the head or they are displaced more or less far forward on the outer side of the tentacles, rarely they lie completely at their anterior ends (*Terebellum*, Terebridae), when they are frequently contained in swellings or the common bases of the eye-bearers and tentacles can be greatly elongated and separated only terminally (most strombids). The tentacles in prosobranchs are as a rule more or less long, cylindrical processes; they are absent in the hydrocenids, in *Homalogyra*, *Olivella*, and *Diplomeriza*; they are cleft in *Janthina*, whereas in rissoellids a pair of similar processes is developed between the tentacles. They are specially modified in the pyramidellids, sometimes short and broad, sometimes more elongated, they possess a groove on the outer side, which in any case contains a special sense organ. The head of the Cephalaspidea has acquired a shield-shaped expansion, under the anterior and lateral margins of which lie the sense organs, and near the mouth opening sometimes there is a somewhat fold-shaped elevated area, which serves as a tactile organ, and more laterally there is an olfactory

1038

organ which in most cases shows fine transverse folds which occasionally have a bipectinate arrangement (*Haminea*). Occasionally the head-shield has 1 or 2 pairs of lateral processes. In *Paraplysia* the form is similar to that in *Haminea*, so that the anterior tentacles correspond to the anterior corners and the posterior ones to the lobes of the cephalic shield; in *Aplysia* the form is further modified. Most frequently the opisthobranchs have an anterior pair of tentacles and a posterior pair of rhinophores, which often show a lamellate structure, although sometimes only one pair of processes is developed, whose homology with one or the other pair is occasionally doubtful.

Among the pulmonates, the basommatophorans are in most cases distinctly characterized by the position of the eyes in the head beside the tentacles, only in *Otina* does the head bear a pair of short processes containing the eyes; on the other hand, in the stylommatophorans the eyes are borne in the tips of the invaginable tentacles. Small anterior tentacles are in most cases present in land snails, although they can be occasionally developed independently of the others, as in the Soleolifera; they are absent in the oncidiids, athoracophorids, and some vertiginids. Strikingly large oval lobes are rarely developed (some oleacinids).

Some snail groups have rudimentary eyes, in most cases as a result of adaptation to life in the deep sea, in caves, or burrowing life-mode. In the most primitive snails, they are in the form of open vesicles, which in patetlids and acmaeids because of being covered by the shell have remained as shallow pigment cups, in *Pectinodonta* and lepetids they are hardly indicated any more. Most of the cocculinaceans are blind, in only one species (*Cocculina fragilis* Thiele) have eyes been found. The pelagic janthinids have rudimentary eyes. In the pyramidellids they are situated in the head between the ear-shaped processes. Burrrowing habits are the cause of a more or less extensive reduction of eyes in the naticids, in *Olivella*, and in the cephalaspideans. Pteropods have no or very rudimentary eyes. The cave-dwelling *Zospeum* species are blind.

On the small head of the scaphopods the leaf-shaped processes at the mouth opening seem to represent a new structure, whereas the folds, along with the cirri, situated at its base are probably homologous with the head-fold of *Haliotis*, but it is possible that the tentacles have also contributed to it; the scaphopods lack eyes.

In the bivalves the head is reduced, but this is only true for the process containing the mouth opening, because the upper lip, which is produced into more or less large oral lobes, has to be considered as a homologue of the head-fold of primitive snails, which has here acquired a new structure in the lower lip. The small cup-shaped eyes at the ends of the oval lobes, retained in some primitive bivalves, could be homologous

with the eyes of snails; such eyes have not been observed in the nuculaceans, which on the other hand possess more or less long appendages arising at the ends of the oral lobes, each with a strong ganglionic nerve, they are probably homologous with the head-tentacles of snails.

1039   The head of *Nautilus* has become greatly modified through the cephalic hood and the cirri with their sheaths, so that the homology of its individual parts is uncertain; there is hardly any doubt that the open eyes correspond to those of the primitive snails but it seems doubtful whether in this case homologues of the head-fold and the cephalic tentacles are ascertainable. The dibranchiate cephalopods certainly seem to have lost them.

The anterior part of the head along with the mouth opening is originally a short snout, which is still found in many herbivorous mesogastropods, as well as in the opisthobranchs and pulomonates. But already in some families of mesogastropods the snout has become elongated proboscis-like; the channel-shaped prolongation of the lower lip of *Capulus* is special, but is to be considered as a propodium. The proboscis at first can be simply shortened and elongated, later it can be invaginated by means of muscles attached at the mouth opening (acrembolic proboscis), as is the case in some higher mesogastropods. In the most highly developed predatory prosobranchs (doliaceans and stenoglossans), the proboscis has often become very long and is enclosed in a special sheath, the retractor muscles are attached only at median part of the proboscis, so that the temrinal part along with the mouth opening in the retracted condition always remains anteriorly directed (pleurembolic proboscis). The proboscis sheath is a permanently invaginated part, which is as a rule attached to the body wall, only in terebrids it is separated from the thin proboscis. Among the opisthobranchs the pterotans in most cases have a protrusible proboscis of varying shape, in cliopsids it is very long, in pneumodermatids it is provided with suckers, it is otherwise short and often has cone-shaped processes.

The originally short oral tube, actually formed only by the lips, leads into the **buccal cavity**, which mainly contains a tongue, covered with a conchin membrane, implanted into which are hook-shaped teeth of characteristic form; its posterior end extends into a sheath, at the end of which the continuous formation of teeth takes place; as a result the membrane gradually moves forward to the extent that the teeth wear out anteriorly. With the exception of bivalves and some groups of snails and cephalopods, such a **radula** is present in all mollusks, and is a character of great importance in systematics. Its structure is very peculiar in the loricates, in which cutting edges are present mainly on the 5 median teeth, whereas the lateral parts bear scale-like plates, except the 3rd row,

attached to which as a rule there is a shaft with a more or less broad cutting edge. Each transverse row accordingly always has 17 plates, and on the whole the differences are not very great, but are nevertheless important for the systematics of the class. In most cases only the ,5 median plates are taken into consideration, of which the central plate and the intermediate plate lying on either side of it are moderately large, but the following, hooked plate is strong and has a very hard, black, detachable cutting edge. The structure of the rasping plates of lepidopleurids is characteristically variable. The central plate of *Lepidopleurus* species is longer than broad, but is variously shaped, sometimes broadest posteriorly, sometimes in the anterior part, nearly always with a distinct curved cutting edge; the intermediate plate in some species bears a distinct cutting edge, in other species it is
1040 rudimentary or completely reduced; most striking is the variability of the hooked plate, the cutting edge of which is sometimes narrow and unicuspid, sometimes provided with a small, sometimes rather large 2nd point, or also with 3 points. Among these forms, the most primitive ones have to be considered to be those with cutting edges on the central and intermediate plates and with a tricuspid hooked plate, such as in *Lepidoleurus algesirensis* (Capellini). In *Hanleya* the central plate is rather broad, with a distinct cutting edge, the intermediate plate is without such, and the hooked plate is tricuspid. The condition of the radula in *Hemiarthrum* shows a clear relationship with the Lepidochitoninae; the central plate is posteriorly pointed, anteriorly rather broad, with distinct cutting edge, the intermediate plate without such, the hooked plate with 3 cusps, and the cutting edge of the lateral plate is denticulate. The greatest similarity with this is shown by the radula of *Tonicella*, although the species are somewhat variable, but the radula of *T. rubra* (Linné) differs only by the slightly different form of the hooked plate. The groups of the genus *Lepidochiton*, as well as *Schizoplax*, *Mopaliella*, and *Middendorffia*, have cutting edges on the central and intermediate plates and tricuspid hooked plates, the margin of the cutting edge of the lateral plates is sometimes slightly nicked; the radula of *Nuttallina*, *Nuttalochiton* and *Notochiton* also shows similar structure: central plate rather broad, with distinct cutting edge, cutting edge of intermediate plate rudimentary or absent, hooked plate tricuspid, cutting edge of the lateral plate nicked. Of the species of the genus *Callochiton*, those belonging to the subgenus *Icoplax* have a well-developed lateral plate with a smooth-margined cutting edge, as well as the genus *Eudoxochiton*, whereas in *Callochiton* s. s. and *Trachyradsia* the lateral plates have lost their cutting edges.

The same type of radula with slight modifications has been retained in the families of mopaliids and cryptoplacids; in *Cryptochiton* the tricuspid hooked plates are very strong, whereas all other plates have lost their cutting edges. Among the ischnochitonids we initially find not very different rasping plates, but on the inner side of the hooked plates a wing-shaped appendage develops, which is at first inconspicuous, but attains a considerable size in *Pallochiton*, *Dinoplax*, and several Ischnochitoninae. In many *Ischnochiton* groups and in *Lorica* and the chitonids, a small appendage is also developed on the anterior part of the lateral margin of the intermediate plate. The form and size of the central and intermediate plates are often characteristic in the different groups; as a rule the cutting edge of the hooked plate in the ischnochitonids has 3 or 2 cusps, more seldom only a single, pointed cusp remains, or the cusps are obliterated, so that a broad rounded cutting edge is formed, such as that also characteristic of most of the chitonids. Only in the subgenus *Lucilina* (besides *Onithella*) and the genus *Schizochiton* the cutting edges have acquired 4 more or less distinct cusps.

If one compares the rasping plates of the loricates with a primitive condition, such as one must assume for the ancentral conchiferans, it then becomes clear that the former are highly specialized, which is evident mainly in the very characteristic structure of the hooked plates and in the reduction of the cutting edges of the marginal plates. Among the conchiferans, the most primitive snails possess rasping plates with numerous denticles, which are more or less distinctly developed more strongly on the median field than on the lateral fields. The radula of *Pleurotomaria* is characterized by the plates on the median field being more numerous than in the remaining rhipidoglossans, the central plate 1041 and the inner intermediate plates have no cutting edges, whereas the outer intermediate plates are strong and curved hooked-shaped, most lateral plates on their backside near the end bear a tuft of small bristles, which are lacking in all other rhipidoglossans and may represent a special acquisition of the recent pleurotomarians. The radula of the haliotids seems to be quite different, the central plate is broader than long, beside it on either side there are 5 intermediate plates, of which the 2 inner ones are medium-sized, the 3 following ones are very strong and armed with triangular cutting edges; the lateral plates are narrow and numerous. The radula of the scissurellids is also clearly different, besides the central plate, it has 5 intermediate plates, the 4th of which is the smallest and the 5th is the largest, all plates bear finely denticulate cutting edges. Similar characters are shown by the radula of the fissurellids, because here again the 4th intermediate plate is the weakest, and the 5th is the most strongly developed; the central plate of the

Emarginulinae is variably broad, it is broadest in *Fissurellidea*, and like the inner intermediate plates it has only slightly recurved, not or finely denticulate cutting edges, only in *Clypidina* the cutting edges are distinctly denticulate; the large outermost intermediate plate in most cases has only one outer lateral cusp on the pointed cutting edge; in *Hemitoma* there are in addition 2 small outer denticles and in *Clypidina* a small inner tooth. The radula of the Fissurellinae differs by the narrow neck of the central plate and the broad quadricuspid outermost intermediate plate. The first lateral plate has frequently lost its cutting edge.

The radula of the patellaceans is very peculiar, because the bases of the median plates bear detachable, very hard and brownish-yellow cutting edges, and because the radula is narrow and sometimes very long. The most original form has 5 plates in a row with simple cutting edges, somewhat farther posteriad on either side one plate with a broad, split quadricuspid cutting edge, the margin on either side bears three simple plates with small, nondetachable cutting edges (cf. Fig. 23). The central plate has a tendency towards reduction, it becomes narrow and loses its cutting edge, so that in most of the patellids it appears only as an inconspicuous longitudinal ridge; in the Nacellinae the innermost intermediate plate has disappeared; the lateral plates here are often only weakly developed. The radula of the acmaeids has the greatest similarity with that of the Nacellinae: central plate rudimentary, in most cases completely lost, on either side only one anterior intermediate plate with simple cutting edge and one posterior plate with bipartite cutting edge; of the lateral plates, in *Patelloida* there are 2 on either side, in *Lottia* and *Collisella* a small one is retained, they are absent in others. In *Pectinodonta* the outer cutting edge of the posterior intermediate plate is cuspidate and is fused with the other two to form a more or less long oblique cutting edge (cf. Fig. 27). The reduction of plates proceeds still farther in the median part of the radula of lepetids, in which the two inner cutting edges have become fused to form a common cutting edge which is truncated straight or is pointed, whereas the two outer ones are situated alongside and in most cases remain separate, in *Cryptobranchia concentrica* Middendorff they have united with the inner ones to form a single long cutting edge; lateral plates similar to *Patelloida*, with smooth or denticulate cutting edges, are always present.

In the series of trochaceans, the median part of the radula is in most 1042 cases represented by a central plate and on either side 5 intermediate plates, however the number of intermediate plates in the Margaritinae has become reduced to one (*Basilissa*, *Seguenzia*, *Guttula*), as in cyclostrematids, more seldom they are more numerous (*Cittarium*, some *Calliostom* species). The central plate in most cases has a constricted

neck with more or less broad lateral lamellae and a pointed cutting edge, rarely it assumes other forms (Umboniinae) and its cutting edge may become rudimentary (several turbindis); in *Phasianella* the central plate has become a narrow ridge or is completely reduced, and in *Eulithidium* a secondary central plate has developed by fusion of the two inner intermediate plates. In their form the intermediate plates in most cases resemble the central plate, and in the lateral plates are in most cases, narrow, although in the turbinids the innermost become often more or less strong. The radula of *Angaria* is characterized by the large size of the 2 outer intemediate plates, which are similar to those of *Haliotis*.

Among the neritaceans, the median part of the radula has undergone distinctly differentiated development, but as a rule on either side there are 4 intermediate plates, followed by numerous lateral plates. The central plate is weak, without distinct cutting edge, the first intermediate plate in the neritids is sometimes greatly broadened, with smooth cutting edge, in helicinids it is small, similar to the two following plates, which are also weakly developed in the neritids, on the other hand the outer intermediate plate is very strong, with large smooth or denticulate cutting edge and an outer process of the basal part. In hydrocenids, titiscaniids, and neritopsids the plates in the median part of the radula have become reduced, so that only a few outer intermediate plates are retained.

In the stirps of cocculinaceans, the cocculinids still have a typical rhipodoglossate area[1] with numerous narrow lateral plates, whereas the outermost of the 4 or 5 intermediate plates is large and strong, on the other hand in the Lepetellidae the lateral plates are reduced and the remaining plates strikingly differ not only among the known genera but also from the Cocculinidae.

Because in the trochaceans the number of intermediate plates on either side is already reduced to one, and the number of lateral plates is decreasing, the taeniglossate type differs but slightly from this condition, because in this case as a rule on either side there is one intermediate plate and 2 lateral plates.

The rasping plates of cyclophorids can be derived from a form which has been retained in some subfamilies (cf. Fig. 84): central plate anteriorly rather broad, with pentacuspid cutting edge, intermediate and inner lateral plate with 4, the outer one with 3 cusps. More or less modified is the form of the plates and the number of teeth, which occasionally decreases; the genus *Alycaeus* is characterized by large

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[1] "Gebiet" = area, in the original text is probably in error for "Gebiß" = dentition. —Editors.

lobe-shaped cutting edges with indistinct lateral cusps and the greatest modification is seen in the dentition of *Cochlostoma*, in which the plates are rather narrow and have large simple cutting edges, whereas the outermost plate has become rudimentary.

The other families of architaenioglossans, which live in freshwater, have highly variable dentition, the viviparids have in most cases rather large and thin plates with finely denticulate cutting edges, but the 1043 Campelominae have smaller plates with simple cutting edges; in the ampullariids the central plate is short and broad, with pointed, cuspidate cutting edge, intermediate plate with inner and outer adjacent cusps, lateral plates with strong, pointed cutting edges, in most cases with a small inner adjacent cusp; the radula of lavigeriids (Fig. 90) is also very different, outermost plate similar to that in the melaniids with several cusps.

Among the marine taenioglossans, the radula of the lacunids shows considerable similarity with that of some cyclophorids, so that one can think of a certain relationship; the base of the intermediate plate of the Littorinacea always has an outer identation, in littorinids the radula often reaches considerable length, whereas the form of the plates is modified, it is peculiar in *Tectarius* species. In the large stirps Rissoacea, which lives not only in the sea but also in freshwater, and partly even having invaded the seashore and land, the central plate on its posterior part has on either side often 1 or a few small denticles, but which can also be absent. The typical form of dentition, such as that occurring in the families of hydrobiids and rissoids, shows a posteriorly broadened central plate, in which the cutting edge in most cases has a few adjacent cusps, an intermediate plate with a more or less long lateral process, and lateral plates as a rule with finely denticulate cutting edges. The micromelaniids always lack the posterior denticles of the central plate. A certain similarity is also evident in the radula of the valvatids, but they also lack the posterior denticles and the intermediate plate is only slightly broadened, in *Valvata* s. s. all plates are finely denticulate, in *Borysthenia* the lateral plates have a slender tip, without denticles. Among the Barleeinae, the dentition in a few genera is similar to that in the Rissoinae, on the other hand are those in *Eatoniopsis*, *Boogina*, and *Eatonina* characteristically modified. The structure of the rasping plates of adeorbids, as far as known, also approaches that of rissoids. The same is also true of the Assimineinae, in which the central plates in part have retained the posterior denticles and in part have lost them; the form of the plates and their cutting edges varies rather strongly, as a rule they are cuspidate, the outermost plates being more or less finely denticulate, in the more original groups they are moderately broad, in the more highly developed

groups they become very broad and the denticles very fine and numerous, secondary larger denticles are formed due to several deeper incisions (Omphalotropidinae).

This radula is very similar to that in the pomatiasids, mainly through the very broad outer lateral plate (Fig. 102). The denticulation of which differs in the two subfamilies.

In the planaxids and Batillariinae, we find on the central plate a pair of posterior teeth, which however seem to be scarcely homologous with those of the Rissocea, also noticeable is the presence of a broad thin lamella on the outer lateral plates, which is similar to that in the pomatiasids; a corresponding lamella is also developed in *Cerithidea*. Among the cerithiaceans, the Litiopinae may represent the most primitive group, the dentition of which shows some similarity with that of the lacunids; the form of the plates within the stirps shows considerable differences, the intermediate plate is often produced into a more or less long process. Such a condition is also shown by the radula of Amaltheacea, in which the plates bear fine denticles, but the lateral plates have a tendency to become elongate and pointed, and in related groups as a rule we find pointed, more or less strong lateral plates, sometimes with only a few lateral denticles, as also in the Triviinae, whereas the other subfamilies of cypraeids have retained the characteristically formed lateral plates, of which those of the Amphiperasinae remind of the pomatiasids on account of the strongly broadened outermost plate.

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Some larger or smaller groups have deviated from the normal form of the taenioglossate radula, either in the very peculiar structure of the plates, or in their different number. *Microdiscula*, the rissoellids, the mathildids, and the solariids of the genera *Torinia* and *Philippia*, have only 5 plates in each row, in the homalogyrids, in *Turritellopsis* and *Lamellaria*, the lateral plates are completely lacking. On the other hand, in the choristids on either side there are 3 or 4 lateral plates and a small scale-shaped marginal plate (Fig. 164); in *Turritella* species on either side there may be 3 lateral plates, the struthiolariid genus *Perissodonta* has 5 lateral plates on either side. The genus *Solarium* differs from *Philippia* by the loss of the central plates and a considerable increase in the number of the remaining plates. The radula of the triphorids has undergone still greater modification, with its very small bi- or tricuspid plates in several rows, in the trochaclidids with numerous thin, pointed lamellae, in the ptenoglossans (Figs. 222 and 224) with more or less numerous uni- to tricuspid teeth which are sometimes fairly strong, and in *Aclis* and *Liostraca* with numerous, very small, needle-shaped teeth.

From the taenioglossan radula the stenoglossan radula is derived by loss of the intermediate plate and one lateral plate, so that the typical

stenoglossan radula has one central plate and a pair of lateral plates in each row. Very probably the central plate primitively has 3 teeth and the lateral plates are simply pointed, because this form is present in various families, and the other forms can be derived from it. The number of teeth on the central plate may increase, in some muricids through smaller secondary denticles, in a different way in *Pseudanchis* (Columbellidae), in some buccinids, in nassids, in *Olivella* (Olividae), in some mitrids, and in marginellids. On the other hand, the teeth decrease in number and may disappear completely, mainly in the columbellids (*Pyrene* and *Columbella*) and some buccinids (*Liomesus*, *Beringius*). The central plate of *Halia* and *Volutomitra* (Volutidae) has a single long cusp, and in *Cancellaria* this plate has assumed the form of very long and narrow lamella. In toxoglossans originally the central plate is still well developed, but in most cases it becomes small or disappears completely. In some families the lateral plates have developed teeth on the posterior margin, as in the columbellids, nearly all buccinids, galeodids, nassids, fasciolariids, mitrids, and in the 2 last mentioned families the lateral plates are very broad. In the toxoglossans the more or less elongate lateral plates have often acquired a wing-like, thin process (Turrinae), in the Brachytominae and the remaining conids they are modified into groove-shaped teeth often with barbs, their basal membrane is reduced, so that they project singly into the end of the proboscis and are used as stylets. The teeth of the terebrid genus *Hastula* are similar, whereas in *Diplomeriza* they are simply pointed, solid structures. The lateral plates are completely lost in *Cylindromitra*, most of the volutids, and in *Cancellaria* and marginellids. Several groups of prosobranchs have completely lost the radula, such as the partly parasitic melanellids, the stiliferids and Thycinae, the pyramidellids, as also magilids and the genera *Scaphella*, *Admete*, and *Terebra*.

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A survey of the phyletic development of the dentition in the prosobranch series shows that, apart from the few groups with abnormal structure, the number of plates in the transverse rows has consistently decreased, so that the extreme form shows only one central plate without lateral plates or only one pair of lateral plates without central plate; as a result of the loss of a homogeneous basal membrane, the toxoglossans have attained the most peculiar structure.

The opisthobranchs show an independent parallel development of the rasping plates. One can assume that, like in the ptenoglossans, first of all a form developed with numerous plates, differing from the normal taenioglossan form. The great variability of dentition among the genera of actaeonids is striking both in the form and size, as well as the number of plates, which may be considered as the primitive condition. They lack

a central plate, as in the ringiculdis, hydatinids, and notodiaphanids, and in most of the philinids, philinoglossids and gastropterids. On the other hand, the diaphanids have a well-developed central plate, in *Toledonia* in addition on either side there is a scale-shaped lateral plate, which is lacking in *Newnesia*. Approaching the latter are the sacoglossans with one longitudinal row of plates, while the bullariids have 2 plates with cuspidate cutting edges and a small scale-shaped plate on either side of the broad, denticuilate central plate, the atyids, aplysiaceans, most of the Pterota, the umbraculids and pleurobranchids have numerous plates. To these are related the Doridacea, in which the central plate is sometimes well-developed, sometimes lost, and the Aeolidiacea, in which the lateral plates have a tendency toward reduction, so that some of its families have a single-rowed radula, like the sacoglossans.

Some opisthobranchs have no radula: the retusids of the cephalaspideans; the genera *Corolla*, *Gleba*, *Laginiopsis* of the pteropods, also, the Oleidae, Phyllidiidae, Dendrodoridinae, Tethyidae, and Rhodopidae.

In certain groups of pulmonates we come across a form of radula which may possibly be considered as the initial form, in which all plates have an inner and an outer cusp on the pointed cutting edge. Very often the plates closer to the margin have become more or less strikingly differentiated from those of the median part, but on the whole, the modifications of the radula within this subclass are less extensive than in the other two.

Among the ellobiids the lateral plates of *Carychium* have a small inner and outer cusp on the pointed cutting edge, the broader marginal plates have a few small cusps; in the Pedipedinae the lateral plates lack the outer cusps; the radular plates of the Ellobiinae are more modified, their cutting edges tend toward enlargement and simplification (Fig. 558). The radula of the Amphibolacea (Fig. 560) is peculiar. The cutting edges of the lateral plates of the chilinids, latiids and physids are broadened and denticulate and are arranged in oblique rows, whereas in the lymnaeids and planorbids they have retained the more original form and arrangement; among the ancylids some still have a similar dentition, in others it is considerably modified (Figs. 579 and 580).

1046   The most striking modifications of the rasping plates have taken place in some terrestrial pulmonates associated either with predatory habits or with arboreal life. The radula of the predatory snails is characterized by more or less strong, narrow, claw or thorn-shaped plates arranged in oblique rows; such are found in the rathouisiids, in oleacinids and testacellids, in daudebardiines, trigonochlamydids and in the Streptaxacea. The dentition of tree snails shows enlarged, especially

broadened cutting edges on the plates which are arranged in oblique rows; such a form has developed in genera belonging to several groups [*Peruinia* (Fig. 626) (Clausiliidae), *Rhinocochlis* and *Sasakina* (Fig. 692) (Xestinae), *Oxychona* and *Zaplagius* (Fig. 710) (Bulimulinae), *Gaeotis* (Fig. 721) (Amphibuliminae), the Urocoptinae (Figs. 727 and 728), *Amphidromus* (Fig. 739) and *Calycia* (Fig. 741) (Pleurodontidae)]. A peculiar development has taken place in 2 helicid groups (*Vidovicia* and *Allognathus*), wherein the large radula is beset with numerous rows of very small, narrow, hook-shaped denticles.

The radula of the scaphopods is very uniform, always with 5 plates in each transverse row, of which the central one and the two outermost have no cutting edges (Fig. 786). The cephalopods also do not show great variability. Each transverse row of the radula teeth in *Nautilus* consists of 13 plates with simple, partly long, partly short, cutting edges (Fig. 868). The dibranchians possess 7 plates, in most cases with simple pointed cutting edges, occasionally also with a pair of toothless marginal plates in each row. In some groups the bases of the 3 median plates form pointed outer cusps. Only the octopods have undergone distinct modifications, the most striking of which is the strong broadening of the plates in the Bolitaenacea (Fig. 887); rarely the radula has become distinctly rudimentary (*Thaumeledone*) or has completely disappeared (Spirulidae, Cirroteuthacea).

In patellids, below the anterior end of the radula, there is a transversely pleated bulge (sublingual organ), the individual folds of which bear a strong cuticula on their anterior side; in acmaeids this organ is variable, in most cases it is covered by a denticulate cuticula, the area around the mouth opening may also show similar denticulations. Such structures also occur in the neritids, and in *Cocculina* species they are in the form of small bristles. Some of the doridids possess a special armature of the lips.

The **jaw** is a plate situated on the dorsal wall of the buccal cavity, opposite to the anterior part of the radula. In most cases it consists of parallel rods and a cuticula and originally it is bipartite. It protects the epithelium it covers against injury from the radular teeth. In loricates such a jaw is not yet developed, in bivalves it has been lost, like the entire buccal mass. Among the snails also in many groups it has become rudimentary or has been totally lost. It shows a peculiar condition in the docoglossans, in which the layer of rods is lacking, the anterior marginal part is outwardly reflected, so that here a sharp edge is formed, whereas a large portion does not lie free toward the buccal cavity, but is covered by cartilage, muscles, and the sensory palps, which are attached to it. The cymatiids and doliids have a pair of jaws which are completely

separate from one another, those in the latter are produced anteriorly into hooks. Among the Trochinae a few genera have lost the jaw, as also the Neritacea and Cocculinacea, in which it is developed merely as a simple cuticula. It is weakly developed in the littorinaceans and is not or

scarcely present in the pomatiasids, assimineids, trochaclidids, melanellids, stiliferids, pyramidellids, heteropods, most of the cypraceids (except Triviinae) and stenoglossans. Among the opisthobranchs also, the jaw has been lost in several groups: the Diaphanidae, Retusidae, Scaphandridae, Philinidae, Philinoglossidae, Aglajidae, of the pterotans the Clionidae, Thliptodontidae, Anopsiidae and Laginiopsidae, also the sacoglossans, the umbraculids, some polycerids, doridids and the phyllidiids, and finally the hedylids, *Tethys* and *Rhodope*. Among the pulmonates the jaw is lacking in the amphibolids, .gadiniids, most of the oncidiids and achatinellaceans, and some predatory snails: rathouisiids, oleacinids, systrophiids (?), trigonochlamydids and Streptaxacea.

Occasionally the rods of the jaw are peculiar, in the rissoellids they are rhombic and are finely denticulate on one side, in *Turritellopsis* they are basally broadened and distally provided with a few small cusps, in *Microdiscula* they are small in number and are arranged arch-shaped, the outermost are the largest, more or less long knife-shaped with finely denticulate anterior margins. The rods of some opisthobranchs also have denticulate margins. The jaw of aeolidiaceans is sometimes strongly developed, the two halves may fuse together and acquire a cutting edge. In the buccal mass of *Acera* and aplysiids, besides the jaw, there are numerous minute teeth on the dorsal wall, and most of the Pterota have evaginable hook sacks.

The jaw of pulmonates is in most cases a half-moon-shaped, more or less strong structure, it is rarely distinctly composed of rods (ellobiids) or platelets (vaginulids, some endodontids), in the succineids and athoracophorids it has acquired a broad reflected lamella (Elasmognatha); frequently the center of the concave margin has a tooth-shaped projection. More or less numerous folds are developed on the jaw of bulimulids and ribs in many helicaceans. In the lymnaeids and planorbids the jaw has a pair of lateral processes.

The jaw of scaphopods is horseshoe-shaped, with sharp edge, and overlies an epithelial fold. The jaw of cephalopods is much more strongly developed; the upper jaw, corresponding to the jaw of gastropods, consists of a broad palatal plate and an outer plate which is fairly broad only in the center and rapidly narrows toward the sides, the cutting edge forms a pointed tooth; besides the upper jaw, the cephalopods also possess a lower jaw, the two together serve for biting like a parrot's beak, in *Nautilus* the internal esophageal lamella is not broader than the

outer plate in contrast to the Dibranchia, in which the outer plate is distinctly narrower than the esophageal lamella. The form of the jaw undergoes little modification, in the bolitaenaceans the jaw is softer than usual. The radular sack bears a horny cuticula armed with thorns.

In mollusks the buccal cavity and lips, or the oral tube, are as a rule provided with stomodeal glands, which develop from epithelial mucus cells. The loricates, on the anterior part of the dorsal wall, possess only one pair of mucus glands in the form of sacks, which are simple in small animals, and more or less folded in large animals; the posterior part of the subradular blind sack is also covered by glandular epithelium; salivary glands are absent.

Similar mucus esophageal sacks are developed not only in rhipidoglossans but also still in the lower taenioglossans, they are disappearing in the higher forms. Opening beside their anterior ends are a pair of **salivary glands**, which are very rarely absent (Neritacea and Cocculinacea, Trochaclididae, Melanellidae). They may be simple tube-shaped glands or they may be more or less highly branched; their structure may be partly correlated with the size of the animal, but also with their phylogenetic relationships. Among the primitive snails, *Pleurotomaria*, *Haliotis* and fissurellids have branched glands, among the trochaceans such glands have been reported in *Calliostoma*, they probably also occur in others, on the otherhand, simple tubes are present in others like *Gibbula* and *Monodonta*. In patellids the glands are profusely branched and each is divided into 2 parts, which open close together into the anterior part of the buccal cavity, each with its narrow duct; the two parts probably provide different secretions. In scalids 2 pairs of tube-shaped glands are present, one pair of which opens into the sheaths of a pair of horny stylets and probably produce a toxic secretion, and in addition some other glandular tubes lie on the outer side of the jaw plates. The glands in *Recluzia* are similar, but the true salivary glands form distinct lobes, whereas in *Janthina* both pairs are tube-shaped, the ducts near the jaw are more weakly developed and the stylets are lacking. The glands of the doliaceans are very strongly developed and produce an acidic secretion—in most cases sulfuric acid; in *Dolium*, at the beginning of each excretory duct, also lies a small acinous accessory gland. The salivary glands of the rhachiglossans as a rule have a similar, compact structure; besides these, several groups also possess agland which is sometimes paired, sometimes unpaired, in *Volutocorbis* it is considered as the 2nd pair of salivary glands, in *Melo* there is a pair of small elliptical glands with long, terminally joined excretory ducts; in *Cancellaria* there are 2 pairs of tube-shaped glands, the longer of which discharge at the mouth opening; *Oliva* has an unpaired gland with narrow

excretory duct and the Mitrinae have a long tube-shaped protrusible poison gland. It is not certain whether all these glands are homologous and whether they all have the same function. The structure of the salivary glands of the toxoglossans is very different; here they are very unequally developed, the right one is medium-sized, simple tube-shaped, in contrast the left one is modified into a large poison gland with a very long excretory duct and an unbranched gland surrounded by strong musculature, with the secretory cells probably situated in the outer part of the muscular sheath.

In the opisthobranch series the oral tube glands are often strongly developed; the salivary glands in most cases represent a pair of simple tubes, in oxynoids they form a pair of bundles of fine tubules. In the notaspideans the two salivary glands are in the form of more or less branched, often interconnected masses and their excretory ducts in most cases have an ampulla (Pleurobranchidae) or a transverse connecting duct (*Umbraculum*); in addition, there is an unpaired, often very strongly branched gland opening into the oral tube, its secretion contains sulfuric acid. The salivary glands of nudibranchs are variable, they are sometimes very small, in other cases they are strongly developed, as in *Sphaerostoma* and especially in *Armina*, where they form many small tubes.

In the pulmonates they are in most cases lobed, more seldom roundish.

In scaphopods the oral tube forms a glandular pouch on either side. They lack salivary glands. In the bivalves, along with the buccal mass, the glands have also disappeared. The pharynx of *Nautilus* on either side of the tongue contains a broad, flat, somewhat lobed gland with very short excretory duct; this gland cannot be considered homologous with the salivary glands of snails. Similar glands are more or less developed also in the Dibranchia, in *Spirula* as minute irregular depressions in the posterior part of the buccal mass and on the subradular organ; they are best developed in the octopodids, where they have moved out from the buccal mass and are in the form of paired masses, the excretory ducts of which open into the radular sack. In addition, the dibranchians possess a poison gland lying behind the buccal mass and opening into the subradular organ by a long duct; occasionally it is paired and the excretory duct is bifurcated; this again is a new structure, which is not homologous with similar glands of some snails.

The **foregut** of the primitive mollusks is not a simple esophageal tube, but is provided with 2 glandular sacks, which are connected with it on both sides. They are distinctly developed in the loricates, scaphopods and most of the prosobranchs. In the former the sacks are separated by muscle bundles posteriorly from the esophagus, so that they are connected

only with its anterior part; its epithelium forms villous elevations. The foregut of the prosobranchs has undergone a rotation of about 180°; in the primitive groups the glands are connected throughout their length with the median part which is separated only by longitudinal folds; internally it has villous or fold-shaped elevations. The longitudinal folds are variably developed; when they are distinct both dorsally and ventrally, the glandular sacks appear to be lateral, when the ventral folds are reduced so that only a dorsal groove is present, which may happen mainly in the posterior part of the esophagus, then the gland is to be considered as a ventral structure. The esophageal pouches of the neritids are rather short, internally with numerous folds, in *Hydrocena* they are long and only slightly lobed, posteriorly in the form of a blind sack. *Cyclophorus* has esophageal glands, which are anteriorly channel-shaped, posteriorly sack-shaped; in *Pila* they represent rounded sacks, which open at the beginning of the esophagus through short ducts, in one *Ampullarius* species the esophagus is greatly widened. The esophageal glands of *Viviparus* are moderate expansions without sack-shaped part, of the longitudinal folds only the dorsal ones are developed. In the assimineids (*Pseudocyclotus*) the esophagus anteriorly has a pair of lateral grooves, which then fuse ventrally and posteriorly terminate as blind pouches.

The turritellids and solariids have a long and narrow esophagus, but in the groups Amaltheacea, Calyptraeacea, Strombacea and Heteropoda also the esophageal glands are weakly or scarcely developed. In contrast, the Naticacea, Lamellariacea and Cypraeacea have a very well-developed gland with numerous lamellae. The esophageal gland of the Doliacea represents a ventral bulge with many folds, delimited by a pair of longitudinal folds; in *Dolium* there are also numerous gelatinous pads on the longitudinal folds, and in the blind sack at the posterior end of the gland fine folds with special epithelium are developed.

The Rhachiglossa also possess well-developed foregut glands. In muricids these consist of a smaller part situated directly on the esophagus and a larger part opening into it by a duct (Leiblein's gland). It is in most cases a more or less large tube-shaped appendage of the foregut. Because, according to more recent opinion, the poison gland of the 1050 toxoglossans represents one of the two salivary glands, it cannot be homologous with Leiblein's gland and hence the esophagus lacks special glands. In the opisthobranchs also it is in most cases simple, sometimes distinctly widened; some sacoglossans have a more or less large suctorial crop on the buccal mass and a glandular tube may be present on the esophagus. The esophagus of *Nautilus* is greatly enlarged, in decapods it is thin, in octopods it often has a lateral crop-like dilation.

The more or less enlarged **stomach** receives the originally probably symmetrical excretory ducts of the large digestive gland, although this symmetry of the stomach is more or less greatly disturbed. In general it is wider in herbivores than in carnivores. The stomach of snails is often sack-shaped, wherein the cardia and pylorus have come close together. The pleurotomariids possess a well-developed spiral blind sack; such a structure is also found more or less distinctly in many trochaceans, but the scissurellids and fissurellids also possess a blind sack, on the other hand it is lacking in the docoglossans and most neritaceans. Sometimes, folds or constrictions separate different parts. The stomach shows the most striking differences in the series of opisthobranchs. Whereas the primitive groups (Actaeonidae, Ringiculidae, Hydatinidae, Diaphanidae and the subgenus *Laona* of the Philinidae, also the Gastropteridae and Aglajidae) possess a simple sack-shaped stomach, in other groups hard plates are developed in its anterior part, which can be worked against one another by strong musculature. Their form and number is important for systematics. In *Bullaria*, besides 3 strong, quadrilobate plates, there are also a few cone-shaped spines, the 3 plates of the atyids are keeled and are more or less strongly transversely furrowed; in *Haminea*, anterior to these, there are also 3 pairs of small denticles; the form of the 3 plates in the Retusidae and Scaphandridae is somewhat different, in *Scaphander* and *Philine* s. s. the plates are calcified, one smaller than the other two. The stomach of Runcinidae contains 4 cuspidate plates; several pyramid-shaped plates in 2 to 3 transverse rows are present in *Acera* those in the Aplysiidae are similar. The thecosomate pteropods also possess a few masticatory plates. The stomach of the umbraculids is armed with numerous small teeth. The plates or teeth occurring in some nudibranchs are not homologous with those of the pleurocoels; *Marionia* has numerous narrow plates, *Scyllaea* and *Melibe* have a ring of plates and *Bornella* longitudinal rows of thorns in the posterior part of the stomach.

In the shell-less sacoglossans, the **liver** has lost its compact form, in *Hermaea* it forms 2 lateral canals with processes which branch in the dorsal appendages, in elysiids the branches extend into the lateral folds; in the limapontiids the digestive gland is not greatly branched, but is divided into 2 anterior and 2 posterior main parts. In the aeolidiaceans also, this gland has undergone a similar modification to a variable extent, in *Heterodoris* it forms 3 main lobes with short terminal branches, in the stomach of *Armina* on either side opens a small and posteriorly a large branch, similar to a few other groups. In the hedylids and pseudovermids the branches are not very developed; the liver of the phyllirrhoids has 3 or 4 simple branches. The branches form a network in the body wall of the zephyrinids and notaeolidiids; in a few groups the branches extend

into the dorsal appendages and open externally at their ends, on each of their ends an expansion is formed, which is covered with characteristically modified cells. The contents consists of cnidocysts, which have been derived from granules of the liver cells.

The stomach of pulmonates has undergone fewer modifications. In the basommatophorans it is in most cases strongly muscular and is provided with a small blind sack. The stomach of the rathouisiids forms a long blind sack, which, along with the hepatic ducts opening into it, occupies the entire posterior half of the body.

A certain similarity with this is shown by the stomach of the dentaliids. As in some snails, the stomach of bivalves in most cases has a blind sack, which contains a crystalline style, rarely also an additional blind sack (Adesmacea). The cephalopods also have a blind sack, which opens into the posterior chamber of the stomach, and is sometimes roundish (*Nautilus, Sepia*), sometimes long and more or less spirally inrolled, as in most of the dibranchs. The liver of *Nautilus* consists of 2 halves, which are further divided into lobes, in the spirulids and sepiids also the 2 halves are separated, it is otherwise in most cases undivided, in the loliginids it is traversed by the esophagus. The pancreas constitutes a part of the liver, adjacent to the beginning of the excretory ducts or is developed within them.

The **intestine** in the primitive herbivores always forms at least one loop. Among the loricates, the simplest form shows 2 loops, which become more complicated in the higher groups, most strongly in the family Chitonidae. A single loop is formed by the initial form in snails, as also still happens in the series of trochaceans. The intestine of fissurellids is somewhat longer, and very long in the patellids. Among the taenioglossans a few old forms still have a moderately long intestine, but in most cases it is short and scarcely coiled, as also in the stenoglossans; the terminal part of the intestine is often distinctly thickened. *Actaeon* also has a short intestine, in a few other pleurocoels it forms 1 or 2 loops, in nudibranchis it is short; in *Calma* lacking. Among the taxodont bivalves, *Arca* as a single loop, similar to some nuculaceans, whereas in *Nucula* the loop has become elongated by inrolling; the intestine of *Solenomya* is very short, also in poromyaceans; in most it forms few loops. Among the cephalopods the intestine is as a rule short, in *Nautilus* with one loop and in *Tremoctopus* with several coils.

On the rectum of some snails, blind sack-shaped evaginations have developed, which do not have any great phyletic significance, thus there is a narrow tube in the fissurellids, a branched gland in the naticids and muricids; among the pulmonates, some oncidiids have a glandular tube. Much more strongly developed is the ink-sack of the dibranchiate

cephalopods, which however in lacking in the cirrate octopods and in the Bathypolypodinae.

The condition of the **nervous system** is of great importance for the recognition the phyletic interrelationships of mollusks, mainly its form in the different classes and its development in the series of snails. The nervous system of loricates shows a primitive structure, which in most cases reminds of some worm-like animals, especially Solenogastres, mainly through the presence of a pair of gangliar ventral cords and a pair of lateral cords which posteriorly merge into one another above the rectum. The head contains a gangliar ring around the oral tube, which is anteriorly and especially laterally much stronger than in the posterior part. The anterior half of the ring gives off 3 series of nerves, above those to the perinotum, in the center to the horseshoe-shaped head fold, and below those to the lips, corresponding to those from the posterior half of the ring. From the initial parts of the latter arise connectives to the ganglia of the subradular sense organ and to the buccal ganglia, which innervate the musculature of the buccal mass. These ganglia also form an esophageal ring and originally consist of 2 pairs of small ganglia; the posterior commissure lies above the beginning of the radular sheath. From the lateral parts of the large esophageal ring arise posteriorly both the ventral as well as the lateral ganglionated cords, which are originally joined with one another by several transverse connectives, although the connectives between the ventral and lateral cords tend toward reduction, at any rate in some species only a few or none have been found. While the ventral cords supply the foot, the lateral ones innervate the perinotum, the musculature between the shell valves, the aesthetes and the gills, at which small ganglia may be present in the lepidopleurids.

Among the conchiferans, the nervous system of only the most primitive gastropods shows enough similarity with that of loricates that definite homologies are ascertainable; mainly the esophageal rings and the pedal ganglionic cords differ little. Because in *Haliotis*, which is especially suitable for comparison, the epipodial folds terminate at the cephalic tentacles and, unlike the perinotum of loricates, are not continuous anterior to the head, the nerves corresponding to those going from the anteriormost part of the esophageal ring to the perinotum are lacking; the ganglia of the subradular organ and the anterior commissure of the buccal ganglia are also absent. The nerves corresponding in the two groups are those to the head fold and to the anterior part of epipodium = perinotum, in this connection it only needs to be considered that the loricates lack epipodial tentacles and eyes, whereas in *Haliotis* the lateral swellings of the esophageal ring give out nerves to the large cephalic

1052

tentacles, to the eyes, and on either side one nerve to the dorsal body wall. In the anterior part of the ventral gangliar cords the cells have become sparse, so that this part is to be designated as cerebropedal connectives, nevertheless the latter on either side give out a pair of nerves to the epipodium and to the dorsal body wall. Beside these connectives, a 2nd pair of connections between the esophageal ring and the ventral cords has developed, running over the cerebropedal connectives and reaching the dorsal part of the ventral cords. This part is joined with that of the other side by a strong gangliar commissure, and it gives off another nerve to the dorsal wall, a nerve into the mantle and a gangliar strand, the so-called visceral commissure, which has assumed the form of an 8 as a result of the peculiar twisting of the visceral sack along with the shell against the foot and head, in which the part arising from the right pedal cord runs left above the intestine, and that arising from the left cord runs to the right below the intestine. The dorsal initial part of the pedal cords and of the visceral commissure, giving off the mantle nerves and the upper connectives to the esophageal ring, is known as the pleural ganglia. The pedal cords are connected with one another farther posteriorly by several commissures arising from the ventral half and send nerves to the foot, to the epipodium, and nerves proceeding dorsally from 1053 the inner side of the dorsal half, which correspond with the anterior nerves to the dorsal wall and probably also to both mantle nerves from the pleural ganglia. The epipodium contains a gangliar nerve net, which serves the sense organs and the musculature. The visceral commissure innervates the inner margins of the two mantle lobes as well as the viscera, and is connected to a pair of branchial ganglia.

In comparing the most primitive snails with the loricates, if we accept the homology of the epipodial gangliar with the lateral cords, the main difference then is the gangliar visceral commissure of the former, which at all events has arisen along with the mantle lobes and the attached ctenidia; also correlated is the development of the cerebropleural connectives. However, it also needs to be emphasized that the nerves corresponding to those supplying the dorsal body wall of *Haliotis* are not known in the loricates, and that the dorsal musculature in the latter is innervated from the lateral cords.

The nervous system of *Pleurotomaria* differs from that of the haliotids mainly by the fact that the visceral commissure arises not from the anterior end of the pedal cords but from the cerebropedal connectives, and is asymmetrical, extending farther forward on the right than on the left; in addition, the epipodium is more weakly developed and a head fold is absent. In the trochids the beginning of the visceral commissure has a similar position as in *Haliotis*, but in this case, along with the right

gill, the ganglion belonging to it has been lost; at the connective to the branchial ganglion and at the origin of the visceral nerves, the ganglion cells have drawn together to form more or less distinct swellings that are known as the supraintestinal and the visceral ganglion, whereas a subintestinal ganglion is still scarcely delimited; as a rule a connection joining the latter with the right mantle nerve and of the supraintestinal ganglion with the left mantle nerve have developed, as they are present in most prosobranchs. The pedal cords of the Fissurellidae are considerably shortened, and do not lie within but on the musculature; epipodium forms a series of tentacles with sensory hills, the ganglia of which are not interconnected.

In the docoglossans the posterior part of the esophageal ring contains distinct ganglia for innervation of the palps lying beside the oral aperture; the commissures between the pedal cords, besides the anterior main commissure, are in most cases restricted to only one or two in the posterior part of the foot; short gangliar bridges connect the anterior ends of the pedal cords with the well-developed pleural ganglia, each of which as a rule sends out 3 strong nerves into the mantle, in which, along the marginal tentacles, a gangliar nerve ring has developed, which therefore cannot be considered as a homologue of the lateral cords of the loricates. The fairly weak visceral commissure is somewhat displaced to the right hence the connective of the left pleural ganglion with the subintestinal one is distinctly longer than that of the right pleural ganglion with the supraintestinal one, whereas, conversely, the nerves to the gill rudiments situated on the neck are longer on the left than on the right. From the left branchial ganglion a nerve runs out on the underside of the mantle obliquely forward and to the right, corresponding to the left pallial nerve of the zeugobranchs; in the acmaeids from this nerve near its beginning, branches off the branchial nerve.

1054 The nervous system of the neritaceans shows several striking characteristics. Due to shortening of its connectives to the pleural ganglia, the subintestinal ganglion has come so close to them that in most cases it lies between them and in immediate contact with them; and together with the anterior ends of the pedal cords it forms a narrow ring in which the statocysts often lie. In addition, it is quite remarkable that, unlike in the trochids, the gill of the neritids is not served by the supraintestinal ganglion, but that the branchial nerve is a branch of the pallial nerve, which arises from the left pleural ganglion; the hydrocenids and helicinids lack the gill and this nerve.

The nervous system of the cocculinaceans is more concentrated. A labial commissure between the cerebral ganglia seems to be absent, the small pleural ganglia lie above the larger pedal ganglia which have only

one commissure. The posterior part of the mantle is innervated by the pleural ganglia, on the other hand the supraintestinal ganglion gives off a strong nerve into the anterior part of the mantle, a branch from which enters the gill.

Among the architaenioglossans, the viviparids and cyclophorids are close to the trochids, both of them have pedal cords with a few commissures and a normal visceral commissure with weakly developed parietal ganglia, which are connected to the pallial nerves; the labial commissure still retained in the viviparids is reduced in the cyclophorids, whereas the pleural ganglia, which in the cyclophorids lie at the anterior ends of the pedal cords are in the former closer to the cerebral ganglia; the connectives of the parietal ganglia with the pallial nerves have become more shortened in the cyclophorids, especially on the right. The ampullariids also possess a weak labial commissure, the pleural ganglia lie at the anterior ends of the pedal cords, the subintestinal ganglion is fused with the right pleural ganglion and is joined with the left pleural ganglion by a connective situated posterior to the pedal commissure, as is also the case with the supraintestinal and the visceral ganglion. A strong, straight connection between the left pleural ganglion and the supraintestinal ganglion is conspicuous; in its place in *Lanistes* a connective is formed only by a branch of the pallial nerve. Hence in this case a zygoneury has developed on both sides.

Among the marine taenioglossans, the littorinids show close relations to the trochids, but after the loss of the labial commissure, the cerebral ganglia have become displaced farther posteriorly and the pleural ganglia have come very close to them; the pedal ganglia are no longer cord-shaped, but are rounded, anterior and posterior to each ganglion lies a smaller ganglion, of which the posterior ones in *Lacuna* are joined by a commissure; in the visceral commissure both parietal ganglia are well developed and are connected with branches of the pallial nerves.

Approaching this condition, although with certain differences, are some other groups, such as the planaxids, the cerebral ganglia of which have a shorter commissure and are connected with the pleural ganglia, the subintestinal ganglion also closely adjoins the left pleural. In the hydrobiids also these ganglia and the supraintestinal ganglion lie close together; a posterior pedal commissure is in most cases present; the condition in the valvatids is similar. The pomatiasids have a nervous system similar to that in the littorinids, the connectives between the pleural and parietal ganglia are long, small ganglia on the pedal ganglia are lacking. Among the cerithiaceans, in the Pleurocerinae, Melanatriinae, and Melanopsinae there is a long cerebral commissure and distinct connectives between the different ganglia, but the cerebral and pleural

ganglia in most cases lie close together and the subintestinal ganglion on the left pleural ganglion, while it is often joined with the right pleural ganglion by a straight bridge.

Among the ptenoglossans, the scalids have short commissures between the cerebral and pedal ganglia, and attached to the former are the pleural ganglia, with which the supraintestinal ganglion is connected by a shorter left and a longer right connective, whereas the subintestinal ganglion is joined only with the left pleural ganglion. In *Janthina*, as a result of the very large size of the buccal mass, the esophageal ring is greatly widened, the cerebral and pedal commissures are long, the pleural ganglia are fused with the cerebral ganglia and each parietal ganglion is joined with both pleural ganglia, not quite in a straight line with that of the same side.

Both parietal ganglia of the capulids are joined with the pleural ganglia by distinct crossed connectives, and the subintestinal ganglion is joined with the right pleural ganglion by the pallial nerves; the long groove-shaped lower lip is innervated by the pedal ganglia and is therefore homologous with the anterior foot lobe of the Vanikoridae, Amaltheidae, and Trichotropidae. The nervous system is much more concentrated in the calyptraeids, in which the subintestinal ganglion lies near the right pleural ganglion and is broadly joined with it; a left zygoneury is not yet developed in *Calyptraea*, but in *Crepidula* the supraintestinal ganglion lies between the pleural ganglia, connected directly with both.

Originally the nervous system of the Strombacea is less concentrated. Corresponding to the elongated neck region, the parietal ganglia of *Xenophora* are widely separated from the pleural ganglia, the subintestinal ganglion is directly joined with the right pleural ganglion, but already in *Struthiolaria* the subintestinal ganglion adjoins the left pleural ganglion, whereas it is connected with the right pleural ganglion by a rather short connective; the connective of the supraintestinal ganglion with the right pleural ganglion is longer. The nervous system of the Aporrhaidae and Strombidae has greater similarity with that of *Xenophora*.

The nervous system of the naticids is characterized by the absence of right zygoneury, whereas the supraintestinal ganglion is connected with the left pleural ganglion by the pallial nerve; the latter ganglion has a sometimes short, sometimes longer connective to the subintestinal ganglion; the connectives of the supraintestinal ganglion are longer. The ganglia of *Lamellaria* are much more concentrated, with double zygoneury, the supraintestinal ganglion lies over the left pleural ganglion, the connectives to the supraintestinal ganglion, which lies to the right of the remaining ganglia, are somewhat longer. In the cypraeids the supraintestinal

ganglion lies close to the pleural ganglia joined with both of them, the subintestinal ganglion however is more or less distinctly removed, and a right zygoneury is sometimes incomplete; very striking is the condition of the pedal ganglia, which is Cypraeinae are produced into 2 long cords joined together by a few commissures, whereas in the Triviinae they are greatly prolonged posteriorly, but are not rope-ladder-shaped and from their posterior ends send out nerve bundles into the foot. Because the latter group, in general, appears to be more primitive than the former, which is also evident from the longer connectives of the parietal ganglia, and, because there are otherwise no closer affinities between the cypraeids and the architaenioglossans, the assumption lies near that the rope-ladder-shaped pedal cords in this case represent a secondary structure.

1056

Among Doliacea, in the cymatiids the parietal ganglia are rather distantly removed from the pleural ganglia, the subintestinal ganglion is joined directly with both pleural ganglia, the supraintestinal ganglion is connected with the left pleural ganglion by the pallial nerves. The condition in the cassidids and doliids is similar, whereas in the pirulids the ganglia lie more closely together, so that the nervous system is similar to that in the stenoglossans. Corresponding to the small size of the buccal mass, in the latter the buccal ganglia approach the cerebral ganglia and the excretory ducts of the salivary glands lie outside the esophageal ring, whereas they show still great variation in the approach of the parietal ganglia to the pleural ganglia. For instance, in *Clavatula* the subintestinal as well as the supraintestinal ganglion are joined with them by distinct connectives, and in *Conus* the former of these is even more distantly removed, but the latter however adjoins the right pleural ganglion. The subintestinal ganglion in most cases lies between the two pleural ganglia, closely united with them, whereas the supraintestinal ganglion is joined with the right pleural ganglion sometimes by a rather long connective (Volutidae, Cancellariidae), sometimes by a short connective (Buccinidae); this may vary within the same family. All ganglia are most concentrated in olivids and marginellids.

A comparison of such a nervous system with that of *Haliotis* shows enormous differences, although these terminal forms are connected with one another through all possible intermediate forms. Interruption of the labial commissure results in the lateral thickenings of the esophageal ring forming the cerebral ganglia, connected together only by an upper esophageal commissure. The pleural ganglia, originally adjoining the anterior ends of the pedal cords, and innervating mainly the mantle, shift away from them and adjoin the cerebral ganglia. The long pedal cords shorten gradually and lose their numerous commissures, of which the large anteriormost alone is left, likewise the epipodial nerves. In the

visceral commissure develop the parietal ganglia and the visceral ganglion, the former of which first become connected with the pleural ganglia of the same side through pallial nerves, thereafter often giving rise to a direct connection, mainly on the right side (zygoneury). Finally, all ganglia move close together, being separated only by more or less distinct constrictions.

Among the opisthobranchs, the nervous system of the actaeonids shows strong similarity with certain taenioglossans; the pleural ganglia are united with the cerebral ganglia, the latter are also joined together by a fine ventral commissure in addition to the upper esophageal commissure; the pedal ganglia have a strong anterior and a weak posterior commissure, the ring formed by these ganglia and their connectives surrounds the anterior part of the buccal mass, the connectives between the parietal ganglia and the cerebropleural ganglia are rather long and crossed and on either side contain a small pallial ganglion. Already in the pleurocoels there are more or less striking modifications. The anterior position of the esophageal ring is retained in some families, whereas in *Haminea* (Atyidae), *Acera* (Aceridae), and aplysiids it is displaced to the posterior of the buccal mass; the pleural ganglia often remain separate; whereas 1057 the gill shifts toward the right and then posteriorly and the mantle cavity correspondingly widens posteriorly, the supraintestinal ganglion is pulled to the right so that the crossing of the visceral commissure is eliminated. The ganglia contained in the latter in pleurocoels as a rule remain separated from the pleural ganglia by longer connectives, except the right pallial ganglion, which not seldom lies on the pleural ganglion, sometimes (*Aglaja*, *Philine*) the supraintestinal ganglion also adjoins; however, in *Gastropteron* all ganglia of the visceral commissure adjoin the pleural ganglia and are situated lateral to the oral tube. The condition is *Tylodina* is similar, where only the visceral ganglion remains separate, and in *Pleurobranchaea*, in which the supraintestinal ganglion is united with it, from this condition *Pleurobranchus* differs only by the short cerebral commissure, whereas in *Umbrella* and the nudibranchs all these ganglia are united with the pleural ganglia. In *Petalifera* and *Notarchus* (Aplysiidae) these visceral ganglia lie between the pleural ganglia, but ventral to the esophagus. Besides the cerebropleural and pedal ganglia the esophageal ring of sacoglossans also contains 2 or 3 visceral ganglia, the left of these begin sometimes fused with the median; they lie above the pedal ganglia.

Accordingly, the nervous system in the series of opisthobranchs also shows considerable variation, the concentration of the gangliar mass has taken place in different ways. In the nudibranchs the visceral commissure is weak, situated below the esophagus, and the ganglia are aggregated

above and beside the esophagus, whereas in the sacoglossans the commissure with its 2 or 3 ganglia lies above the pedal ganglia.

The variations in the nervous system of the pulmonates are less striking, involving mainly the length of the connectives between the ganglia. In only one species of *Chilina* could an indication of the crossed visceral commissure be demonstrated, which is still rather long in this case, similar to that in *Latia*. The originally independent pleural ganglia are in most cases close to the pedal ganglia, and because the visceral commissure shortens, its ganglia approach one another, in most cases they remain at least partly separated by short connectives or by constrictions, but often some of them fuse together. The cerebral commissure gradually shortens until the two ganglia touch. Among terrestrial snails, especially primitive conditions are present in *Carychium*, the cochlicopids, the clausiliids, also the subulinids and the endodontids, although differences may occur within the same family.

The nervous system of the scaphopods shows a mixture of characters of gastropods and bivalves, but has greater similarity with the latter because it has retained the original symmetry, as well as an uncrossed visceral commissure, and because the pedal ganglia are no longer rope-ladder-shaped, but knot-shaped with a single short commissure. The cerebral commissure is also very short, the initial parts of the visceral commissure on the cerebral ganglia are somewhat swollen (pleural ganglia), their connective to the pedal ganglia is largely united with the cerebro-pedal connectives. However, as in primitive snails, in the scaphopods a lingual commissure is retained, connectives from it go to the buccal ganglia, as also to the ganglia of the subradular organ, as in the loricates. Compared with *Haliotis*, a concentration has taken place here, evidenced by the short commissures of the cerebral and pedal ganglia, the shortening of the latter, and by the proximity of the pedal ganglia to the cerebral ganglia.

1058　　Among bivalves, more or less distinct pleural ganglia are recognizable only in some nuculids, in the same position as in scaphopods. The central commissure is in most cases longer than in the latter; in the limids the ganglia are shifted far to the rear toward the ganglia of the visceral commissure, which correspond to the parietal and visceral ganglia of the snails and in most cases lie close together. Because these innervate the posterior part of the mantle along with the sense organs and muscles, they sometimes attain greater importance over the remaining ganglia. In some bivalves, lying below the cerebral ganglia there is a pair of small ganglia supplying mainly the labial palps; they correspond neither to the labial nor to the buccal ganglia of snails, but are new structures. Accessory ganglia may also otherwise occur in the visceral commissure or in the mantle margin.

In the nervous system of *Nautilus* the three pairs of main ganglia are not separated from one another, the strand lying above the esophagus, corresponding to the cerebral ganglia, laterally divides into the anterior pedal ganglia joined together by a thinner commissure, and the posterior visceral ganglia, both of which form narrow half-rings around the esophagus; separate pleural ganglia are absent. The pharyngeal ganglia, each of which is joined with the cerebral ganglia by 2 connectives, probably correspond to the labial ganglia of snails and scaphopods, on either side they give out a connective to the buccal ganglion. The lateral parts of the pedal ganglia, which innervate the arms and the eye tentacles, will have to be assigned to the cerebral ganglia.

Both ventral half rings are fused together in the dibranchiate cephalopods, whereas the innervation centers of the arms have separated and come to lie anterior to the pedal ganglia, to which they are joined by strong connectives; the latter are rather long in some decapods, but especially in the octopods they are so shortened that the ganglia fused together; in the latter the arm ganglia are joined together by a commissure above the esophagus. In general, they are also joined with the cerebral and upper buccal ganglia by connectives, which are greatly shortened in the octopods. The gangliar arm nerves are connected at the base of the arms by a ring commissure. The visceral ganglia, forming the posterior part of the ventral gangliar mass, innervate, besides the viscera, also the mantle and the gills; for serving the mantle muscles the mantle nerves form the stellate ganglia, which are joined together in some decapods by a commissure probably formed of 2 fused nerves. In this group also the most highly concentrated form of nervous system is to be considered as the most highly evolved.

Some **sense organs** are also important for the recognition of the phyletic relationships among the mollusks. One may assume that the initial molluscan form had simple organs of vision in the form of open pits, because such structures are present in the most primitive gastropods and in nautilids. Because indications of eyes have also been observed in the juvenile stages of loricates, it is probable that originally present eyes have become reduced as a result of the extension of the perinotum over the head. Also, the small eyes at the ends of the labial palps in some bivalves may correspond to the primitive cephalic eyes. The eyes of the 1059 higher snails, and also already those of the fissurellids, turbinids, and neritaceans, are closed and contain a vitreous body, but still have only little functional ability. On the other hand, in the dibranchiate cephalopods they have attained a high level of capability; the anterior wall of the optic vesicle produces a lens and an iris is formed by a circular fold, in addition, a second circular fold forms an anterior eye chamber, which has

a wide (*Spirula*, Architeuthacea, Cirrata, and Bolitaenacea) or narrow (Sepiacea—excluding *Spirula*—and Loliginacea) opening; in the octopodids an eyelid may be formed over the closed cornea by a third integumental fold.

In contrast to these cephalic eyes, the accessory eyes developed in various groups of mollusks are of little phyletic significance, such as the shell eyes of loricates, the dorsal eyes of some oncidiis, and the eyes at the mantle margin of certain bivalves.

An important sense organ for the phylogenetic history of the mollusks are the so-called **osphradia**, which are most closely associated with the ctenidia. Because we have no sufficient reason for assuming that the stem forms of loricates possessed a pair of ctenidia, we cannot consider the sensory elevation situated beside the anal papilla in many species as homologous with the gill sense organs of the conchiferans. The latter originally are bands of sensory epithelium over the branchial ganglion and the nerve in the efferent gill margin, such as those present in the zeugobranch snails and the primitive bivalves. It is only in the snails that this organ at times has undergone a distinct complication, whereas it is reduced in others. Along with the ctenidia, the osphradia of the docoglossans have become more or less rudimentary, they form a pair of symmetrical sensory elevations in the posterior part of the mantle cavity, thus indicating derivation from symmetrical zeugobranchs. Along with the right ctenidium the right osphradium of the trochaceans has become reduced, and to the extent that the left gill rachis fuses with the mantle, the osphradium also joins the latter and then comes to lie as a simple sensory band to the left of the gill. Because the gill of the neritids is not homologous with that of the trochids, it lacks an osphradium, as is also the case with the hydrocenids and helicinids; associated with this is the atrophy of the supraintestinal ganglion.

The sense organ situated near the mantle margin in the cyclophorids is not homologous with the osphradium. The osphradium of ampullariids is rather short, in some groups it is still simple, in others it is bipectinate. It is retained in the terrestrial assimineids and pomatiasids. Whereas in the more primitive taenioglossans it is in most cases a long simple band of sensory epithelium, it has become modified in a few small or large groups; thus, in the solariids it consists of small radial folds forming a semicircle beside the anterior end of the gill, in *Campanile* (Cerithiidae) it is short and broad and is bipectinate; it has assumed a similar form in melanellids, trichotropids, calyptraeids, naticids, lamellariids, in the doliaceans and stenoglossans, and also in the triviines, whereas in triradiate form has developed in the remaining cypraeids.

Whereas the gill of the actaeonids consists of a single lamella, the osphradium forms a small roundish sensory elevation; from this it may be inferred that this gill is homologous with only one of the numerous lamellae hanging on the underside of the mantle in many prosobranchs, and that, correspondingly, the osphradium is greatly shortened. It is 1060 similar in most of the Cephalaspidea and the Anaspidea, and in *Tylodina*, but is lacking in *Umbraculum*, in pleurobranchids and the nudibranchs. In *Newnesia* it has been described as a lamellate organ below the gill, in the oxynoids as a yellowish patch or short band anterior to the gill. It seems somewhat uncertain whether the organs of pteropods described as osphradium are homologous with those of the cephalaspideans.

The aquatic pulmonates have retained an osphradium similar to that in the cephalaspideans, whereas it is lacking in the terrestrial forms. Similar organs have nevertheless been described in some of them, but their homology with true osphradia is improbable.

The osphradium of bivalves is a simple band of sensory epithelium on both gills, which is not specifically modified and becomes rudimentary in the septibranchs. The scaphopods have no osphradium. In *Nautilus* there are 2 pairs of small sensory elevations, one of which lies between the anterior gills, the other further posteriorly near the midline of the body; an osphradium is not known in the dibranchiate cephalopods.

Of the statocysts it should be remarked that they are lacking in the loricates, and in the nuculaceans they are often connected with the surface of foot by an open canal and contain sand grains; in other taxodonts the canal is indicated only by a strand of tissue. Several statoconia are found in the arcaceans, mytilaceans, and pectinaceans, in addition a larger statolith is present in *Saxicava, Lyonsi, Lyonsiella*, and probably also in other pandoraceans; 2 or 3 statoliths are found in *Poromya*, whereas the remaining bivalves in most cases have one. Very rarely the statocysts are reduced. Among the prosobranch series the primitive groups have several statoconia, including also the architaenioglossans and some cerithiaceans, whereas the rest of them possess a single statolith in each statocyst. Most of the opisthobranchs have several statoconia, but the aplysiids have one statolith each.

The statocysts of *Nautilus* are thin-walled, with numerous statoconia. In those of the decapods the sensory epithelium forms 3 elevated plates (crista statica), one of which (the main plate) bears a statolith, whereas numerous statoconia lie on the two accessory plates; in addition, arising from the vesicle wall, there are a few peg-shaped processes (in most cases 11 or 12, 10 in *Rossia*, 6 in *Sepiola*). In the octopods only a horseshoe-shaped crista is developed, without accessory plates and statoconia, the pegs also are nearly always absent.

A few, in most cases primitive, mollusks possess various epidermal sense organs, the phyletic significance of some of which is uncertain. The small sensory elevations present in the lepidopleurids in a row on the outer wall of the gill groove, hence on the morphologically ventral side of the perinotum, are very probably homologous with those on the epipodium of *Haliotis*; they are still retained also on the epipodial tentacles of fissurellids, and trochids, but disappear in higher snails. The lowest snails possess on either side a band of sensory epithelium, which begins near the osphradium and externally continues below the mantle around the pedal retractors (subpallial organ): such structures have been observed in *Haliotis* and patellids, in the fissurellids the organ is a roundish sensory elevation on either side beside the osphradium. In certain trochids on the right side of the gill, below the mantle attachment, there is a row of small sensory elevations which probably correspond to the right subpallial organ of *Haliotis*.

1061

In the arcaceans and anisomyarians, also in *Neotrigonia*, on either side of the anal papilla, there is a sensory elevation (abdominal sense organ) provided with long nonmotile cilia, the epithelium of which is similar to the olfactory epithelium of vertebrates. A corresponding organ is not known in snails; it seems doubtful whether the so-called osphradia of loricates, which do have a similar position, are homologous with it. In many siphonate bivalves a sense organ of similar function is present at the retractors of the incurrent siphon.

The phyletic significance of the **nephridia**, which has remained uncertain for a long time, is now clear. They represent modified gonoducts, because the gonads were originally associated with the pericardium, which was only the enlarged initial part of the gonoducts. After the pericardium had separated from the gonads, so that it was no longer in contact with the germ cells, the gonoducts assumed excretory function. The nephridia thus formed completely lost their association with the gonoducts, or it was more or less distinctly retained, or it could have been secondarily restored.

In the loricates the original position of the pericardium posterior to the gonoducts has persisted, although they have acquired their own exit ducts, which are connected neither with the pericardium nor with the nephridia. The latter represent a longitudinal canal with numerous branches, which communicates with the pericardium through an inner limb and below the 7th shell piece with the sea water by a short exit duct, the outermost part of which probably has ectodermal epithelium. Both limbs are directed anteriorly and in most cases the lateral main-canal is longer, so that anteriorly it more or less surpasses the renopericardial dust. In the lepidopleurids the nephridia are short and as

a rule do not extend beyond the 6th shell piece, in the higher groups they are longer and in most cases terminate below the 3rd, sometimes below the 2nd shell piece. Mainly in the Acanthopleurinae, anterior to the excretory duct, the main canal gives off a branch running anteriorly above the pedal musculature and extending nearly as far as the main-canal. This form represents the highest level attained by the loricate nephridia, although also *Cryptochiton* has attained a peculiar condition, wherein the posterior parts of the main-canals have become considerably widened and have united together and their anterior parts have loop-shaped connections with the inner limbs. The nephridia of loricates have only minor value for the recognition of phylogenetic relationships, because they may be similar in rather different groups and may be dissimilar in related groups.

The nephridia of snails are very strongly affected by the torsion of the viscera against the foot and head; the originally right nephridium is enclosed anteriorly on the left between the rectum and the mantle cavity and is separated from the digestive organs, consequently it cannot give out any outer processes and an enlargement of the glandular surface has been brought about by internal club-shaped papillae; in contrast, the left nephridium infiltrates with numerous processes among the viscera and has thus acquired a much more favourable position. From such a condition, as is present in *Haliotis*, that of the fissurellids is to be derived, in which the left nephridium has become considerably reduced and has also (always?) lost the connection with the pericardium, whereas the right nephridium has enormously enlarged. The nephridia of the docoglossans are very similar, except that in most cases both of them have retained their connection with the pericardium.

1062

The trochids also are related to the zeugobranchs with a spirally coiled shell, but in this group, along with reduction of the right gill, the rectum moved more to the right, thereby leaving a large space for the left nephridium, whereas the right one is correspondingly restricted and receives a lesser quantity of blood; its apertural part is not excretory (uninary chamber). On the left nephridium, a part has especially developed with canals, which open into the nephridium and are surrounded by blood lacunae (nephridial gland).

The condition in the neritaceans is fundamentally different, because they no longer possess a right nephridium functioning as excretory organ; in contrast, the left nephridium is more highly developed, sometimes surpassing the rectum, the papillae in most cases have become branched folds and often the outer part is differentiated into a nonexcretory urinary chamber; in *Hydrocena* the two parts are connected by a long loop-shaped canal. The apertural part (ureter) is sometimes covered with

ectodermal glandular epithelium. The nephridium of the cocculinaceans is simple sack-shaped.

A corresponding nephridium is also present in all higher snails. A nephridial gland is absent in some groups (Viviparidae, Rissoacea, Valvatidae, Pomatiasidae, Cerithiacea). In the viviparids and valvatids a long ureter is developed. In *Turritella*, running from the nephridium to the mantle margin there is an elevated ciliated groove, which may (?) function as a ureter; similarly in the solariids. The nephridium of ampullariids consists of 2 different parts communicating by a narrow aperture, certainly a special acquisition of the family. Like the littorinids, the strombaceans possess a nephridial gland, as also most of the higher prosobranchs. The nephridium of the doliaceans is divided by the rectum into 2 parts, which in *Dolium* are almost completely separated but identical. However, in naticids there are 2 lobes differing in structure, the right one showing a network of lamellae, while the left one, which adjoins the nephridial gland, having papillae similar to those of the left kidney of *Haliotis*. In cypraeids the right part is similar, the other one is occupied by numerous parallel lamellae and is separated from the nephridial gland. In stenoglossans also 2 lobes are more or less distinctly separated and unequally developed; designated as the highest stage is the condition in muricids and buccinids, where the left lobe forms a marginal lamella with secondary lamellae which infiltrate among the lobules of the right lobe.

The nephridium of the Cephalaspidea lies in the mantle between the pericardium and the gill, as a compressed sack with internal folds, without a separate ureter and without a nephridial gland, similar in other shelled groups; in the shell-less forms it is displaced into the body. The renopericardial duct is sometimes more or less long (Pleurobranchidae, Duvauceliidae, Polyceridae, Dendronotidae), sometimes very short (Aeolidiidae, Elysiidae); in *Elysia* there are several such connections. The kidney sack, which is originally simple, may in various groups of nudibranchs give out a few or numerous processes, similar to the right nephridium of *Haliotis* and both nephridia of loricates.

The nephridium of the most primitive pulmonates (Ellobiidae) is very similar to that of the Cephalaspidea: a sack lying in the mantle beside and anterior to the pericardium, internally with a few folds, anteriorly opening into the mantle cavity with a papilla, without ureter (Fig. 894). In the series of basommatophorans in most cases the anterior part has become lengthened and in it an excretory epithelium is absent, although folds are present in its interior; this part is to be considered as the urinary chamber, which represents a part of the true kidney chamber.
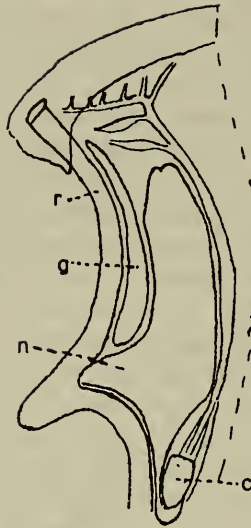
Fig. 894. Roof of the mantle cavity of *Marinula juanensis* N. Odhner.
c, heart; g, pallial gland; n, kidney; r, rectum
(after Odhner).

In the stylommatophorans, as a rule, a tube, known as ureter, has separated from the opening of the kidney chamber onwards on the underside of the mantle, which transports the excreted materials toward the opening of the lung cavity. Such a ureter is represented in a few primitive groups only by a posteriorly running ciliated groove, whereas, as in the basommatophorans, the kidney sack extends far forward, where it serves as urinary chamber. A distinct boundary between the latter and an (ectodermal) ureter constricted from the mantle is often formed by a pore, corresponding to the original opening of the nephridium, but occasionally it is not readily clear whether it is a kidney chamber or a ureter, or as to where the boundary between the two lies; thus in the athoracophorids it seems uncertain whether the long many-limbed ureter is entirely or partly of ectodermal origin. In the oncidiids the kidney sack opens through a short and very narrow duct into a papilla situated in a short process of the anus; this process thus represents a ureter. The condition in the soleoliferans, which lack a lung cavity is more difficult to understand. In the rathouisiids the three-limbed ureter opens through a narrow terminal tube on the right side between the foot and notum,

rather far anteriorly together with the rectum, into a slight depression above the ♀genital opening, separated from the latter by a small fold; a pore is not present at the beginning of this duct, and the ventral part of the terminal limb is surrounded by a subepithelial cell mass.

In *Vaginina*, which is probably the most primitive form among the vaginulids, the kidney sack and the three-limbed ureter are very similar, but the rectum and the ureter extend further to the back within the notum, the former opening externally with a wide aperture to the right of the posterior tip of the foot, the latter with a narrow opening in the midline of the animal posterior to the foot; soon after leaving the body cavity, that is, in the region where they open in the rathouisiids, the intestine upwardly gives out a short process, and the ureter gives out another process, opening into the former with a narrow aperture. This condition thus has a similarity to the kidney opening of oncidiids, if the intestinal process of *Vaginina* is compared with the gut opening of the latter. It may thus be concluded that the three-limbed ureter of *Vaginina* and the remaining vaginulids actually represents a urinary chamber, evidently a difficulty is posed by the presence of the subepithelial gland should this be regarded as ectodermal, although it probably does not represent a homologue of the hypobranchial gland of cephalaspids; rather, this aggregation of cells may represent a blood gland. At any rate, the ureter situated posterior to this connection, which is also present in a few other vaginulids (*Pseudoveronicella*), has, when compared to rathouisiids, to be considered as a secondary acquisition; in *Vaginina* it is still connected with the rectum by a few tubules arising from the latter and opening into the ureter through narrow pores. Hence, in this case the intestine running within the notum appears similar to a cloaca, whereas in most *Vaginula* species the intestine and the ureter unite only at their ends.

In the shell-bearing stylommatophorans the form of the kidney sack is variable, sometimes short, sometimes more or less long, the pore lying in the vicinity of the pericardium and the pulmonary vein. From it the ureter as a rule runs backward on the right margin of the kidney sack and then often more or less far to the front beside the rectum; this latter part is designated a secondary ureter. It has probably developed in various groups which are not closely related with one another, so that its presence alone has no great phyletic significance, although compared to its absence it generally has to be seen as a more advanced condition. The wall of the ureter is sometimes smooth, sometimes more or less richly folded.

The scaphopods possess a pair of symmetrical, somewhat lobed nephridia, which are connected neither with one another nor with the

pericardium and open into the mantle cavity beside the anus; they are primitive, the absence of pericardial ducts alone is a secondarily acquired character.

The nephridia of the more ancient bivalves also show primitive conditions. Similar to in the scaphopods and zeugobranch snails, the original form seems to comprise 2 more or less folded and entirely separated sacks, communicating with the pericardium through one ciliated canal each, and opening externally without distinct ureters; an indication of a connection with the gonoducts may be present, in *Solenomya* these open into the anterior parts of the proximal ducts. The nephridia of the nuculaceans appears as two-limbed tubes, connected to one another and opening externally together with the gonoducts, and this urogenital cloaca is in most cases connected with the proximal part by a short canal or a perforation of the walls. The nephridia of the arcaceans, mytilaceans, and trigoniids are sack-shaped, separated from one another, and open together with or beside the gonoducts. In the pectinids they have a short proximal and a sack-shaped distal limb, the latter being connected and receiving the openings of the gonoducts. In limids these open in the ends of the proximal limbs, similarly in anomiids. The form and location of the openings as well as their positional relationship with other organs are variable and of little phyletic significance, nevertheless the eulamellibranchiates uniformly have the nephridia situated posterior to the pericardium and in lacking any connection with the gonoducts. Just as nuculaceans differ from arcaceans because of the loop-shaped nephridia, those of the unionaceans, in contrast to the trigonaceans, have assumed a loop shape and beside the posterior bend the proximal limb forms folds covered with excretory epithelium, the distal limb connected with that of the other side. The nephridia of the corbiculids also consist of an arch-shaped proximal and lateral and an additional distal limb connected with that of the opposite side; from this the form of the nephridia of sphaeriids is to be derived, with a complicated loop formation (Fig. 895). In most heterodonts, as well as in the Anomalodemata, the distal limbs are sack-shaped and connected to one another, as also in the pholadids, whereas in the teredinids, the nephridia are elongated and are reflected anteriorly over the pericardium, so that both limbs merge into one another behind the adductor muscle and the internal and external openings are posterior in position; a connection between the two nephridia is here lacking.

In the cephalopods also the nephridia represent sack-shaped cavities, of which in *Nautilus*, corresponding to the 2 pairs of gills, there are 4, the posterior of these being homologous with those of other mollusks. Because their excretory parts are developed at the afferent branchial vessels, the division of the gills into two also resulted in a division of the kidney
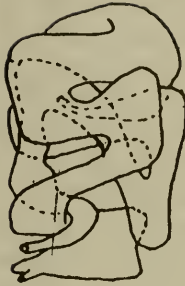
Fig. 895. Kidney of *Pisidium henslowanum* (Sheppard)
(after Odhner).

sacks. A direct communication with the pericardium is not present, but the posterior larger sacks open into the mantle cavity immediately beside the exit ducts of the pericardium, so that it may be assumed that these have only secondarily detached from the kidney sacks. The dibranchiate cephalopods have one pair of nephridia, which in octopods remain separated from one another and possess each an accessory chamber, with which they stand in open connection. In the decapods both nephridia are united without another, and a wide dorsal dilatation may develop, which extends posteriorly below the shell; this contains various veins with glandular appendages. The exit ducts of the pericardium open into the initial parts of the nephridial ducts, which open beside the anal papilla.

Because the **pericardium** of mollusks has arisen from enlarged initial parts of the gonoducts, and because, like the gonads, these were originally paired, it is to be assumed that initially the pericardium also consisted of 2 parts, which however almost always fused with one another. It may also seem doubtful whether the originally paired condition has still maintained itself in any group; nevertheless the species of the genus *Arca*, in which alone 2 completely separated pericardia occur, are so primitive in their entire make-up, that one can assume it to be also of this character as well as the fact that the two nephridia are entirely separated, whereas in the nuculaceans and most of the bivalves they are interconnected.

As a result of misinterpretation of homologous parts, the pericardium together with the nephridia of mollusks, was declared equivalent to the body cavity and the segmental organs of annelids, but it cannot be doubted that the molluscan nephridia correspond to primary gonoducts, which have disappeared in annelids, and that in addition the body cavity

1066

(coelom) does not agree with the pericardium of mollusks. As a rule the latter is no larger than what the heart needs for its expansion; among the snails it has attained an extrordinary extension in *Septaria*, stretching out into the posterior part of the animal from the left side, where the heart lies, between the viscera up to the right side. In a similar fashion, but to a still greater extent, the pericardium of *Nautilus* has become enlarged; and one can assume that it pushed with one of its lobes between the gonad and gonoduct which is largely or completely formed from ectoderm, so that the gonad seems to lie in the body cavity, which represents an enlarged pericardium and extends between the viscera; by means of the suspensory band of the gonad, an incomplete septum is formed between the body cavity and the true pericardium, the latter of which encloses the heart with its 4 auricles.

The decapods also have a wide body cavity, which may sometimes (cranchiids) extend very far anteriorly. In octopods, on the other hand, the body cavity is considerably restricted and the true pericardium is reduced, the heart being enclosed only by a connective tissue capsule; the gonadal part is connected by a pair of canals to 2 bottle-shaped pouches, which contain the glandular appendages of the gill hearts and are joined to the nephridia by ciliated funnels.

The **gonads** of mollusks are originally paired, symmetrical, and with separate sexes. Their original position anterior to the pericardium has been retained in the loricates, but they are almost always fused with one another, remaining separate only in *Nuttalochiton*, so that here they are similar to the solenogasters. The gonoducts in all loricates are entirely separated from the pericardium and the nephridia and open into the gill groove anterior to these. They consist of an inner part which derives from the gonad, and an outer part formed by ectoderm, and is covered in the ♀ by glandular epithelium and at times presenting an enlargement; this part is in most cases much larger than the inner, but in *Lepidopleurus* the latter forms the entire portion lying within the visceral cavity. One can assume that this condition is the more original.

The gonad of the snails is always single; because, in contrast to the loricates, it always has only a single exit duct, it is probably homologous with only one of the two original gonads, the left one, which however after torsion lies on the right. In the primitive groups (zeugobranchs, patellaceans, and trochaceans) it still shows a distinct connection to the right nephridium, opening as it does into its terminal part or in the renopericardial duct. At the opening into the mantle cavity, in the ♀ an ectodermal glandular duct develops.

Considerably altered are the conditions in the neritaceans. They are simplest in hydrocenids. In the ♀ sex the oviduct gradually becomes

glandular and opens into another duct which is surrounded by subepithelial glandular masses and anteriorly opens into the mantle cavity beside the anus; beside the opening on the oviduct into this duct there are also openings of 3 other tubes; one of these is a blind-sack-shaped gland, the 2nd is an anteriorly narrow, posteriorly somewhat widened blind sack,

1067 which is to be called bursa copulatrix and opens into dorsal side of the glandular duct; the 3rd is, in the posterior continuation of the glandular duct, a fairly wide tube which through a narrower terminal opening passes into a sack-shaped cavity, the epithelium of which consists of glandular cells without supporting cells. It is close to consider this sack a homologue of the right kidney of trochaceans, because like the latter, it is connected with the glandular duct by a direct passage. However, it must be emphasized that a connection to the pericardium has not been proven and that the oviduct does not open into this sack, but that a connection is effected only through exit ducts which are covered with ectodermal glandular epithelium.

From this condition the structure in the helicinids can be derived without difficulty, if one assumes that the bursa copulatrix has acquired a separate opening into the mantle cavity, which lies more or less deeply within the interior, and that it has remained connected with the glandular duct by an in most cases short duct; attached to this may be a seminal vesicle and at its posterior end there is a more or less well developed sack, which in view of its position and the nature of its epithelium corresponds with the sack of *Hydrocena*.

The conditions in the neritids are more difficult to understand. As a result of a fertilization by spermatophores, the bursa copulatrix has become greatly enlarged and its opening has moved forward beside that of the glandular duct (ootype), the connecting duct with the latter, short in helicinids, is also more or less lengthened and complicated, and as a rule has a receptaculum seminis. The oviduct in most cases communicates with the pericardium through a ciliated funnel. It is uncertain whether there is in this case a homologue of the sack lying at the end of the glandular duct of helicinids, such as the peculiarly lobed part of the connecting duct between the ootype and spermatophore sack of *Nerita*. In some groups even a third opening of a duct has been formed, leading to the receptaculum seminis. It is evident that such a condition is much most divergent from the normal than that of the littoral hydrocenids.

The ♂ apparatus of *Hydrocena* consists of a strongly coiled sperm duct, which leads into a wide glandular tube; posteriorly the latter has a glandular blind sack, and another one opens into it near its anterior end. The ♂ organs of the helicinids are similar; in the neritids a lobed prostate is found at the opening of the sperm duct into the spermatophore gland,

and beside the right cephalic tentacle a lobe-shaped copulatory organ is developed. There probably is no indication of the right kidney remaining.

The gonoducts of the Cocculinacea are very simple; the hermaphroditic gland has a single exit duct, the epithelium of which consists of glandular and supporting cells, it opens into the mantle cavity near the anus; a variously shaped depression of the mantle cavity serves as bursa copulatrix. At the right tentacle sometimes a ♂ copulatory organ may be developed; in *Bathysciadium pacificum* Dall this appears as a tube, the inner epithelium of which is partly glandular and presents an enlargement before forming a narrow and long terminal tubule. The ♂ duct of *Titiscania* is simple, only the gland is more strongly developed and near its opening lie about 12 spherical seminal vesicles; the coiled sperm duct runs to a small elevation behind the right eye.

The ♂ gonoducts of the higher prosobranches are essentially similar in structure; often a receptaculum seminis is present near the opening of the oviduct into the glandular mass and at its opening the gland is connected to a blind sack, known as bursa copulatrix. In *Littorina* a connection of the pericardium to the end of the oviduct has been demonstrated and it is possible that such a connection also is present in other groups, because it is developed in ♀ calyptraeids, whereas it is absent in the preceding ♂ gonoduct and also in the ♀ *Capulus*. Thus it is uncertain whether such a gonopericardial duct is always to be regarded as an inheritance of zeugobranchs and trochaceans or sometimes as a secondary acquisition. The same applies to the question whether the receptaculum seminis represents a rudiment of the right kidney. Such an interpretation is possible in cases like *Littorina*, where it is a sack-shaped structure and is connected to the pericardium; but in other cases it may be absent or cannot be interpreted in this way because of its position. In *Pomatias* the oviduct is widened in its median part and receives the sperm; in *Pila* (Ampullariidae) the oviduct forms several spiral coils within a bean-shaped body formed of connective tissue. In *Calyptraea* however a bundle of vesicles separates from the posterior end of the "uterus," similarly in *Crepidula*; and in *Marsenina* and lamellarines several vesicles are present, similarly in *Trivia*. These are apparently structures of a different nature, which have possibly arisen in different groups and being not always of equal value. These conditions are still poorly known among higher prosobranchs; in *Oliva* the receptaculum seminis represents a coiled, tube-shaped appendicular structure with lateral sack-shaped extensions, surrounded by a thick fibrous connective tissue layer, hence somewhat similar to that in *Pila*; in *Concholepas* the oviduct in the middle has a thick-walled sack-like bean-shaped extension, perhaps representing

1068

a receptaculum; in *Melo*, at the end of the oviduct, there is a fairly large sack-shaped appendage with thin walls of doubtful function.

The glandular mass into which the oviduct opens, in most cases considered as the uterus, consists as a rule of a proximal albumen gland and following it a capsule- or shell-gland, to which at times a jelly gland is added. The latter in closely related species may be sometimes developed, sometimes absent; thus in *Littorina rudis* a non-glandular brood space is present in its plate. These glands also show other differences, which in most cases have only little phyletic significance. The anterior part of the uterus sometimes has a long cleft-shaped opening (cyclophorids, pomatiasids), but in most cases it is tube-shaped with an anterior opening. A separate vagina with a bursa is not seldom absent but frequently the anterior part of the glandular tube is considered as the vagina, where the glands are absent or they are more weakly developed. In *Strombus* the glandular tube is very long, posteriorly blind-sack-shaped; opening into it along with the oviduct is a receptaculum seminis and a thin glandular tube; from the outer opening a ciliated groove runs to the anterior part of the foot; the ♀ organs of heteropods are similar. Some melaniids show brood care; in *Tanganyicia* a brood pouch is formed opening below the right eye.

The sperm duct is usually long and coiled, but there are some differences. A widened part, which serves as vesicula seminalis, is sometimes present in the proximal, sometimes in the distal portion. A prostate can be developed as an open glandular groove or as a closed tube; in this respect species of the same groups can be different.

1069   The ♂ copulatory organ shows some peculiarities. In viviparids it is developed at the right tentacle; it is connected with the testis by a closed, rather short sperm duct which passes into a thick-walled expansion and a thin-walled terminal part; it has certain similarity with that of *Bathysciadium*. The penis of *Cyclophorus* is cone-shaped, attached below the right tentacle, connected with the genital opening through a seminal groove and supplied by a nerve from the right pleural ganglion. A penis situated behind the right tentacle is present in the Vanikoridae, Trichotropidae, Capulidae and Calyptraeidae, in the first of these families with closed sperm duct, in the others with a sperm groove. In the pomatiasids it is located rather far to the near on the right side and is innervated from the subintestinal ganglion; the sperm duct is closed, with a pear-shaped prostate. The ♂ copulatory organ of ampullariids is unique, lying on the inner side of the mantle margin; it is variably strong developed and as a rule consists of a more or less long, thin process with a sperm groove, at the base of the process a tubercle or a lobe being

present; the process is surrounded sheath-like by a rather thick extension with a groove. The condition in the hydrobiids is also peculiar, for here the penis is situated in the neck region; its shape is varied, in some groups it is leaf-shaped, in others with a basal process. Its innervation still appears uncertain, in *Pseudocyclotus*, where the penis is also located at the neck, the nerve appears to arise from the connective between the right cerebral and pedal ganglion, but close below the cerebral. In most of the taenio- and stenoglossans the penis is located on the right side not far from the right tentacle, more seldom farther away from it, and is innervated from the right pedal ganglion. In view of the condition in *Pseudocyclotus*, it seems possible that the innervation from the pedal ganglion is not to be regarded as fundamentally different; thus in the case of *Oliva* it has been stated that the nerve arises at the place where the right pedal ganglion merges into the cerebral ganglion. Nevertheless, it can be considered as certain that mainly in the lower groups of the prosobranchs a ♂ copulatory organ has developed in various ways. It is absent in the Cerithiacea and Ptenoglossa.

Seldom has hermaphroditism developed in the series of prosobranchs. Whereas in the cocculinaceans, and probably in the pyramidellids, the gonoduct remains simple, at times complications appear in various ways, in which the ♂ part has developed alongside of a complete ♀ part, as is the case in the valvatids. The hermaphroditic duct divides and both branches bear appendicular organs, the prostate is a club-shaped blind sack; a similarly formed appendage of the ♀ part may be a bursa copulatrix, and another one a shell gland. Among the lamellariids, in lamellariines the sexes are separate, in both of the other subfamilies they are combined and their form shows considerable variability in the genera and species, *Marsenina* is most similar to *Lamellaria*.

In a similar fashion the hermaphroditism of the opisthobranchs and pulmonates developed. In *Actaeon* there is a glandular duct (uterus) opening into the mantle cavity, and a bursa copulatrix, as well as a closed sperm duct and a non-retractile penis lying on the right side, similar to that in some prosobranchs, with the only differences that both sexes are here combined; the penis, as in all opisthobranchs, is innervated from the right pedal ganglion. The ringiculids and hydatinids also have a closed sperm duct but a retractile penis; but in all other cephalaspideans as well as anaspideans and pteropods, it is connected to the genital opening by a ciliated canal, sometimes it has a prostate. The form of the gonoducts and the appendicular glands shows considerable differences, at the sperm duct in most cases a vesicula seminalis is developed and on the outer part of the stalk of the bursa copulatrix a sack-shaped expansion may be present, but an equivalent of the receptaculum seminis of

prosobranchs appears always to be absent. *Haminea* agrees with *Acera* and the aplysiids in having a special nidamental gland at the terminal part of the gonoduct.

The sacoglossans have a closed sperm duct, which is partly glandular in the oxynoids and is connected with a large seminal vesicle, whereas the vagina receives the duct of a double bursa copulatrix. The glands in this family are massive; in the shell-less sacoglossans the hermaphroditic gland and the albumen gland are branched, and the ♀-duct divides in some genera and opens with an anterior exit duct of the mucus gland (ootype) and with a posterior vagina, which is connected with a larger spherical bursa copulatrix; accordingly the reproductive apparatus here is very complicated.

In the notaspideans the sperm duct is also closed and the penis has approached the ♀ opening, which is occasionally divided into the anterior vagina and the posterior opening of the mucus gland, but the ♀ duct is undivided; it has a bursa copulatrix, and the sperm duct has a prostate. Next to these stand the nudibranchs, among which there are certain differences that must be noted for systematics.

The genital apparatus of the primitive pulmonates is similar to that of the cephalaspideans, here again the retractile penis is connected to the genital opening only through a sperm groove. Variations are already found in the ellobiids, in which the hermaphroditic duct at times remains united up to its opening, sometimes it is divided, to a varying extent, into a female and a male duct, opening at times together, at times separately; a bursa copulatrix in most cases is long-stalked and is attached not far from the opening, but in *Tralia* and *Melampus* is rather far away from it. The retractile penis is very probably homologous with that of the opisthobranchs, hence its innervation from the right cerebral ganglion in pulmonates is to be explained by a displacement along the pedal connective. In ellobiids a sperm duct is in most cases present at the penis, extending from the groove to the inner end of the penis. In *Otina* the sperm duct is already closed, and this also is the case of most basommatophorans. In *Siphonaria* the penis opens together with the genital duct without an inner sperm duct, a prostate is present; in *Amphibola* also both openings lie close together, but an inner sperm duct is present, as is also a long and thin prostate at the proximal end of the penis, whereas a bursa copulatrix is absent. *Gadinia* has separate openings and a closed sperm duct; in this case a gland lying beside the ♀ shell gland at the opening of the hermaphroditic duct serves as the prostate. The condition in the hygrophilic basommatophorans is similar. These are often expansions present at the hermaphroditic duct which have been called vesiculae seminales or fertilization pouch and are probably not always homologous; also

improbable is a homology with the receptaculum seminis arising from the right kidney in some prosobranchs, even though their location may be similar.

Because of the separation of the ♂ copulatory organ from the ♀ opening, the oncidiids approach the basommatophorans; however, this separation has here reached its peak, wherein the ♀ duct has shifted posteriorly with the lung and rectum, whereas the ♂ duct has shifted anteriorly, opening beside the right tentacle. The hermaphroditic duct receives the exit ducts of albumen and mucus glands (spiral glands) and has a sack-shaped or internally folded appendage of variable size, probably a prostate; after separation of the sperm duct from the oviduct, the latter has a spherical bursa copulatrix, whereas the former runs under the skin forward to the penis. The ♂ copulatory apparatus is very differently developed within the family; in some species a penis gland is developed, probably from a blind sack of the penis sheath, similar to the prostate of *Amphibola*, sometimes of considerable size, terminally with a spine.

In the soleoliferans also the genital openings are away from the one another; in the rathouisiids the female opening lies on the right side below the anus. The gonoduct has some resemblance with that of oncidiids, it receives the exit duct of a large gland and has bursa copulatrix, while a prostate is present at the beginning of the sperm duct. The ♂ copulatory apparatus, which lies at the head, is also similar to that of the oncidiids in having a more or less large tube-shaped gland, which opens into the penis sheath; a similar gland is often also developed on the left side. The opening of the ♀ genital duct of vaginulids lies on the underside of the notum in about the middle of the right side, the fertilization pouch is represented by a widening of the hermaphroditic duct, the oviduct is long and coiled, the sperm duct in most cases provided with a club-shaped prostate and directly connected with the bursa copulatrix through a short tube (canalis junctor). The penis of *Vaginina* has only slightly developed glandular tubes, which open into its posterior end; in the remaining genera these tubes are much more strongly developed and open into a special cone-shaped process of the penis pouch, which is called a stimulatory structure.

In all remaining groups of land snails the opening of the penis sack is united with the ♀ opening or is at least very close to it. The ♀ and ♂ ducts are more or less united and are separated only by a pair of internal folds; the ♀ part receives the secretion of the albumen gland and its wall is often folded and glandular, it sometimes serves as uterus in which the eggs develop into embryos. The bursa copulatrix, which is variable in size, sometimes with a short, sometimes long stalk, has in

some groups acquired a blind sack on the stalk for the reception of a spermatophore. The ♂ part is glandular (prostate) and then runs as a sperm duct to the penis; also associated with it are often glands (epiphallus) and at its opening into the penis a thin tube (flagellum). Like these parts, in some groups stimulatory organs are developed, in the form of a "love gland" (glandula amatoria) often with dagger-like tip, or as a calcareous spine (Gastrodontinae), or love dart in association with a simple or multipartite gland (Fruticicolidae, Helicidae).

1072   The terminology of homologous parts in the literature and also in the first two parts of this handbook is not uniform; the copulation pouch (bursa copulatrix) principally has often been called the receptaculum seminis; the fertilization pouch, not seldom developed on the hermaphroditic duct, is very different from it. Similar structures developed in various groups are to be considered analogous, not homologous, even if they have received the same designation.

The conditions in the scaphopods are uncommonly simple: the unisexual gonad is unpaired, in *Dentalium* lying only on the dorsal side, in *Siphonodentalium* also in ventral part of the mantle, it does not have its own exit duct; at maturity it fuses with the right kidney and after dissolution of the wall it releases its germ cells through the kidney into the mantle cavity. The unpaired nature of the gonad, as well as its position in the posterior part of the body, and especially the mode of release, are not to be regarded as primitive.

The gonads of the bivalves are paired symmetrical, originally unisexual and lying in the visceral sack, rarely extending more or less far into the mantle; their short and simple exit ducts open together with the kidneys or near them; in some primitive groups they open into the kidneys, through which they empty into the gill cavity. This is the case in *Solenomya* and in the pectinaceans, to which the anomiids are close; however it seems somewhat doubtful whether this is to be viewed as an original condition, because the taxodonts and mytilaceans, as well as the trigoniids show only common openings for the kidneys and gonoducts. At any rate, the gonoducts of the bivalves correspond only to that part of primitive snails, which is formed from the gonad and opens into the kidney or into its connection with the pericardium, so that as a rule they have no ectodermal part, just as they always lack copulatory organs. Hermaphroditism has arisen in various groups, sometimes in entire families, sometimes only in single genera or species; even in species which are otherwise unisexual, hermaphroditism may develop under special circumstances; all Anomalodesmata are hermaphroditic, with the exception of *Cuspidaria*.

The gonad of cephalopods is always unified and the sexes are separate; because the gonoducts are originally paired, it may be questioned whether the gonad corresponds to the sum of the paired anlagen, which have fused together as in most of the loricates, or only to one of them, the other having completely disappeared. The genital sack containing the gonad opens in *Nautilus* into the body cavity, but opposite to this opening lies the beginning of the gonoduct which receives the germ cells, without itself being situated in the body cavity. The left gonoduct has no connection with the gonad and represents a pear-shaped vesicle opening into the mantle cavity. The oviduct is short and wide, glandular in the outer part, and opens at the base of the mantle cavity. The sperm duct forms a spermatophore gland, then a spermatophore sack, and ends in a penis-like process posterior to the funnel in the gill cavity. The "spadix" is employed for copulation; this is a group of 4 cirri of one body side, which represent the ventral part of the inner system and are peculiarly modified.

In the dibranchiates the ♀ gonoducts are in most cases paired, but in the Sepiacea and Loliginacea, and also in the cirrate octopods, the right oviduct has become reduced, in *Pterygioteuthis* in contrast it is the left one; its terminal part is glandular. The ♂ gonoduct is paired only in
1073 *Calliteuthis*, otherwise only the left one is retained. Its initial part is narrow and coiled, followed by a trilobate spermatophore gland, thereafter a "Rangir gland" and finally the spermatophore sack (Needham's pouch). In the decapods the gonoduct communicates with a pouch-like depression of the epidermis through a narrow ciliated canal arising between the two glands; the glands are enclosed in this depression; in the Architeuthacea it is anteriorly open, in others it forms a closed capsule. The octopods are more divergent; here the end of the gonoduct forms a penis-like process, on which there is a gland which is sometimes strongly developed, but a genital pouch is lacking.

For the transfer of the spermatophores to the female, use is made as a rule of a more or less modified arm, or more rarely a pair of arms. Nothing a known about this in some genera, as for instance in most of the Architeuthacea and the cirrates. In decapods, in most cases one of the ventral arms is hectocotylized, rarely both of them (*Spirula, Idiosepius, Todaropsis*), in sepiolids and histioteuthids on the other hand the dorsal arms are hectocotylized. The modification of a 3rd arm of octopods has taken place in a different way, in the Octopodacea by the development of a spoon-shaped terminal part, in Argonautacea by a considerable elongation and detachment from the body in the mature state.

Outline of the Phylogeny of the Mollusks

There is no doubt that the mollusks developed in Precambrian times from shell-less animals. In order to determine how these animals were constituted, one can draw conclusions through a comparison of some still living animals pertinent to this problem. Among these, principally the Solenogastres are important, which together with the loricates have been grouped as Amphineura, and in comparison with the latter even have been considered by Pelseneer as secondarily simplified, although this viewpoint is untenable and has been given up at present.

The Solenogastres are completely shell-less and their regular dermomuscular tube proves that they could not have descended from shelled animals. They are in most cases cylindrical covered with a more or less strong cuticula with embedded calcareous needle- or scale-shaped bodies; but running ventrally between the mouth and anus in most cases there is a ciliated groove, into which subepithelial glands open. The mouth opening often lies at the base of an atrium provided with sensory cirri, occasionally separated from the latter; the anus also lies in a cavity which may contain gills. The nervous system consists of an indistinctly paired upper esophageal ganglion and 4 ganglionic longitudinal cords, of which one pair is positioned ventrally and the other laterally; as a rule they are connected by several transverse commissures; in addition, a pair of buccal ganglia is present. The foregut has various glands and often a radula, which is in most cases small and without a uniform basal membrane. The midgut runs as a straight tube toward the rear, not seldom with regular lateral expansions. The heart consists of a posterior auricle and anterior ventricle; true blood vessels are not developed; the space between the dorsal body wall and the gonads serves as an aorta and ventrally, above the ventral groove, there is an incompletely delimited sinus. The gonads comprise a pair of elongated sacks lying side by side, rarely fused with one another, or as series of pouches with longitudinal ducts lying between the intestinal sacks; the initial parts of the exit ducts are widened and fused with one another to form a space which surrounds the heart and thus simultaneously serves as pericardium and uterus. The following part of the exit ducts recurves anteriorly, then forms evaginations serving as sperm containers and turns backward, opening into the posterior cavity below the anus; this terminal part is glandular and often unpaired, the ducts fusing together before their opening.

Some of these conditions are characteristics which the Solenogastres share with the "worms," and which distinguish them from mollusks, such as the cylindrical form, the absence of a shell, the regular dermomuscular tube, the elongated midgut, the long nerve cords, the gonoducts with their

1074

widening serving as pericardium, and the cloacal chamber; hence the Solenogastres are to be excluded from the mollusks.

The loricates are closest to the Solenogastres. They agree with them mainly in the basic form of the nervous system with the 4 longitudinal cords and in the position of gonads under the dorsal body wall and anterior to the pericardium, as well as in the possession of a cuticula with calcareous bodies. However, there are important differences, foremost the calcareous shell which has developed as separated calcareous embeddings in the cuticula, lying one behind the other; these remained joined to one another by muscle bundles which have separated from the dermomuscular tube, so that inrolling was possible. In the region of the shell, the calcareous structures embedded in the cuticula disappeared and the epithelial papillae extended to the surface (aesthetes). The shell parts then formed 8 entirely external plates, which at the attachments of the connecting muscle bundles and the musculature of the perinotum, developed projecting margins and correlated differentiations in the structure of the plates.

Because of the formation of the shell, the cuticula, which previously covered the entire dorsal side, was restricted to the body margin. It ends at the fold which surrounds the gill groove of the loricates. This fold originally formed the lateral margin of the body and probably terminated anteriorly at the head; gradually a muscular bulge developed above it, and this assumed the shape of an edge which then formed a secondary body margin and closed itself in the form of a ring anteriorly above the head as well as posteriorly above the anus.

From the fact that the cuticula covered only the dorsal side of the loricates and left the ventral side free, it may be deduced with much probability that the loricates derive from flat animals similar to turbellarians. Hence, it will be assumed that the Solenogastres too were originally more flattened and protected by a cuticula only dorsally. Besides this, the common ancestral forms probably possessed longer midgut processes, between which muscle bands descended; the midgut glands of the loricates may be considered to have been desired from such processes. The foot of the loricates derived from the ventral dermomuscular tube and the transverse muscles, the sole corresponding to the ciliated groove of the Solenogastres. Because the formation of the anterior pit (atrium) and the cloaca of the Solenogastres probably is a consequence 1075 of the cuticularization of the ventral side, these invaginations are lacking in the loricates. The gill groove has formed through the development of the foot and the perinotum. The gills lying within it are not homologous with those of Solenogastres.

While the 4 ganglionic longitudinal cords in both animal groups are so similar that their homology does not seem doubtful, the anterior parts of the nervous system show considerable differences. The Solenogastres have a pair of adjacent upper esophageal ganglia and a pair, of small buccal ganglia, the loricates on the other hand have an esophageal ring with lateral swellings and 2 pairs of buccal ganglia, which also form an esophageal ring; in addition they have the ganglia of the subradular sense organ which is lacking in the Solenogastres. In the latter the anterior parts of the lateral cords are often more or less swollen and these swellings correspond to those of the esophageal ring of the loricates; other differences are due to the development of the perinotum.

The digestive organs of the two groups are considerably different. The radula which is present in several genera of the Solenogastres never attains such a size as in loricates. Moreover, in the latter it has attained a much higher condition, not only by the development of a basal membrane and a complicated musculature, but also by the differentiation of the plates in the individual rows, mainly of the large hooked plates with especially hardened and detachable cutting edges, and the reduction of the cutting edges of the marginal plates. The esophageal glands of the Solenogastres are various, and homologous glands are lacking in the loricates. The alternations which the midgut has undergone are very great: with the sack-shaped anterior glands, the midgut gland (liver), and the long, more or less coiled intestine of the loricates; the latter does not open into a cloaca. The heart of the loricates can be derived from that of the Solenogastres, perhaps by reduction of the simple posterior auricle and the new development of 2 lateral auricles in connection with the development of gills. The haemocoel of the Solenogastres is at a very low stage, and in loricates a complicated vascular system has developed. Whereas the pericardium of the Solenogastres is a part of the gonoducts, in the loricates it has separated from the latter and its exit ducts have assumed excretory function; the gonads, on the other hand, which in most case have fused together, have received their own secondary gonoducts.

Through all these differences, especially the shell, the foot, the reduction of the complete dermomuscular tube and the stronger transverse musculature, the perinotum, the fore- and midgut glands and the coiled intestine, the separation of the pericardium from the gonads, also the paired auricles of the heart, the loricates first acquired the essential features of the molluscan type.

The phylogeny of the loricates begins with forms that did not yet possess insertion margins, so that the shell was entirely external except for the small apophyses of the 2nd to 8th pieces; probably the surface of the most primitive forms had only minute warts, which corresponded to

aesthetes, and the narrow perinotum was covered with minute scales, scattered among which were small needle- or club-shaped bodies. On the outer wall of the gill groove there was a row of sensory elevations. Originally the hooked plate probably had a tricuspid cutting edge. The 1076 nephridia and the gill rows were short. These characters have been retained in the group of *Leptochiton*, to which are joined the other sections of *Lepidopleurus*. The rasping plates in this genus show considerable variability. *Hanleya* has larger apophyses and a smooth insertion margin at the anterior margin, also a stronger perinotum. A very remarkable transitional form is *Hemiarthrum*, with smooth insertion margins on both end pieces, with groups of longer needles on the fairly strong perinotum at the margin of the anteriormost shell piece and between the following pieces; the radula with tricuspid hooked plate and notched cutting edge of the lateral plate is very similar to that in *Tonicella*. The condition attained in the Lepidochitonidae distinguishes these and all other loricates from the lepidopleurids: the development of incised insertion margins on all shell pieces. The surface is more or less distinctly granulated; the perinotum like that of the lepidopleurids with minute scales or needles and small groups of larger needles; the cutting edge of the hooked plate of the radula is tricuspid, that of the lateral plate in most cases notched or comb-shaped. *Nuttalochiton* is a remarkable group, the shell of which is sculptured with ribs or rows of warts and has connected apophyses and which differs from all others by the paired gonads, apparently a feature of very primitive organization, but this does not put the genus at the beginning of the phyletic development. At the same time it indeed shows striking affinities with various groups of loricates. The Callochitoninae likewise have connected apophyses; in *Icoplax* species the median areas may bear similar longitudinal ribs as in *Nuttalochiton martiali*, but the shells contain small intrapigmental eyes, the insertion margins have many incisions; lateral plates of the radula with rather small smooth cutting edges or without these.

Like *Nuttalochiton*, the mopaliids as a rule possess 8 incisions of the anterior margin, corresponding to which there are often radial ribs, the apophyses are more of less large, sometimes connected, the covering of the perinotum may also be very similar, the cutting edge of the hooked plate is tricuspid, that of the lateral plate is smooth. Otherwise the genera of the family are fairly variable. The posteriormost shell piece sometimes has a few normal incisions, sometimes only 2 or none at all. In *Katharina*, and especially in *Amicula*, the tegmentum is reduced, the insertion margins and apophyses are greatly enlarged and the perinotum is strengthened. In *Placiphorella* the anterior part of the perinotum is considerably broadened. Such characters are special acquisitions of the individual groups.

Some similarity is shown in the development of the series of cryptoplacids, which differ from the mopaliids in the smaller number of anterior incisions, of which there are 5 in Acanthochitoninae, and in most cases 3 in Cryptoplacinae. Among the genera, *Craspedochiton* shows affinities with *Nuttalochiton*, in particular the covering of the upper side of the perinotum is strikingly similar, the granules of the shell surface are enlarged, the apophyses are separate, the posterior margin is irregularly notched, the cutting edge of the lateral plates of the radula may be notched. The tegmentum in *Cryptoconchus* s. s. is very narrow, in *Cryptochiton* it is completely reduced, so that the shell consists only of the large articulamentum + hypostracum, hence this genus presents an extreme in a certain direction; in addition, besides the large hooked plate, all the cutting edges of radular plates are reduced and the nephridia are fused together. The perinotum in this family has become very strong, and in the Cryptoplacinae the body has become more or less elongated, so that in some species of the genus *Cryptoplax* the 4 or 5 posterior shell parts have moved apart; in this genus only the anteriormost shell part has incisions in the margin.

The sculpture of the shell in Chaetopleurinae often shows great similarity with *Nuttalochiton*, the number of anterior and posterior incisions is somewhat variable, and the covering of the upper side of the perinotum sometimes consists of small scales, sometimes of needles, scattered among which are larger needles or those with more or less long double cups; the lower side has smooth small scales. The hooked plate of the radula has a tricuspid cutting edge, in *Chaetopleura* s. s. a bicuspid cutting edge, and on the inner side of the shaft an in most cases weak expansion, which in *Dinoplax* represents a rather large wing. Approaching the forms with ribbed scales on the perinotum are the Ischnochitoninae in which these scales are more or less enlarged and aggregated, so that the needles with double cups are restricted to one row at the margin. In this species-rich group the shell and the radula have undergone some modifications; the shell may be smooth, granulose, or ribbed; in *Stenochiton* it is very long and narrow; the intermediate valves sometimes have more than one incision on either side, exceptionally the insertion margins may be notched comb-like. The cutting edge of the hooked plate is sometimes tricuspid, in most cases bicuspid, the outer cusp may become a small accessory cusp or entirely disappear; the wing-shaped appendage on the innerside of the shaft is in most cases large and often a small wing is also developed on the outer side of the intermediate plate.

The Chitoninae are not very different from *Ischnochiton*, the insertion margins being notched comb-like, which is seldom the case in the

Ischnochitoninae, the marginal scales are in most cases larger, and the cutting edge of the hooked plate is broadly rounded; exceptionally, intrapigmental eyes may appear in the shell.

The end forms of this developmental series are represented by the Acanthopleurinae, in which the shell contains extrapigmental eyes and the marginal scales of which are in most cases either elevated in the form of more or less long thorns or are reduced to minute needles; the radula is either similar to that in *Chiton*, or the hooked plate has received a quadricuspid cutting edge.

Schizochiton is to be regarded as a special end form of this phyletic series, with large eyes which, corresponding to the incisions of the insertion margin, are arranged on the anteriormost shell piece in most cases in 6 rows, and on the intermediate valves in 2 rows. The shell is greatly elongated and the perinotum is broad, posteriorly divided by a deep sinus which corresponds to a sinus in the posterior margin of the last shell piece. The perinotum is covered above and below with small needle- or club-shaped calcareous bodies, and at the margin and in groups on the upper side stand larger longitudinally grooved needles. These characters and also the complicated intestinal coils show a remarkable similarity with *Cryptoplax*, which is probably to be explained by a similar mode of life, but in any case does not represent a sign of closer relationship.

1078   All the remaining mollusks stand in opposition to the loricates, so that they can be combined as *Conchifera*. They can be derived from ancestral forms about whose nature a comparative study mainly of the most primitive gastropods and bivalves can give some information. Like the latter, their body was bilaterally symmetrical with paired nephridia and gonads as well as with 2 auricles of the heart; it is uncertain whether the ventricle and the pericardium may also be assumed as having been paired; at any rate the latter arose from an originally paired· anlage, corresponding to the gonads and nephridia, to which it was connected. If the intitial portions of the anterior aorta, which lay above the intestinal tract, were paired in accordance with the divided heart chambers, one may assume that the posterior aortae arose as branches running below the intestine, so that the latter was embraced by the aortae, as a result of which the pierced heart chamber developed, frequently found in lower conchiferans. Also bilaterally symmetrical was a pair of gills (ctenidia) near the anus. The primitive shell which was overlying only the visceral sack but not the head, is to be conceived as flat, but not bipartite as in bivalves, and was posteriorly produced into 2 lobes to which a pair of mantle lobes corresponds, on the lower side of which the gills were attached.

As in the gastropods, the ancestral form had a soled creeping foot, the ganglia of which were rope-ladder-shaped as in the loricates; the ganglia of the head were also similar, but a ganglionic cord, the visceral commissure developed, issuing from the anterior end of the pedal cords; at all events it developed in connection with the formation of the mantle lobes and ctenidia, which it mainly innervates. An equivalent of the perinotum of the loricates is the epipodium, which appears as a fold on the sides of the body proceeding from the head backwards, provided at the margin with tentacles and on the lower side with sensory elevations, but it lacks the covering of the upper side with a strong cuticula and calcareous bodies. The digestive organs begin with the mouth opening situated in a short snout-like process and a buccal mass, which contains a well-developed radula with near-identical teeth, opposite to which on the dorsal wall of the oral cavity lie a pair of jaw plates; the glands of the midgut are similar to those in the loricates.

From such an ancestral form the gastropods descended by an asymmetric turreting of the visceral sack covered by the shell. The asymmetry may have been the consequence of reduction of the left gonad. At any rate, the shell became spirally inrolled and gradually assumed the form of a broad, rounded cone. Because, with the enclosed visceral mass, it attained a considerable weight, it had to tip over to the left and thus came into contact with the substratum, and hence dragged during crawling, resulting in rotation until the shell acquired the most convenient position possible; this happened with the part touching the substratum had reached a position to the right beside the end of the foot. In this way one can conceive the displacement of the originally posteriorly situated parts: the shell aperture with the slit, the mantle lobe and gills, together with their centers of innervation, and the rectum along with the heart, the pericardium, and the kidneys. The gill cavity now lies over the dorsum, the gills are forwardly directed, and the visceral commissure has assumed the shape of the figure 8, the kidneys have developed in various ways.

1079   The group of marine gastropods which preserves most of the primitive features in the shape of shell is that of the pleurotomariids, which has maintained itself with a few species into the present. These living species of course do not correspond in their organization entirely to the picture that we have to make of the most basal animals, thus the epipodium is only rather weakly developed, the attachments of the visceral commissures have become displaced somewhat anteriorly, and the radula too may be especially developed. With their only slightly coiled shell having a row of holes and the loss of the operculum, the haliotids have indeed altered externally in a fashion similar to that of

Stomatia and *Gena* among the trochids, but on the whole they have retained such a primitive organization as no other group of snails; this is true especially of the well-developed epipodium and the nervous system. The eyes are open cups, as in *Pleurotomaria*.

The scissurellids are more varied, and have developed partly in the direction of fissurellids and partly in the direction of trochids. They are always small, in *Incisura* the shell is only slightly coiled, with wide aperture and short slit; the epipodial folds are reduced, whereas a few tentacles and below them small club-shaped sensory elevations are retained; the eyes are closed vesicles.

In several genera of fissurellids, as also in some trochids, a tentacle-like process of unknown function is found behind the right eye tubercle in both sexes; perhaps the ♂ copulatory organ of neritids is derived from it.

Among the fissurellids, judging from the shell, which is characterized by its bilateral symmetry, the forms with backwardly inclined apex and anterior slit with adjacent slit band show the most primitive characters. The central plate of the radula is more or less broad, with smooth or finely serrate cutting edge, the large outermost intermediate plate with an outer lateral cusp on the large pointed cutting edge; the related genera *Hemitoma* and *Clypidina* have acquired a cup-shaped shell with an indistinct slit and the radular plates differ distinctly, especially in the latter genus. *Puncturella* is also close to *Emarginula*, its slit is anteriorly closed; in *Fissurisepta* the thus-formed hole occupies the center of the shell, so that the apex is reduced. According to Odhner, the crop in these groups is very asymmetrical, the left half forming a large sack with internal villi, whereas the right half is greatly reduced; on the other hand, the crop of *Diodora* is less strongly twisted and in its interior provided with dense folds, so that this genus as well as *Lucapina* and *Fissurellidea* approach the Fissurellinae; hence they can be separated as the subfamily Diodorinae. In some groups the shell is covered by a broad fold of the mantle margin. Whereas the shell in the more primitive groups completely covers the animal, it becomes smaller in the higher groups and the hole becomes larger, as in *Fissurellidea annulus* Odhner, where the shell represents only a fairly narrow ring, and in *Macroschisma*, so that these forms are to be placed at the end of the phyletic development of the fissurellids, although without any immediate relationship to one another.

The patellaceans, similar to *Clypidina*, have a cup-shaped shell, although it is sometimes more, sometimes less deep and the apex sometimes approaches the anterior margin, but in most cases it lies in about the center. Most important for the systematic placement of the stirps is the presence of two gill rudiments together with the osphradia

lying symmetrically in the not very deep mantle cavity, a fact which indicates a derivation from animals with a pair of symmetrical gills, such as only the fissurellids possess. As a consequence of the reduction of the gills, the heart has undergone considerable modification, it is displaced from the middle somewhat to the left, whereas the rectum has turned to the right, hence the ventricle is no longer traversed by the intestine; of the two auricles the right has become reduced and the left one has shifted anterior to the ventricle. One can assume that a ring of lamellae has developed on a ring-shaped blood sinus such as it occurs in fissurellids, which projected fold-like from the site of the mantle attachment and which took over the respiratory function. On the left side, anterior to the shell muscle, this sinus emptied into the auricle of the heart. In this area in the acmaeids a bipectinate gill has developed, probably from a larger lamella, and in *Lottia* and *Scurria* in addition to this a circle of gills, like in patellids is present. The efferent blood vessel of the gill is a branch of the mantle sinus and the gill nerve is a branch of the mantle nerve, which corresponds to the left anterior mantle nerve of *Haliotis*. The relationship of patellaceans with fissurellids is also decisively indicated by the condition of the kidneys, the left of which is very small, the right in contrast is very large. Both groups have a ring nerve in the mantle, provided, especially in patellids with tentacles; but the epipodium has disappeared. The two groups differ as far as the pedal cords are concerned; in patellids, they have retained the more original position within the musculature, whereas in the fissurellids they overlie it. Sensory palps have developed in the mouth, the jaw has become uniquely modified by the development of a cutting edge and by the attachment of cartilage and musculature on its inner side. This is also true of the very long and narrow radula, attached on the median band of which very hard, yellow-brown, detachable cutting edges appear, which occur nowhere else. The esophagus is strongly twisted, following the crop, separated from it by a constriction, is an anterior part of the stomach with the opening of the liver, then the only slightly widened main stomach and the strongly coiled intestine.

In the phyletic development of the patellaceans 2 organs are especially important: the radula and the gill. The first of these in the family of patellids very clearly shows a development which begins with *Scutellastra* and ends with the Nacellinae; in the former there are on each side of a well-developed central plate 2 similar intermediate plates and somewhat behind this a plate with a large quadricuspid and uniquely bipartite cutting edge; the margin on either side bears 3 plates with simple, non-detachable cutting edges. In the remaining Patellinae the central plate becomes narrower and loses its cutting edge, in the

Nacellinae it is always rudimentary, and the adjoining intermediate plates have also become reduced, so that on either side there is only one anterior intermediate plate and one posterior one with bipartite cutting edge; the marginal plates are also sometimes rather weakly developed. The acmaeids approach this condition. In most cases the central plate is lost without leaving any trace, and the intermediate plates have come closer together, the anterior one with a simple, the posterior with bipartite cutting edge; of the marginal plates, sometimes 2 (*Patelloida*), more often only one or none at all are retained. *Potamacmaea* and *Pectinodonta* have uniquely modified dentition. The radula of lepetids has the greatest similarity with *Patelloida*, because always 2 marginal plates are present on either side, but one pair of plates is always fused to form a single cutting edge, whereas the other pair in most cases has separate smaller, simple cutting edges, which in only one species are fused with the others to form a broad cutting edge.

1081

Just as it is impossible to derive the dentition of *Scutellastra* from that of *Lottia* or *Acmaea*, it also seems impossible to derive the rudimentary gills of the former from the condition existing in the latter. One will have to assume that the original ctenidia were so affected by a reduction of the mantle cavity that they lost their function, whereas respiration was taken over by the mantle, on which a ring of lamellae developed. The strong development of the digestive organs may have given the impulse to the flattening of the gill cavity. The gill rudiments of the patellids are less distinct in the acmaeids; also, a subpallial sense organ, which the patellids inherited from the rhipidoglossans, has been lost in the acmaeids. The auricle of the heart in *Scutellastra* lies largely in the roof of the gill cavity and extends far on the right, in contrast the heart of acmaeids has shifted considerably farther to the left. Accordingly, there can be hardly any doubt that among docoglossans, the patellids are more primitive than the in most cases smaller acmaeids and lepetids, the latter of which have entirely lost their gills.

The trochids approach zeugobranchs with spiral shell and operculum, in which the right gill and shell slit tend towards reduction, similar to the condition in the scissurellids. In trochids the right gill has disappeared, it is indicated only by a blood vessel corresponding to the gill vein and the right auricle; but the left gill in the posterior part has fused with the mantle, so that the upper series of lamellae has disappeared and the lower lamellae are attached at the underside of the mantle. As in the scissurellids and fissurellids the radula on either side of the central plate in most cases has 5 lateral plates in each row, which in this case are at first not very different. The epipodium is anteriorly broadened, often asymmetrical, in the posterior part with few tentacles are similar sensory elevations as in *Scissurella*; the nervous system is also similar.

Among the currently living genera, *Margarites* most strongly reflects the primitive condition, it is more or less broadly cone-shaped with rounded whorls, with weak, not strikingly colored outer layer, smooth or spirally sculptured, aperture roundish without thickenings of the margin; the number of intermediate plates varies between 4 and 6, they have well-developed, laterally cuspidate cutting edges and their shape does not distinguish them much from the lateral plates, the first of which has only occasionally lost its cutting edge. Approaching this group, which lives mainly in the cold seas, are various phyletic series: primarily one with sometimes similar, sometimes more strongly sculptured shell, represented mainly by the genera *Calliotropis*, *Euchelus*, *Solariella* and *Seguenzia*; in this series the number of intermediate plates has become increasingly reduced, so that finally only one has remained, the radula thus approaches that of the taenioglossans from which it differs only in having a larger number of lateral plates. Coming close to this series are the in most cases cone-shaped Calliostomatinae, in which the radula likewise bears a varied number of intermediate plates.

Among the Trochinae, *Gibbula* can be regarded as most closely related to *Margarites*. In this series the size, shape, and sculpture are
1082 variable, the outer shell layer tends to be distinctly colored, the apertural margin not seldom has tooth-like thickenings and the umbilicus may be partly or completely covered by callus. Jaw plates are often reduced, the radula as a rule has 5 intermediate plates on either side (except in *Cittarium*) of a shape similar to that in *Margarites*, but the cutting edges are sometimes larger. The Umboniinae may be considered as another series, the shell of which is sometimes very similar to *Gibbula*, in some genera with an umbilical callus; their main characteristic is the form of the median radular plates, the cutting edges of which are not or only slightly projecting and lack a narrowed neck part. The Stomatiinae also seem to approach *Gibbula*; they are characterized by the loss of the operculum and by the progressive reduction of the spire, so that the terminal forms have become cap- or cup-shaped. The genus *Angaria* resembles *Liotia* in the shape of the shell, but has an uncalcified operculum, and the form of the radular plates is considerably different; the genus seems to approach the *Gibbula-Tegula* series.

The anatomically little-known, generally small, Skeneinae differ from most genera of the heretofore mentioned groups to trochids by their non-nacreous shell, but exceptionally this character can also be found in the trochids, as for instance in *Fossarina*; their operculum is uncalcified. The radula in these genera shows differences, in most cases the central plate is broad, with only slightly curved cutting edge which is not demarcated neck-like and is smooth or finely cuspidate, 4 or 5 intermediate

plates with cuspidate cutting edges. Because of the colorless, smooth or finely spirally sculptured shell, which is sometimes and probably originally cone-shaped, this group reminds of *Margarites* and may have diverged very early from the other trochids. Perhaps approaching them are also the cyclostrematids, previously united with them, and the radula of which has only one intermediate plate and few weak lateral plates.

The turbinids differ from trochids mainly by a more or less strong calcareous deposit on the operculum; in *Liotia* it consists of a spiral row of pearl-like granules which do not form a solid, continuous layer; in *Mölleria* it is only thin and spiral like the inner layer; in *Leptothyra* in most cases with a callous covering; in *Bothropoma* externally forming only a broad whorl around a median pit. The operculum of the Turbininae and Phasianellinae is thick and externally the inner whorls are in most cases not recognizable, these rapidly increase in the latter group. *Liotia* is thus closest to the trochids, perhaps in particular to the *Gibbula* group, with which the radula also agrees; *Mölleria* and *Leptothyra* are related here; *Bothropoma* is distinguished by a different form of the radular plates, which however also deviates little from certain trochids and shows rather primitive characters. The more or less large species of the genera *Turbo* and *Astraea* have often lost the cutting edge on the central plate of the radula, the strongest plates here are not the intermediate but the inner lateral plates; both genera are closely related with one another. In contrast, *Prisogaster* is considerably different; the two species show striking similarity with certain *Tegula* species from the American west coast, such as *T. gallina* (Forbes) and *funebralis* (A. Adams), not only in the nature of the shell but also in the shape of the radular plates, so that one can think of a relationship, but the operculum is calcified, externally greatly bulging, internally somewhat concave, with nearly 1083 marginal nucleus, thus showing the same characters as in the Phasianellinae; the genus has therefore to be placed with that group, although the shell is internally nacreous. Of the other genera, the shell of which is not nacreous internally, externally in most cases quite colorful, *Tricolia* as well as *Prisogaster* have a broad central plate of the radula without cutting edge, in *Phasianella* it is modified into a narrow ridge or is completely reduced, and in *Eulithidium* the two inner intermediate plates are fused to form a secondary central plate.

Because, according to their dentition, the neritaceans belong to the rhipidoglossans, and show closer relationships neither to zeugobranchs nor to the docoglossans, they can be derived only from the trochaceans, from which however they show important differences. Transitional forms between the two stirps are not known. Because of the low-spired, non-nacreous shell with its callus-covered umbilicus, the Australian

Callomphala (cf. Fig. 41) strongly resembles *Nerita*; but unfortunately the animal is unknown and hence it is uncertain whether this similarity can be considered as an indication of relationship.

The aquatic neritaceans have a bipectinate gill, which however is very peculiar in not being fused with the mantle as in trochaceans and is quite differently innervated, the gill nerve being a branch of the mantle nerve arising from the left pleural ganglion; it also lacks a distinct osphradium. For these reasons the neritid gill cannot be considered as a homologue of the trochid gill; the reduction of the latter is difficult to explain, perhaps it came about through adaptation to life on the seashore, such as *Hydrocena* leads, whereupon a return to the sea or to freshwater resulted in the new development of a gill. *Hydrocena* is more primitive in the nature of the reproductive organs than the neritids, and hence one may accept the idea that the latter descended from the hydrocenids; in the latter, however, the right auricle of the heart, which is present in neritids, has disappeared and the ventricle is not traversed by the intestine; thus in this respect the hydrocenids are farther removed from the common stem forms than the neritids.

The operculum is uncalcified only in *Pseudhelicina*; its form in this genus is similar to the initial form: about semicircular, forming less than one whorl; in the hydrocenids and neritids a process is present internally at the nucleus, in helicinids the growth often becomes concentric. The strongly calcified operculum of *Neritopsis* is very unique; the operculum is absent in the cap-shaped phenacolepadids, the completely naked titiscaniids, and the proserpinines.

The buccal cavity does not contain jaw plates comprised rodlets, which are also lacking in some trochids, and also no salivary glands, but only the anterior glandular pouches and a pair of esophageal sacks which correspond to the crop of the trochids, etc., and which are considerably shorter in neritids than in hydrocenids and helicinids. The normally developed radula has 4 intermediate plates on either side, the outermost of which is very strong, especially in helicinids, the others are in most cases small, but in many neritids the innermost also reaches considerable size; on the other hand in *Neritilia* and *Neritopsis* the central plate, in *Titiscania* also the inner intermediate plate, have reduced and in hydrocenids only a few weak plates are retained in the median part. The nervous system is characterized mainly by the compression of the subintestinal ganglion and the pleural ganglia above the anterior ends of the pedal cords, in helicinids are probably also hydrocenids by interruption of the supraintestinal part of the visceral commissure.

The position of the kidney, which undoubtedly corresponds to the left one of the trochids, somewhat varies according to the extent of the

mantle cavity, and similarly its shape and the urinary chamber; instead of the club-shaped papillae of the trochids, here more or less strong folds are developed, a nephridial gland is absent. A right kidney is not present; the blind sack on the gonoduct of *Hydrocena* may be considered a remnant of this kidney, such may also be retained in other neritaceans, but no longer has an excretory function. In neritids the oviduct has retained a connection with the pericardium. The nature of the ♀ genital tract of *Hydrocena*, with its simple opening, is the most primitive in the stirps; the helicinids differ from this in the development of a separate opening of the bursa copulatrix into the mantle cavity and in neritids the bursa is considerably enlarged as a result of spermatophore formation, its opening has therefore moved farther forward, and finally in some groups a 3rd opening is also developed. In contrast, the gonoducts of *Titiscania* are simple; the receptacula seminis are a unique structure. Whereas the hydrocenids and helicinids lack a ♂ copulatory organ, the neritids in most cases have a lobe-shaped process posterior to the right tentacle; in *Phenacolepas* it is finger-shaped.

As a whole, the neritaceans are a highly developed stirps of rhipidoglossans, which are unique in various organs so that they are not in direct phyletic relationship with taenioglossans, even though the reduction of the right kidney does indicate a certain relationship; moreover, the structure of the gonoducts of *Hydrocena* is essentially like those of several taenioglossans.

Considerably more divergent are the cocculinaceans, a group of small, mostly deep-sea, snails with cap- or cup-shaped shell, of which the cocculinids still have a distinctly rhipidoglossate dentition, whereas it is uniquely modified in lepetellids. A ctenidium is absent, and is in most cases replaced either by a larger folded lamella or by few or several leaflets which, similar to the condition in patellids, are attached on the underside of the mantle, but only on the right. The short pedal ganglia, the simple sack-shaped kidney, and the hermaphroditic gonad with simple gonoduct represent characters of a unique development.

The architaenioglossans are interrelated only by the rope-ladder-shaped pedal ganglia and their more or less primitive organization, showing a certain resemblance to the trochaceans, from which they seem to have arisen. Among these the cyclophorids are land snails, which distinctly differ from the remaining families living in freshwater. It is still unclear from which marine snails they derive, although the considerable similarity of the dentition of some cyclophorids (cf. Fig. 84) with that of *Lacuna* may indicate a certain relationship, especially because the shell form does not contradict this and the latter group can be regarded as the most primitive among the marine taenioglossans. As

in the trochaceans, the pleural ganglia of cyclophorids lie at the anterior
ends of the pedal cords, but in some genera (*Poteria, Cyclosurus*) they
move away from them, so that they are connected by distinct connectives;
the rather weak parietal ganglia are removed from the pleural ganglia,
the supraintestinal ganglion farther away than the subintestinal. The jaw
plates and the salivary glands are well developed, the buccal pouches are
small; the kidney has no separate urinary chamber. The oviduct leads
into the widely open glandular duct, attached at the posterior end of
which is a sack-shaped receptaculum seminis, a bursa copulatrix being
absent; the ♂ duct is similarly shaped, it has a spermatophore gland at the
posterior end of the wide terminal part; attached behind the right tentacle
is the penis, connected with the genital opening through a groove and
innervated from the right pleural ganglion. An epipodium is absent.
Accordingly, it may be assumed that a group of marine gastropods, which
still shares the ladder-shaped pedal ganglia with the trochids
—probably from the group of the Margaritinae, in which the radula tends
to a reduction in the number of the intermediate plates (cf. Fig. 31)
—but was approaching the littorinaceans in the structure of kidneys and
reproductive organs, migrated to the seashore and then to land, lost the
gill, and gave rise to the cyclophorids. The interrelationships of the
groups among themselves can be assessed only from the character of the
shell, the operculum, and the radula, because the comparative anatomy
of the animals has in most cases not yet been investigated. Probably the
broadly cone-shaped, medium-sized shells with tightly coiled horny
operculum are to be regarded as primitive, similar to *Leptopoma*,
possibly also *Craspedopoma*, on the other hand a calcified operculum
and turreted shell or the fatty shine of the surface of Pupineae or the
different radular forms (cf. Figs. 81 and 85) indicate secondary
modifications; the European group *Cochlostoma* on the whole seems to
be the most different.

The nervous system of the viviparids differs from that of cyclophorids
by the pleural ganglia having moved away from the pedal ganglia and
toward the cerebral, as well as by the retention of a lower esophageal
commissure. The neck lobes are similar to those of trochids; they receive
their nerves from the pleuropedal connectives, the margin of the right
one also receives a branch of the mantle nerve, in the trochids they are
supplied from the anterior part of the pedal cords; perhaps these nerves,
along with the pleural ganglia, have become displaced farther forward in
the viviparids. The gill is retained here, its leaflets are attached to the
mantle. The form of the radular plates shows little similarity with that
of cyclophorids. A special acquisition of viviparids is the long ureter; the
blood gland, which is otherwise part of the nephridial gland, in this case

lies in the wall of the auricle. Use of the right cephalic tentacle as a copulatory organ as well as viviparity are also peculiarities of the family. It is thus to be assumed that it has retained some primitive characters of trochids but in other organs it has developed so independently that a close relationship with cyclophorids is out of the question. The widely distributed genus *Viviparus* may be the most primitive, whereas the North American Campelominae because of their small radula with simplified plates, the large foot, and the weak neck lobes are the most divergent.

The ampullariids may have derived from similar forms as the viviparids, for the two agree in their habitat in freshwater, similar shell, operculum, as well as in the neck lobes, but in other organs they have undergone a unique development. Especially striking is the division of the mantle cavity, the right part of which contains the gill, whereas the left serves as a lung. In the nervous system the lower esophageal commissure and the fusion of the pleural ganglia with the anterior parts of the pedal cords is a primitive character, but the union of the subintestinal ganglion with the right pleural ganglion is a peculiarity. The condition of the kidney and the development of a ♂ copulatory organ at the mantle margin are also unique. Among the genera, the West African *Afropomus* may be especially primitive, however its anatomy is not known. As higher and divergent characters may qualify: the disk-shaped (*Ceratodes*) or sinistral (*Lanistes*) shell, the calcified operculum (*Pila*), the reduction of neck lobes (*Asolene*), and the bipectinate osphradium.

There are divergent opinions of the systematic position of the lavigeriids, which inhabit Lake Tanganyika; in most cases they are included in the melaniids, but, according to Moore, the nervous system is considerably different from that of melaniids and resembles that of viviparids, with the rope-ladder-shaped pedal ganglia, a lower esophageal commissure, and the pleural ganglia lying close to the cerebral ganglia. The outer lateral plate of the radula is similar to that in melaniids, less so the other plates, but this can be viewed as an analogy, and perhaps *Lavigeria* can be seen as a form, sculptured similar to *Paramelania*, derived from a *Viviparus*-like gastropod.

Among the marine taenioglossans, the littorinaceans show some traits of primitive organization. The shell is not nacreous, in most cases with medium high spire, more seldom flat or turreted above, aperture roundish, operculum uncalcified, in most cases with few whorls. The pleural ganglia adjoin the cerebral ganglia, the pedal ganglia are not rope-ladder-shaped but roundish and each with 2 small ganglia attached to it, the posterior pair of which in *Lacuna* is connected by a commissure.

This posterior pedal commissure seems to be of special interest, because it is also found in some other groups and is thus important for the recognition of their relationships. The ganglia of the rather long visceral commissure are only indirectly connected with the anterior mantle nerves. Because some littorinids live on the seashore, their gill, which in *Lacuna* together with the osphradium and the hypobranchial gland are well developed, tends toward reduction; *Cremnoconchus* has climbed into the mountains. The radula of lacunids is moderately long, whereas in littorinids it often attains an enormous length. The intermediate plate always has a sinus on the outer margin; the cutting edges in most cases have several cusps. The salivary glands each have a very narrow efferent duct; on the esophagus on either side lies a somewhat folded buccal pouch anterior to the cerebral ganglia, its posterior part is narrow. *Lacuna* has a well-developed anterior pedal gland with a blind sack; it may also be of significance that in the left mantle margin lie a number of subepithelial glands, which open on the underside. It is uncertain whether the tentacle-shaped processes of the opercular lobes of *Lacuna* may be considered as remnants of the epipodium; anterior lobes are lacking. The oviduct of *Littorina* —that of *Lacuna* has not been studied— is connected with the pericardium at its end lies a receptaculum seminis embedded in the albumen gland, which forms the posterior part of the "uterus" and which is joined by a capsule gland and in most cases a jelly gland; the blind-sack-shaped bursa copulatrix also opens at the opening of the uterus. In the ♂ the penis is connected with the sperm duct
1087   sometimes by an open ciliated groove, the glands of which serve as prostate, sometimes through a closed canal; in *Littorina* species the penis has special cement glands. Among the littorinids, *Laevilittorina* and *Haloconcha* may be primitive forms, *Cremnoconchus* and *Tectarius* the most modified.

The pomatiasids shows striking similarity in the nervous system to littorinaceans; moreover, like *Lacuna*, they have in addition to the main commissure of the pedal ganglia, also a weaker posterior one, but the small accessory ganglia are not separated. Because they are land dwellers, they lack a gill, but a bulge-shaped osphradium is retained. Their operculum is varied, rarely thin and horny, more often calcified; the shape of the shell is also varied. The division of the foot-sole by a median furrow is only a reinforcement of the condition in *Littorina*. However, in other organs there are considerable differences, such as in the form of the radulars plates, the outermost of which is greatly broadened, the esophagus having a ventral conducting groove with basophilic glandular cells, whereas the remaining part has an epithelium similar to the crop of rhipidoglossans; the kidney has no nephridial

gland, the uterus is largely groove-shaped, the penis is attached farther to the back on the right side and is innervated from the subintestinal ganglion. Hence, it is hardly possible to directly relate pomatiasids with the littorinaceans. The center of their development probably lies in the Indo-African region; among the Pomatiasinae, *Leonia* may be the most divergent form, whereas in the series of the Chondropomatinae unique forms of sculptures have developed, among which *Blaesospira* needs to be mentioned (cf. Fig. 110).

The relationship of planaxids is also unclear, the nervous system of which, according to Bouvier, is very similar to that of *Littorina*, which is true especially of the pedal ganglia; the subintestinal ganglion has moved toward the left pleural ganglion and the cerebral commissure is shorter. The shell aperture is strikingly different, as also the scarcely spiral operculum and especially the radula, the central plate of which bears a couple of basal cusps similar to the condition in Batillariinae, the lamella on the outer lateral plate has some similarity with *Pomatias*, but is probably only analogous with it.

The hydrobiids can be related to the littorinaceans with greater certainty. Their nervous system is more concentrated because of a shortening of the connectives, and the parietal ganglia may touch the pleural ganglia; a posterior pedal commissure often connects a pair of accessory ganglia. With few exceptions, the animals are small, with a more or less high shell and in most cases roundish aperture; the operculum is originally horny and spiral, with few whorls. The central plate of the radula has as a rule two or more basal cusps, the intermediate plate a sometimes very long lateral process and almost always a cuspidate cutting edge, the lateral plates in most cases finely serrate cutting edges. A majority of the hydrobiids live in freshwater, but they belong to the large stirps of the Rissoacea, of which many groups are marine. Anatomically they are still poorly studied, so that their classification is based on the condition of the shell, operculum, and radula; it may be that marine rissoids are intermediate between lacunids and hydrobiids. Among them, the groups united in the genus *Cingula*, some of which are widely distributed, may be considered as most 1088 primitive, the shell of which is not or weakly sculptured and has no sinus at the end of the columellar margin. Like *Rissoina*, which according to the radula is not different from *Rissoa*, the Barleeinae and Hemistomiinae have an internal process on the operculum, whereas their radula has a more or less divergent form. Of the hydrobiids, some genera are close to *Hydrobia*; their penis is simple, attaching in the neck region somewhat on the right, the operculum spiral, thin, with few whorls. The largest forms have developed in Lake Baikal. The penis has sometimes attained

a lateral process or is broadened leaf-shaped. *Truncatella* species inhabit the seashore and *Geomelania* the dry land. Because of the tightly coiled operculum and the shape of the radular plates, the Australian genus *Hydrococcus* is transitional to the Stenothyrinae; the calcified operculum is the main character of the Bithyniinae. The micromelaniids, likewise living in freshwater, have a somewhat more concentrated nervous system with simple pedal ganglia and a radula similar to hydrobiids, but without the basal cusps of the central plate. Because the genus *Emmericia* also has such a dentition, it can be placed in the latter family; the shell shapes are different.

Another family of the Rissoacea are the assimineids, which in part live on the seashore, in part on land. The basal cusps on the central plate of the radula are originally distinct but often become lost, and the initially moderately broad outer lateral plate is considerably broadened, with very numerous fine serrations, which makes it similar to that of pomatiasids. As in the latter, the gill is reduced, whereas the osphradium is retained. A posterior pedal commissure is present, the parietal ganglia are fused with the pleural ganglia. As in the related groups, the salivary glands are simply tube-shaped, the esophagus has a posterior blind-sack-shaped gland, homologous with the crop. The closed sperm duct has a strong prostate; the large penis, attached on the neck, receives a nerve from the right pleuropedal connective; before opening into the glandular uterus, the oviduct is connected with a sack-shaped receptaculum seminis. There seems no doubt that in this family the littoral species of the genus *Assiminea* are the most primitive, the land-dwelling Omphalotropidinae are less primitive. The latter, which were earlier united with the pomatiasids, do not seem to be closely related in spite of certain similarities; their foot-sole is undivided, their nervous system considerably more concentrated, and the esophagus is different.

Bouvier believes that the hydrobiids are so closely related to terrestrial acmids that they may be considered as aquatic acmids; but the latter are anatomically still poorly known, their radula may betray a certain resemblance to that of assimineids, to which they are perhaps closest.

According to the condition of the radula, the family of the adeorbids, the shell of which in case is low-spired, also come close to the marine rissoids. A striking peculiarity is shown by the gill, which is bipectinate and extensible as in trochids, but, in view of the concentrated nervous system a close relationship of the latter can hardly be assumed to such an extent that this gill is an inheritance from the trochids; it has probably to be considered a special acquisition as a consequence of the burrowing mode of life. In other organs too the adeorbids resemble the rissoids, but

1089 a ♂ copulatory organ is stated to be absent; on the right mantle margin of *Adeorbis* 2 finger-shaped processes are located. Because in some genera the animals are unknown, their interrelationships remain uncertain, the same is true of the affiliation of the fluviatile genus *Phaneta* to this family.

It is very remarkable that a similar bipectinate and extensible gill is also present in the valvatids, which also have a finger-shaped process on the right mantle margin; their radula differs mainly by the absence of basal cusps on the central plate and their nervous system is similar. The kidney has attained a ureter opening at the mantle margin, and the reproductive organs have assumed a special peculiarity, wherein the two sexes are combined under retention of those parts present in related families, such as a receptaculum seminis on the ♀ part, and on the ♂ part a prostate and a penis attached below the right tentacle. The viviparous group *Borysthenia* is an offshoot from *Valvata*.

A phyletic series, which probably arise from rissoid-like forms, includes mainly the Cerithiacea, to which the ptenoglossans are probably allied. Their shell is in most cases turreted, the aperture originally roundish or ovate and without lower canal, although this feature and sometimes a short siphonal process has developed in some groups. A special character is the absence of a ♂ copulatory organ. The nervous system is in most cases characterized by the approach of the pleural ganglia to the cerebral ganglia and of the subintestinal ganglion to the left pleural ganglion, whereas the supraintestinal ganglion is rather distantly located; the pedal commissure is simple; but the nervous system of ptenoglossans is very different. The radula shows some similarity with that of rissoids, sometimes the central plate also shows indications of basal denticules, but these are in most cases lacking; its cutting edge has next to the median main cusp, on either side an accessory cusp, or 2 or 3, rarely more, as in turritellids; the intermediate plate is variably broad, often with a shorter or longer lateral process and with denticulate cutting edge, the lateral plates are varied, sometimes pointed, sometimes with broadened cutting edges, which often bear a few identical cusps. The plates of cerithiopsids are more irregular, in *Triphora* the taenioglossate dentition is replaced by numerous identical, very small plates with 3 or 2 cusps. The ptenoglossans have assumed the dentition of predatory snails, the buccal mass of which is characterized by large jaw plates, special glands and often by unique stylets. Among the turritellids also an abnormal formation of the radula may occur (*Turritellopsis*), and in the solariids, which like the mathildids probably approach the turritellids, a larger number of radular plates has developed, which show some similarity with those of ptenoglossans. In this series of snails, the non-

retractible snout otherwise being more or less long, some forms have attained a long retractible proboscis in adaptation to a predatory mode of life; the esophagus shows differences corresponding to the nutrition. The osphradium, which is in most cases cord-shaped, can become bipectinate.

In this group of prosobranchs various developmental series probably separated early, in which in most cases the initial forms still showed no or only a weak apertural sinus. Most remained in the sea. Of these, the small Finellidae, whose organization is little known, and the Litiopinae seem to be primitive forms. It is doubtful whether the cirri arising on the foot of *Litiopa* can be considered as the remnants of an epipodium. The shell of *Diala* has resemblance with some rissoids, the operculum and the radula are also not very different. Standing close to them are probably first *Bittium* and various *Cerithium* groups. *Plesiotrochus* and *Trochocerithium* may also have come from litiopines. It is uncertain whether the large *Companile* is related here—the form of the shell and of the aperture appear to indicate this. The potamidids, in most cases living in brackish water, with several whorls of the operculum, represent another series, which probably branched very early; *Pirenella* and *Batillariella* have weakly indented apertural margins, whereas in other genera a distinct sinus and a columellar process have developed, apparently independent of the cerithiids. A similar condition exists in the freshwater melaniids, which however have more often retained the non-indented aperture, although here again forms with distinct sinus have developed in some groups.

Less closely related with these groups are the turritellids, which always live in the sea and, with the exception of *Protoma*, have roundish shell aperture and an operculum consisting of several narrow whorls. Connecting to similar forms, besides the in most cases likewise turreted mathildids, are the low-spired to disk-shaped solariids as well as the in most cases very irregularly formed but sometimes initially still distinctly spiral vermetids, among which *Tenagodus* is characterized by the slitted shell, and perhaps also the very small caecids.

The ptenoglossans, which probably stand close to the cerithiaceans, have posed considerable difficulties for the systematists. Originally based on the radula alone, the group included families which not have to be excluded, so that only the scalids and the janthinids belong here. That these two are closely related is beyond doubt because of the wide agreement in the condition of the highly peculiar buccal mass of *Scala* and *Recluzia*. They have however assumed a divergent mode of life; whereas the scalids crawl on the ground like most snails, the janthinids produce a foam raft with their pedal glands by which they swim on the

ocean surface, where they feed mainly on the relatively large *Velella* and *Porpita*; hence their proboscis has become wider and shortened, which necessarily resulted in a widening of the ganglionic esophageal ring. In this case from a "brevicommissurate" nervous system a "longi-commissurate" has developed. The zygoneury in the two families is also dissimilar; it may be that a left zygoneury is not always developed in scalids. The lateral folds on the foot of *Janthina* are probably a new structure, which is not homologous with an epipodium. The eyes and statocysts tend to reduction. Both families agree in the possessions of mantle glands which produce a purple-like secretion and both have protandrous hermaphroditic gonads without penis, within which character-istic motile "spermatozeugmata" are developed through which fertilization takes place. The shell of scalids is in most cases turreted, the aperture roundish without distinct spout, the operculum spiral with few whorls; among them the genus *Acirsa* may be the most primitive. The genus *Recluzia* stands closer to scalids then *Janthina*; the latter is peculiar in the

1091 color and shape of the shell, the clefted tentacles, the large buccal mass, and the condition of the nervous system.

Aside from the radula, the anatomy of cerithiopsids is still unknown. According to a figure of the animal of *Cerithiopsis tubercularis* by Forbes & Hanley (Fig. 896b), is has no projecting snout, the eyes lie on the dorsal side of the head at the base of the finger-shaped tentacles, the foot is anteriorly strongly produced, clefted at the margin, and has the opening of a gland in the middle of the sole. It is not known whether a penis is present. Thus is view of the considerable differences from cerithiids, it seems probable that, in spite of similar shell shape (cf. *Bittium*, Fig. 896a), *Cerithiopsis* is not closely related with them, whereas the animal of *Triphora* (according to Chiaje) appears to be similar to that of Bittium. Judging from the figures of melanellids, their head and foot is rather similar to that of *Cerithiopsis*, they have a long retractile proboscis with rudimentary buccal mass, a well developed labial and sole gland in the foot, a bipectinate osphradium, and separate sexes with a penis behind the right tentacle (Fig. 896c). Hence, a relationship between the two groups seems possible. Coming close to the melanellids are the stiliferids, which are more or less adapted to a parasitic mode of life. The very small aclidids are also probably closely related to melanellids, but whether the pyramidellids are also related to them, seems somewhat uncertain on the basis of our present knowledge of their anatomy, but it is indeed possible. They also have a long retractile proboscis without a radula, it is closely surrounded by the esophageal ring, but there is a hermaphroditic gonad; the small species lack a gill just like the aclidids. According to the shell and the

operculum, among the melanellids, *Niso* has strong similarity with certain pyramidellids and may be most closely related to them. It is uncertain to which taenioglossans the entire group belongs; according to the shell and the operculum one could think of the Rissoacea.
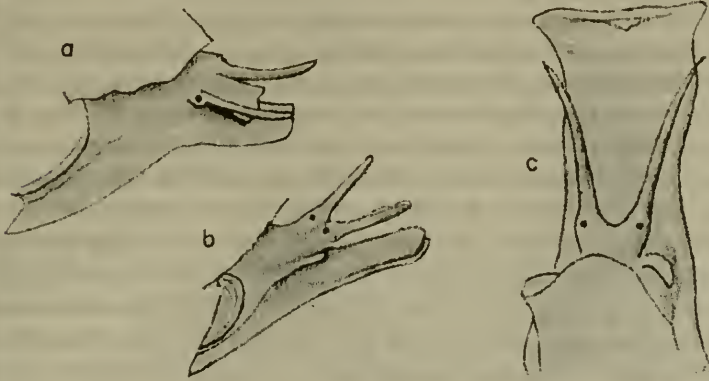
Fig. 896. a, *Bittium reticulatum* (Da Costa); b, *Cerithiopsis tubercularis* (Montagu); c, *Eulima* (= *Melanella*) *alba* (Da Costa). Head and foot, after Forbes & Hanley.

Another series of taenioglossate snails, which may have arisen from the primitive groups of Lacunidae-Rissoacea, begins with the Fossaridae, the anatomy of which is unfortunately still scarcely known, except for the radula. Based on the shell form, the genus *Megalomphalus* among them can be considered as the most primitive (cf. Fig. 246), its radula, like that of *Couthouyia* (Fig. 247), is similar to that of rissoids and adeorbids; the operculum has a nearly or completely terminal nucleus. According to the shell and the radula, the Vanikoridae stand close to the 1092 Fossaridae. Their typical species, *V. cancelata*, has a leaf-shaped propodium and on either side a wing-shaped lamella on the foot; the head forms a rather short snout and the eyes lie in the posterior part of the tentacles, the penis attaches behind the right tentacle. It is not known whether the fossarids have an equivalent of the anterior pedal lobe, but such a lobe is also present in related families, because the "lower lip" of trichotropids and capulids is innervated by the pedal ganglia and corresponds to the propodium of vanikorids and amaltheids. The trichotropids still have a spiral shell and an operculum, the amaltheids and capulids a cap- or cup-shaped shell without operculum. The lateral plates of the radula are in most cases simply pointed; the esophagus is narrow; the animals are often protandrous hermaphroditic. The pleural

ganglia adjoin the cerebral ganglia and both are connected with the subintestinal ganglion, the right alone with the supraintestinal ganglion. The osphradium in amaltheids is thread-shaped, in trichotropids and capulids it is bipectinate.

The calyptraeids also belong in this group of snails; the propodium in its median parts is fused with the under side of the head, so that it has the form of two lamellae, which anteriorly terminate below the tentacles; there is no doubt that these lamellae are not homologous with an epipodium but with the propodium of the related genera. The nervous system is highly concentrated, the parietal ganglia lying close to the pleural ganglia and connected to both. The shell in the more original forms is still distinctly spiral with central apex and flat or concave underside, it later assumes a cup-like form with funnel-shaped basal lamella, or the apex approaches the margin, giving rise to the slipper-shape; the more or less large salivary glands are sack-shaped and do not traverse the ganglion ring; the lateral plates of the radula are cuspidate or smooth; the esophagus has no glands. The gill consists of long filaments, the osphradium is short and bipectinate.

The xenophorids have a shell very similar to that of *Calyptraea* (*Trochatella*) (cf. Fig. 256), with the free shell margin separating the lower side from the upper side. Like the latter, they have a propodium but which here is not fused with the head, and like them they have a gill consisting of long filaments; the radula with simply pointed lateral plates. is also similar, likewise the sack-shaped salivary glands and the long thin esophagus; the similarily shaped penis, situated on the right side, has a ciliated groove. Contrasting these similarities, there are nevertheless some differences: the retention of the operculum, the loss of the creeping sole, the long thread-shaped osphradium, the long connectives between the pleural and parietal ganglia corresponding to the lengthened neck region. However, it is to be assumed that a relationship exists between calyptraeids and xenophorids in that both groups have originated from common ancestors which still had an operculum, a creeping sole, a simple osphradium, and distinct connectives between pleural and parietal ganglia, so that as a whole they had greater similarity with xenophorids. Because, according to the form of the foot and the other characters of the animals, they belong to the strombaceans, this stirps cannot be placed in relationship with the Cerithiacea but with the Calyptraeacea. The shell form of the Strombacea is varied; that of struthiolariids, which still have a normal creeping foot with poorly developed propodium, has similarity with trichotropids (cf. Figs. 251 and 260). In other genera the spire is elevated turret-like and the aperture has acquired an elongated channel, in *Strombus* and *Pterocera* and apertural margin is often widened and is

1093

sometimes produced into processes. The ciliated groove, which in the ♂ leads to the penis, in the ♀ ends at the propodium.

The heteropods also, which have shifted to a swimming mode of life, are very probably related to these groups provided with a propodium; based on the shell one could think of a relationship between *Protatlanta* and *Lippistes*. The pterotracheids, which have completely lost the shell, represent the most highly developed forms among them.

In contrast to this series in which the esophagus is narrow and more or less long, the naticids have a strongly developed esophageal gland, which corresponds to the crop of the primitive prosobranchs. They also have a kind of propodium, but it is basically different from that of Strombacea, etc.; on the anterior part of the foot a shield-like thickening has developed, which is laterally separated from the lower part by a groove and posteriorly has a free margin which overlies the head. This unique structure is correlated with the mode of life of the naticids, which plough the sand in order to drill into bivalves and snails present in it and to suck out their contents. The drilling is effected by a gland at the mouth opening, the tall epithelium of which produces an acidic secretion. The pleural ganglia adjoin the cerebral ganglia, the commissure of which is sometimes rather long, whereas the parietal ganglia are connected with them by distinct connectives, the subintestinal ganglion only with the left pleural ganglion, the supraintestinal ganglion not only with the right pleural ganglion but through the mantle nerve also with the left one. The osphradium is bipectinate. In the naticid series, the small Antarctic *Frovina* may be the most primitive; its shell and operculum have similarity with *Lacuna*, and also according to the radula one can think of a relationship with the lacunids and rissoids; still it has a bipectinate osphradium and probably an indication of the propodium. In the more highly developed naticids, the foot has gradually become enormously enlarged; the operculum is sometimes distinctly calcified and the radular plates can lose their accessory cusps. Occasionally the eyes are reduced.

The lamellariids and cypraeids are to be derived from similar initial forms; both of them have lost the operculum, their mantle is often strongly developed and can partially or completely enclose the shell; they lack a propodium. The shell of lamellariids is only weak, with a wide aperture, spiral with few, rapidly increasing whorls, or cap-like. The radula has variously formed plates, the lateral plates are in most cases rather short and pointed; in *Lamellaria* they have disappeared. The nervous system is more or less concentrated, in *Lamellaria* the two parietal ganglia are connected with the two pleural ganglia by short connectives. Whereas the Lamellariinae have separate sexes, they are combined in the Marseniinae and Velutininae.

Among the cypraeids, especially the Triviinae betray a close relationship with lamellariids. The only slightly coiled shell is, however, differently formed, with low spire and narrow, terminally groove-shaped aperture, and the mantle anteriorly has an elongated siphonal canal, whereas in lamellariids it forms only a fold. In addition to the usual shell muscle, there is also a smaller one lying anteriorly and to the left. The osphradium is bipectinate. A narrow tube-shaped gland opens in the foot-sole. The buccal mass contains jaw plates and a radula with short pointed lateral plates; the esophagus has a strong gland. The bipartite kidney and the ♀ organs with a few seminal vesicles are also similar. According to Pelseneer, *Trivia* has an uncalcified larval shell which, as in *Lamellaria*, is enrolled in one plane and surrounds the initial whorls of the *Helix*-shaped calcareous shell.

The remaining cypraeids have developed more or less divergently; whereas in *Trivia* the osphradium lies rather far forward transversely in the mantle cavity and the gill forms a moderately deep arch, the mantle cavity has deepened, so that it extends almost to the posterior end, the gill forming a deep arch and the osphradium having become triradiate. In the nervous system, the pleural ganglia adjoin the cerebral ganglia and the supraintestinal ganglion is sometimes closer to the left, sometimes to the right pleural ganglion, connected to both, whereas the subintestinal ganglion is more or less removed and is sometimes directly connected with both pleural ganglia, sometimes only with the left. The most striking character of the nervous system of higher cypraeids is the presence of rope-ladder-shaped prolongations of the pedal ganglia, which however do not contain a continuous cortex of ganglion cells and do not contain any cells in the posterior parts; corresponding with them in *Trivia* there are only simple nerves which are not interconnected. These cords of the cypraeids have been considered as indication of primitive organization, and this group has been placed with the architaenio-glossans; they however have no closer relationship with the latter and because as a whole the triviids are the most primitive cypraeids, one will have to assume that their posterior main nerves in the foot have secondarily become partly ganglionic and have retained some transverse connections. It is incorrect that the heart and 2 auricles; according to Pelseneer one assumed auricle is "... une ecbolie anormale du ventricule." The radula has undergone modification in the subfamilies; in the Pediculariinae it is still most similar to the Triviinae, the division of the intermediate plate of Jenneriinae is striking, whereas the lateral plates show transitions to the Amphiperasinae, in which the outer lateral plate is greatly broadened and is comb-shaped serrate; the radular plates of Cypraeinae have assumed greatly divergent forms, whereas the jaw plates have disappeared.

It appears uncertain, to which taenioglossan group the Doliacea are related. Bouvier considered it probable that they have developed from chenopodids (=aporrhaids) through the extinct columbellinids; in these intermediate forms the osphradium may have become modified from the thread-shaped to the short bipectinate one. According to the shell one can also think of the struthiolariids, the foot of which still does not posses a distinct propodium. Aside from the modification of the osphradium, one must assume that the development of the long pleurembolic proboscis is the result of a transition to a predatory way of life and a better development of the salivary glands and the esophageal gland. The nervous systems of aporrhaids and doliaceans are zygoneurous, both parietal ganglia being removed from the pleural ganglia. Among the doliaceans, the genus *Oocorys* may as a whole be the most primitive; as noted by P. Fischer, the shell on the one hand bears similarity with *Liomesus* and *Buccinum*, and on the other hand with *Cassidaria*, *Dolium* and *Linatella*, and the operculum is spiral. Most closely related to it would be *Cassidaria*, to which the other cassidids and cymatiids connect, 1095 then the bursids, doliids and finally the pirulids, the nervous system of which is most concentrated and according to Bouvier is similar to that of vasids and volutids.

One can interpret the mentioned resemblance of the shell of *Oocorys* with buccinids and also with some other stenoglossans as a sign of relationship, for instance with *Lathyrus* (cf. Fig. 275) etc. because it cannot be doubted that stenoglossans have developed from taenioglossans and that among the latter and Doliacea are closest to them. They agree in the following characters: shell and mantle with siphonal process, osphradium bipectinate, proboscis retractile, buccal mass small, esophagus with gland (rarely reduced) the efferent ducts of the salivary glands do not traverse the ganglion ring, nervous system zygoneurous, statocysts with one statolith, a penis present.

The original form of the stenoglossan radula, which occurs in some families, consists of a central plate with 3 cusps at the posterior margin and on either side a simply pointed lateral plate (cf. Figs. 309, 381, 385, 393, 407, 409 and 411).

The concentration of the ganglion mass is somewhat varied, in *Lathyrus* it is similar to *Pirula*; the buccal ganglia have approached the cerebral ganglia.

The families belonging to the stenoglossans are more or less closely interrelated. The toxoglossans have a nervous system similar to certain muricids, also the shells may be rather similar and the radula of some Turrinae with simply pointed lateral plates is comparable with that of muricids; thus one can assume that the toxoglossans stand closely to the

muricids, and here first the Turrinae, and then the groups with arrow teeth without basal membrane, and the terebrids which have in most cases lost their radula. The magilids without radula have also originated from muricids. The radula of the buccinaceans as a rule has one inner or more cusps on the lateral plates and these plates may be sometimes greatly broadened (cf. Figs. 365, 376 and 377); there are occasionally small tubercles or folds on the columella. The foot is often strongly developed, as also in olivids, of which *Pseudoliva* has an anterior margin delimited by a groove, corresponding to the propodium of *Oliva*; the lateral parts of the foot may be greatly broadened and can be used for swimming, but in most cases the animals plough through sand similar to naticids. The shell form of the olivids is sometimes similar to that of certain buccinids, the radula of *Pseudoliva* also shows similar characters (cf. Figs. 343 and 383), but in most cases the lateral plates have only one cusp. The nervous system of *Oliva* is highly concentrated. On the whole the olivids may be most closely related to muricids because of the shape of the radular plates, the presence of an accessory pharyngeal gland and an anal gland.

The shells of the mitrids, vasids, volutids, cancellariids and marginellids in most cases shows distinct columellar folds. The radula in more primitive forms can be very similar to that in muricids; an accessory pharyngeal gland is present only in some groups, whereas it is lacking in others. Among the vasids, the genus *Metzgeria* may be the most primitive, but its relationship with *Vasum* seems uncertain. The lateral plates of the radula are reduced in *Cylindromitra*, *Harpa*, most of the volutids, the genus *Cancellaria* and marginellids; the entire radula is lacking in the genera *Scaphella* and *Admete*. The nervous system has undergone distinct modifications in some families: Bouvier thought that volutids and turbinellids (= fasciolariids) stand at the beginning of two developmental series, which connect to the taenioglossans, because their nervous system with the supraintestinal ganglion rather distantly removed from the pleural ganglia, is still less concentrated than in other stenoglossans; but this view seems too one-sided, because the modifications within the families have not been taken into consideration; thus the supraintestinal ganglion of *Murex trunculus* is considerably farther removed from the right pleural ganglion than in some other muricids; on the other hand in *Melo indicus* (Gmelin) = *Cymbium melo* (Solander) according to Fleure, it lies directly at the right pleural ganglion, whereas Bouvier found a long connective between the two in *Cymbium* (*Cymba*) *neptuni* (Gmelin). *Cancellaria* approaches volutids, the connective of the supraintestinal ganglion being long; a pair of accessory pharyngeal glands is present and the radula is very unique. The shell of marginellids, because of the low spire, the inflected apertural margin, and the mantle

1096

covering it, has attained some similarity with cypraeids, which however is not an indication of relationship.

Concerning the interrelations between prosobranchs and opisthobranchs, agreement has been recently reached to the extent that the actaeonids are on the whole closest to prosobranchs and are to be considered as transitional forms to the shell-bearing opisthobranchs from which then the shell-less forms have developed. However, at the same time the question as to which prosobranchs are closest to the actaeonids is still in dispute. Mörch and other malacologists have placed the pyramidellids with the tectibranchs, in contrast Pelseneer has claimed that these two groups are not related with one another. After an examination of *Odostomia* species he says that these are hermaphroditic, but that this is the only character in which they agree with actaeonids, for in contrast to the latter, the cerebral and pedal commissures are short, the esophageal ring does not lie anterior to the salivary glands, and the statocysts contain a statolith. Hence, according to him, the tectibranchs are closest to trochaceans. This argument is completely insufficient and untenable. The degree of relationship cannot be based on the length of the commissures alone (cf. the ptenoglossans). It can be stated with certainty that a relationship exists between pyramidellids and actaeonids. The shells are in part so similar that one could be in doubt as to which of the two groups they belong; thus certain *Leucotina* species are hardly separable from *Actaeon* by the shape and sculpture of the shell, and it seems possible that this group, the anatomy of which is still unknown, is intermediate between the two families (Fig. 897). The operculum is also very similar. In one *Pyramidella* species from Papeete, the ganglion ring embraces the anterior part of the invaginated proboscis, which widens considerably posteriorly and here instead of the radula contains numerous small thorns. In the mantle cavity are found 2 opposing folds each of which bearing a band of tall ciliated epithelium, quite like that in *Actaeon*; to the right of the dorsal fold lie few gill lamellae. The dorsum bears a median fold. The pedal ganglia have 2 commissures. The closed hermaphroditic duct opens on the right side of the head in a fold, which perhaps corresponds to the penis of *Actaeon*; opening nearby is a blind sack, which lies above the cerebral ganglia and may be a seminal vesicle. The ear-shaped cephalic appendages fo pyramidellids may have modified into the lobes on the head of *Actaeon*; the position of the eyes in the head and the histology of the nervous system also agree. Both families have assumed a different mode of life and undergone modifications as a result; so far as they have been examined more closely, one cannot consider one of them as precursor of the other, but derive both of them from common ancestors, which certainly had no closer relationship with trochaceans.

a   b
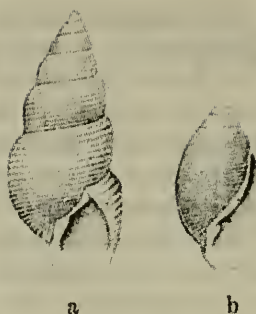
1096   Fig. 897. a, *Leucotina gigantea* (Dunker); b, *Actaeon tornatilis* (Linné). The species included in *Leucotina* are variably high-spired, the typical species *L. niphonensis* not much taller than *Actaeon*.

Whereas the shell of pyramidellids is in most cases more or less turreted, in cephalaspideans there is an increasing tendency toward shortening of the spire and elongation of the aperture, so that the opening of the mantle cavity widens and the gill shifts to the right and the posterior. It is followed by the supraintestinal ganglion and as a result the crossing of the visceral commissure, still clearly noticeable in some primitive groups, is annulled. This condition of the gill is made possible due to its extremely simple leaf-shape in contrast to cypraeids and marginellids, the shell of which has a similarly elongated aperture, whereas their mantle cavity is very deep and the gill correspondingly large. Only in more highly developed opisthobranchs can the gill become greatly enlarged and perfected, mainly in the notaspideans; on the other hand, in nudibranchs it is reduced and can be replaced by other structures. An anterior pedal gland, as in prosobranchs, is also present in cephalaspideans. The buccal mass of actaeonids is very different from the normal condition of the prosobranchs, it lacks the characteristic cartilages in the tongue.

Remarkably large are the differences between the radula of the actaeonids and that of families most closely related to it, in which a central plate is sometimes lacking, sometimes well developed; the lateral plates, which are only weakly developed and without cutting edge in *Toledonia*, are completely lacking in *Newnesia*, likewise in sacoglossans, on the other hand they occur in considerable number in atyids, anaspideans, notaspideans and some nudibranchs. In the series of doridaceans, the central plate often disappears, whereas in aeolidiaceans the lateral plates tend toward reduction.

Even if the actaeonids as a whole stand at the base of the phyletic development of the opisthobranchs, they differ from all of them by the non-retractile penis and from the most closely related families by the complete fusion of the pleural ganglia with the cerebral ganglia. The position of the ganglion ring anterior to the buccal mass is retained by most of the cephalaspideans, but in atyids and acerids it has shifted posterior to it, as in anaspideans. The ringiculids and the genus *Toledonia* still have a distinctly elevated spire and stand close to the actaeonids; their stomach contains no hard parts. The shell of the bullariids and atyids has a sunken spire and shows already in the latter family distinct reduction, the stomach is equipped with chewing plates; the scaphandrids are related to the philinids, of which *Philinoglossa* perhaps forms an off-shoot with completely reduced shell. The animal of *Paraplysia* is similar to that of *Haminea*, the small posterior tentacles correspond to lobes of the cephalic shield; certain affinities with the anaspideans are shown also by the acerids and according to Odhner also by diaphanids, the radula of which is however entirely different. It is to be assumed that the thecosomate pteropods have branched off from the cephalaspideans, their operculum indicating a relationship with actaeonids, but the latter have no parapodia and have a closed sperm duct; the radula of *Spiratella* is comparable to that of *Toledonia*. The Pterota are ranked with the anaspideans. They have variously differentiated in several developmental series. One of them begins with *Pneumodermopsis*, the hook sacks and gills of which are little developed and whose suckers lie directly on the pharyngeal wall, whereas the other genera of the family are more highly developed. *Cliopsis* may be close to pneumodermatids, but it has a long proboscis without suckers, with short hook sacks and a rudimentary median lobe of the foot. *Notobranchaea* has a weakly developed pharynx without special organs, very weak hook sacks and well-developed median and lateral lobes of the foot; coming close to them are the clionids and the more modified thliptodontids with a highly developed head which is not delimited from the rump, with hook sacks and pharyngeal vesicles and with epidermal pouches for the foot and the fins. *Anopsia* is greatly divergent because of the development of the anterior part of the rump, into which the head can be withdrawn, because of the lack of special pharyngeal organs and hook sacks and, besides certain anatomical differences, also by viviparity. *Laginiopsis* seems to be a very divergent form.

There is hardly any doubt that the shell-bearing sacoglossans are close to the cephalaspideans and possibly nearest to the Diaphanidae of which *Newnesia* is similar in the form of the shell and the radula; of course several organs have undergone considerable modifications, the

1098

ganglia have moved closely together and the buccal mass has attained a crop-like appendage. Opinions vary on the interrelationships of the naked sacoglossans; they are sometimes related with oxynoids, sometimes with aeolidiaceans, but the latter, in spite of their similarity with stiligerids, do not seem to be directly related with them; at all events the nervous system of the naked sacoglossans agrees with that of the shelled ones and the caliphyllids can be considered as transitional forms.

In the nervous system of the notaspideans a tendency is seen toward shortening of the cerebral commissure, whereas the pedal ganglia move apart, come close to the cerebral ganglia, and the parietal and visceral ganglia fuse with the pleural ganglia (notoneury); the same condition is shown by the shell-less Doridacea and Aeolidiacea, which accordingly are related to notaspideans. Because the main difference is the absence of the lateral gill, one can assume that the closest relations of pleurobranchids had a similar body form without a gill; this applies best of all to *Doridoxa*, a small Nordic form, which could perhaps dispense with the gill because of its small size. In this form, the anus still lies below the right margin of the notum, the buccal mass contains strong jaw plates and a radula with strong central plate and several simply pointed lateral plates. The Duvauceliidae are placed here because of the position of the anus on the right side and the condition of the jaw and the radula, and are considered as intermediate between Doridacea and Aeolidiacea. Their dorsal appendages are often similar to those in *Dendronotus*, whereas in most Doridacea they are arranged around the anus, which lies in the mid-dorsal line; among them *Bathydoris* is a related form. The radula of the others has no central plates, in *Dendrodoris* and phyllidiids it has disappeared. The latter family differs from all Doridacea by the development of gill lamellae below the notum. Odhner wants to group the families Heterodorididae, Doridoididae and Arminidae together as Arminacea and places Goniaeolididae, Charcotiidae and Heroidae close to them; on the other hand he places the genus *Notaeolidia* as the sole representative of Notaelidiidae in Eolidacea; among the latter he considers the Coryphellidae (= Flabellinidae) as the most primitive with the anus situated on the right, the Eubranchidae and Cuthonidae have an acleioproct anus, the rest of them have a acleioproct one. The Dendronotacea include the Dendronotidae, Duvauceliidae and Dotonidae.

Among the Aeolidiacea, which differ by having separate liver branches and in most cases cnidosacs, the Arminidae have a more or less broad notum, on the underside of which gill lamellae are developed in Armininae, whereas the Dermatobranchinae have no gills, likewise *Doridoides*, the Hedylidae, the Phyllirrhoidae, the Goniaeolididae; in addition the dorsal appendages which are developed in place of gills are

1099

at times hardly indicated. The form and arrangement of such appendages is varied, sometimes being combined in groups and born on smaller or larger stalks (cf. Figs. 544 and 552). The radula occasionally still has several lateral plates, in others only one on either side and in the families Tergipedidae, Fionidae, Aeolidiidae and Myrrhinidae, they are completely absent. In *Calma* the radula forms a continuous series of denticles resembling a bandsaw. The tethyids lack a radula.

The naked opisthobranchs as a whole more or less widely diverge from the normal condition of snails, but are related with them through phyletic series, so that there is no doubt about their belonging to this class. A closer relationship of a few of them is uncertain, as for instance *Vayssierea* and especially *Rhodope*, which at any rate has to be considered as a highly simplified nudibranch without shell, foot, radula, liver and heart; the position of the genital opening and anus on the right side is similar to the condition in nudibranchs and prohibits affinity with turbellarians with which a close relationship, as assumed by Jhering, is completely out of the question.

The most primitive pulmonates are closest to the cephalaspideans. As in the latter, the crossing of the visceral commissure has been annulled, the eyes lie in the head, a small osphradium lies in the mantle cavity, the mantle at the aperture has a lower lobe and contains a gland on the left side, the radula bears numerous small plates, the jaw consists of thin rodlets, the ventricle lies posterior to the auricle, the kidney has no ureter, the gonad is hermaphroditic, its efferent ducts are more or less widely united with one another, the ♀ duct stands in connection with glands and a bursa copulatrix, the invaginable penis is connected with the genital opening by a ciliated groove.

It seems appropriate to look for the most primitive pulmonates among those which still show connections to the sea, such as the Actophila and Amphibolacea. Some ellobiids, such as the Carychiinae, have become entirely land-dwelling, but most live on the sea shore; their shell with the columellar folds is similar to that in some cephalaspideans. An operculum, which is absent in ellobiids and in all other pulmonates, is still retained only in the brackish-water amphibolids. A transition from brackish water into the rivers has happened easily and hence among the inhabitants of fresh water there are very primitive pulmonates, such as the chilinids.

The amphibolids differ from ellobiids by the common genital openings with closed sperm duct and the long glandular tube on the penis, and by the absence of a bursa copulatrix; their mantle cavity contains no gill but is filled with water, a small osphradium lies close to the rather far forwardly situated aperture. They represent a small

offshoot from the pulmonate stem. Even more distantly removed from this stem are the gadiniids and siphonariids with cup-shaped shell, which also live on the seashore. They were placed in the opisthobranchs by some zoologists, but Pelseneer considered them as pulmonates. The mantle cavity of *Gadinia* is without a gill, on the other hand in *Siphonaria* several gill lamellae are developed; in the latter the two genital openings are united. Distinctly developed cephalic tentacles are absent in these groups, as in many cephalaspideans.

As in ellobiids, the shell of *Chilina* as a rule has 1 or 2 distinct columellar folds, the opening of the mantle cavity is rather wide, the nervous system is characterized by the length of the visceral commissure, which occasionally still shows an indication of the crossing. This South American group is on the whole the most primitive among pulmonates living in freshwater, the form of the radular plates evidently appears to be less primitive than in lymnaeids, which stand close to them. Both of them have still not acquired a gill formed by expansion of the lower mantle lobe, as in planorbids and ancylids, and the physids approach them in this respect. The New Zealand Genus *Latia*, the shell of which is similar to that of *Septaria*, has a radula similar to that in *Chilina*, a rather long visceral commissure, widely separated genital openings, a short oviduct with a large bursa copulatrix and a long closed sperm duct with a prostate at its initial position. The physids agree with the planorbids in the sinistral shell and the awl-shaped tentacles, whereas the form of the radular plates is more similar to those of *Chilina*; the reproductive and digestive organs also betray affinities with planorbids. *Aplexa* does not have such mantle lobes as *Physa*; its bursa copulatrix arises close to the opening of the oviduct, and the prostate lobules are also closer to the opening, hence *Physa* is somewhat more modified than *Aplexa*. The lymnaeids are also closely related to chilinids, their radular plates have a more primitive form, their oviduct has a shell gland between the albumen gland and uterus, the prostate is massive; in *Myxas* and *Erinna* the spire is very small. The North American genus *Lanx* represents a very unique offshoot with cup-shaped shell similar to the ancylids. The openings of the mantle cavity and the genital openings in planorbids always lie on the left side, even when the shell is apparently dextral; among them the genus *Isidora* has the most primitive shell form with more or less high spire and left aperture, *Miratesta* stands here, then follow the disk-shaped forms, and finally the forms with the aperture on the right side, the spire of which is to be visualized as so deeply sunken that it projects on the original underside. *Segmentina* is characterized by ridges in the interior of the shell and the appendages on the penis: Among the ancylids, the Ancylinae are to be derived from *Isidora*, with

the whorls of the shell becoming reduced and the aperture widened. Correlated with this is the reduction of the mantle cavity and the approach of the heart to the gill and the tube-shaped multilobed kidney; in *Ancylus fluviatilis* the long sperm duct at its beginning has a prostate with few lobes and the penis has a long and thin process. It seems uncertain as to how the Acroloxinae are related to the Ancylinae.

The ellobiids are placed, mainly by Pelseneer, at the beginning of the phyletic development of the pulmonates, and not only of basommatophorans but also of stylommatophorans. The genera differ considerably from one another not only in the form and size of the shell, but also in the radula and the genitalia. The radula of *Carychium*, the lateral plates of which have small inner and outer accessory cusps and the marginal plates have broader finely denticulated cutting edges, corresponds most with the form occurring in several other groups of pulmonates. *Marinula* and *Pedipes* have similar dentition with numerous narrow plates, the lateral plates in most cases with 2 cusps. The radular plates of Ellobiinae become stronger with increasing body size, their cutting edges become large and simple, but that of the central plate often remains small, and accessory cusps can be retained on the marginal plates. The jaw, still weak in *Carychium*, also becomes gradually stronger, in *Ellobium* it becomes a thick, smooth body similar to stylommatophorans. The genital tracts are also different, but in Pedipedinae they show a less primitive condition than in *Alexia*, with the glandular hermaphroditic duct terminally dividing into an oviduct with a long-stalked bursa copulatrix and a sperm duct, which opens in a ciliated groove anterior to the opening; posterior to the end of the penis begins the terminal part of the sperm duct which leads into the inner end of the penis. *Carychium* has a completely closed sperm duct. On the other hand, in *Alexia*, the genital duct is hermaphroditic up to the end, where the bursa copulatrix is attached, and is connected with the penis through a largely closed sperm duct. In *Tralia* and *Melampus* the glandular hermaphroditic duct is short and divides into 2 ducts, which however combine at the end; the bursa copulatrix is attached to the hermaphroditic duct or at the beginning of the oviduct. In *Ellobium*, below the albumen gland, a glandular duct separates from the hermaphroditic duct, although the two then combine again and near the opening have a very long-stalked bursa copulatrix. Whereas vagina as in actaeonids is in most cases lacking, it is developed in *Marinula* and *Carychium*, a fact which brings them closer to the stylommatophorans.

After an examination of *Alexia*, Pelseneer emphasizes the following characters by which it approaches the stylommatophorans; an indication of anterior tentacles, absence of a "Pavillon respiratoire" (lower mantle

lobe), missing osphradium, single dorsal jaw, long esophagus into the posterior end of which opens the anterior liver lobe, and an anterior pedal gland. On the whole, however, *Carychium* probably stands closest to the most primitive stylommatophorans.

Whereas in Ellobiinae the eyes are situated in the head posterior to the base of the tentacles, *Otina* has only hemispherical processes in which the eyes are contained. The shell is relatively small with rapidly increasing whorls and a wide aperture without columellar folds; the foot, divided by a transverse furrow, is similar to that of Pedipedinae to which *Otina* perhaps stands closest; the sperm duct is completely closed.

The main difference between the stylommatophorans and the basommatophorans is usually considered to be, aside from the mode of life and the position of the eyes, the union of the two genital openings, which are more or less distantly removed from one another in basommatophorans, with the exception of amphibolids and siphonariids. In this respect, standing close to the latter are the "Ditremata," as the group of completely shell-less snails comprising the oncidiaceans and soleoliferans has been called. Their phyletic affinities are uncertain. At any rate they have separated very early from the other pulmonates. Because the oncidiaceans are shore dwellers, they may have developed from shelled littoral forms, somewhat similar to *Otina*, by reduction of the shell, elongation of the eye-bearing tentacles, and the lung opening shifting posteriorly along with the anus, the kidney and the ♀ genital opening. On the other hand, the soleoliferans have completely moved to land; they have become greatly elongated and their very narrow foot has acquired numerous transverse ridges; their mantle cavity is reduced and the openings of the intestine, the kidney and the oviduct originally still lie on the right side (Rathouisiidae); but, in vaginulids the intestine and the ureter have lengthened posteriorly within the notum. In spite of considerable differences, these two groups still permit a certain relationship to be recognized, so that they can be derived from common ancestors, the body of which was still not so elongated as in soleoliferans and the lung, kidney and ♀ opening lay on the right side. The reproductive organs of oncidiids and rathouisiids are essentially similar; noticeable is the presence in both families of unique penis glands, which however are apparently independently acquired in each, although an indication of this may already have existed in the common stem form, just as the glands of vaginulids are already indicated in *Vaginina*. Among rathoudiids, the genus *Rathouisia*, the form of which resembles that of most vaginulids, is probably more primitive than *Atopos*, which has lost the lateral edges. Because this family probably has a predatory mode of life, its buccal mass resembles that of some other predatory snails without a relationship

existing between them. The rathouisiids and vaginulids have at all events evolved from the same stem forms, which already possessed the peculiar notum and a highly concentrated nervous system closely embracing the esophagus; the lung cavity was reduced, it lay on the right side, where the kidney of rathouisiids opens; the tentacles could not be retracted.

Succinea has been in most cases considered a primitive stylommatophoran, mainly because of its amphibious mode of life, very wide distribution, and incomplete separation of the genital openings; although it should not be brought into genetic connection to *Lymnaea*; Pilsbry considered it an independent branch of the pulmonates. The weak shell can be considered an indication of degeneration in contrast to the forms with stronger shells, and so one could reach the conclusion that the succineids are close to a higher group. Such an opinion has been expressed by Odhner who assumes a relationship between succineids and 1103 the Amphibuliminae, to which he allocates the West African genus *Aillya*. The resemblance of the kidney of the latter to that of *Succinea* is noticeable; furthermore the shell, the intestine, the musculature, and probably also the nervous system, are similar in the genitalia, *Succinea* has retained a prostate, which is lacking in bulimulids, as also an "elasmognath" jaw. Moreso than in *Succinea*, the shell of *Homalonyx* has become smaller and flattened, so that it covers only the viscera, in *Neohyalimax* it is completely enclosed by the mantle, similarly in *Hyalimax*. The shell of athoracophorids is completely rudimentary, and because the mantle cavity also has become greatly reduced, it has developed its unique processes. The kidney, as in *Ancylus*, has developed a long many-shanked ureter. The jaw indicates a relationship with succineids and the radula has some similarity with *Hyalimax*; the genitalia are distinguishable from those of succineids by the shortly stalked bursa copulatrix; the penis and vagina open into a more or less long vestibulum genitale.

Even if the succineids are not regarded as primitive stylommatophorans by Odhner, this could perhaps be true of the Achatinellacea, which show strong similarity with ellobiids because of the columellar folds of the shell (cf. Fig. 590); they also have a rudimentary jaw and a straight kidney without ureter. Among them most of the tornatellinids like many vertiginids and some subulinids have a lamella on the penultimate whorl (parietal lamella), it is lacking in the achatinellids. The radular plates do have some similarity with those of *Actaeon*, but this cannot be considered as an indication of relationship— nor is there any with the athoracophorids—but as an analogous development and, compared with the vertiginaceans, etc., as deviating from the normal form. The genitalia show some differences; the sperm duct soon separates from the oviduct, the bursa copulatrix is long stalked;

the often very small development of the albumen gland and the strong development of the prostate and striking; the appendage of the penis is often of considerable size. Pilsbry considered the tornatellinids, achatinellids and amastrids to be very old and assumed their common origin from an extinct group, which is also related with the Vertiginacea and Achatinacea (Ferussaciidae); it may well have been the ancestral form of the stylommatophorans.

The shell form in the family of the amastrids is highly varied; *Leptachatina* approaches *Cochlicopa*, *Carelia* is high-spired like achatinids, whereas *Pterodiscus* and *Planamastra* approach disk-shape; hence from the shell form alone no conclusions regarding relationships can be drawn. In general the following may be considered characters of primitive organization: a kidney without "secondary" ureter and simple genitalia which however, as the result of varied development of different parts can show some differences; and a normal radula, the plates of which nevertheless at times can undergo small changes through the loss of accessory cusps or through secondary cusps of the marginal plates.

The modifications occurring in different families are sometimes so similar that one can be in doubt whether these are to be considered as signs of relationship; this is true of the shape of the shell, the nature of the radula, the presence of a "secondary" ureter and of certain accessory glands or appendages of the genitalia.

1104 The small genus *Pyramidula*, with broad cone-shaped, umbilicated shell, differs from *Vallonia* by the absence of an appendage on the penis and from endodontids by the absence of a ureter; on the other hand the genitalia are so similar to those of *Columella* that it seems to be related with the latter and may represent the most primitive form of Vertigininae. The genitalia of other subfamilies present considerable differences; the Pupillinae like the valloniids, the achatinellids and amastrids, as well as the Eninae and Napaeinae, often have a very long appendix on the penis, the retractor of which is in most cases bifurcated; the bursa copulatrix in most cases has a long simple stalk, in pupillines and enines with a spermatophore sack. Can the strongly developed appendix in these groups be considered homologous and hence can they be considered as directly related to one another? More recent investigators, such as H. Watson and Steenberg, seem to assume this; in that case the Pupillinae would have to be separated from the vertiginids as a special family and would perhaps have to be derived from valloniids, to which the other families with appendix may be joined. On the other hand, the Chondrininae and Orculinae may have developed from Vertigininae through the stronger development of the epiphallus which sometimes has an appendage, whereas other parts, such as the prostate, the radula and the shell, have

also undergone certain modifications. In the family Enidae, which perhaps are most closely related to the Cochlicopidae, a separation of the forms having a spermatophore sack on the stalk of the bursa copulatrix from those without such a structure would perhaps be without significance, but all of the mainly African genera seem to lack this appendage. Their affinities with *Napaeus, Napaeopsis* and *Spelaeoconcha* seem uncertain, but they are not closely related to the North African groups *Maurona-paeus* etc. The absence of an appendage on the penis in Chondrulinae is now to be considered as a secondary phenomenon. It is remarkable that the genitalia sometimes show distinct differences while the shells are very similar, as in *Zebrina, Zebrinops* and *Adzharia*, and also in *Napaeus* and *Napaeinus.*

Whereas the oviduct in valloniids is simple, in Chondrininae and Orculinae it is divided and one part, which contains another type of gland, forms a blind sack. A similar division by means of a fold, in and free margin of which the sperm duct runs, is also found in enids and clausiliids. On the other hand, Steenberg believes that he finds so much overlap in the structure of the gonoducts of *Lauria* and *Balea* that he would like to regard it as an intermediate form between "Orthurethra" and the clausiliids (Sigmurethra). Whether or not this view is accepted, this much seems correct that the clausiliids, in spite of their "secondary" ureter, have developed from enids or vertiginids. Judging by the nature of the penis, with an epiphallus which often has a small process, but without long appendix, and by the presence a spermatophore sack on the stalk of the bursa copulatrix, the clausiliids would stand close to the Chondrulinae. The normal radula agrees in the two groups, only the genus *Peruinia* having acquired a strikingly different dentition. The interrelationships of the subfamilies and genera are still poorly clarified; it appears uncertain whether the presence or the absence of a spermatophore sack is primary; but the Neniinae may be less primitive than the Phaedusinae, and also the purely glandular nature of the process on the stalk of bursa copulatrix in Clausiliinae may be a secondary condition in comparison with the Cochlodininae; a similar condition exists in the case of the apertural folds of the shell, which occasionally become rudimentary.

1105 The phyletic origin of the Achatinacea seems to be highly enigmatic. Pilsbry thought that they have developed in Africa and that they are related to clausiliids, but the latter have few connections to Africa and also in other respects such a relationship appears uncertain. The Achatinacea differ from most of the Orthurethra by the lack of an appendix on the penis, agreeing in this respect with the Vertigininae. The similarity of the shell with tornatellinids and *Carelia* cannot be interpreted

as a sign of relationship. The radular plates of the primitive achatinaceans have outer and inner accessory cusps like the endodontids, and also the kidneys of ferussaciids and the lower endodontids show a certain resemblance; moreover one can point to the lateral furrows on the foot of *Ferussacia*, and because the genitalia are also similar, the stirps of the Achatinacea seems to stand closest to the endodontids, although these in most cases have low-spired shells, but great significance need not be attached to this circumstance. It should be mentioned here that Semper too was struck by the similarity of the dentition, of which he says: "the form of the radula places especially the Philippine species (*End. philippinensis*) in the closest vicinity of the subulines, tornatellines, etc.; on account of the inner apertural teeth, these endodonts could be designated as a flattened tornatellines"; at this point however it should be remarked that Semper, because of insufficient knowledge placed the tornatellines near the subulines.

Among the achatinaceans, the small ferussaciids and subulinids are the most primitive, only few of them attain considerable size, many of them are very highly turreted. Near them are the megaspirids, which in most cases have internal lamellae in the shell, in addition the achatinids, of which some species attain very considerable size, and also the oleacinids, which have shifted to a predatory mode of life. There are *Pseudosubulina* species in which the shell is hardly different from *Subulina*; a jaw is still indicated and the radula bars small plates with 2 cusps; the genitalia show a long and rather thick vagina, long-stalked bursa copulatrix and a very short penis. In this family the animals in most cases become larger, with low-spired shell, which in *Strebelia* has become much smaller than the animal; the foot enlarges, the jaw becomes rudimentary, while the simply pointed radular plates become stronger; the genitalia show some variations, an epiphallus may be absent or present, as also an appendix on it or on the penis. It appears uncertain whether the testacellids stand close to the oleacinids; the small shell situated on the posterior end and the arrow-shaped radular teeth remind especially of *Strebelia*, but no direct relationship exists with the latter.

The group of the endodontids plays a very important role in the phylogeny of the pulmonates. The kidney does not have the straight form as in the "Orthurethra", however some primitive genera do not show the S-shape of the "Sigmurethra", and the kidney and ureter are strikingly variable, so that one can assume that here a development has just begun, which gradually lead to the formation of a "secondary" ureter. In most cases the kidney is distinctly shorter than in "Orthurethra", and the ureter does not reach to the mantle margin, sometimes opening into the posteriormost part of the lung chamber; as a rule however its terminal part

has approached the intestine, a condition which in "Orthurethra" is introduced by reflection of the terminal position but because of the length of the kidney it has not reached the base of the lung chamber and 1106 the intestine. The common ancestors of the endodontids and the Orthurethra (cf. *Pyramidula* and *Vallonia*) probably had only a moderately elongate kidney (cf. ellobiids) which has further developed differently in each of these groups.

The radular plates of the oldest endodontids had the primitive form with an inner and outer accessory cusp, and the weak jaw consisted of a few separated platelets, but the radula and the jaw have already undergone further modifications within the family. The modifications of the shell relate to its height, which is unusual only in *Phenacharopa* (cf. Fig. 657), the provision of the aperture with teeth (cf. Fig. 658), which appeared in a few genera, and the reduction known only in *Ranfurlya*. The foot has a lateral furrow on either side. Appendages on the genitalia are seldom developed.

One can assume that from this widely distributed group in different ways most or all pulmonates that are not "Orthurethra" have developed. The lateral furrows of the foot can be retained or become indistinct, the shell assumes various forms, as also the radular plates; the ureter in most cases reaches the mantle margin, and the genitalia also may undergo more or less striking modifications. Some more or less richly developed series have thus arisen, the origins of which stand close to the endodontids, whereas their terminal forms may present considerable differences.

Like some endodontids (cf. Fig. 662), the polygyrids and sagdids show so much similarity with helicids, that they have been in most cases considered close to the latter, especially because they lack lateral furrows on the foot. Of the corillids, the South African *Sculptaria* species have such lateral furrows, whereas they are lacking in the Asian genera *Plectopylis* and *Corilla*; the latter are distinguished by lamellae in the interior of the shell. The zonitids are closely related to certain endodontids and distinguished from them mainly by the long, as a rule simply pointed marginal plates of the radula, such as those exceptionally occurring also in some endodontids; in the Gastrodontinae a calcareous spine has developed on the ♂ copulatory organ. *Daudebardia* is characterized by the small shell borne only on the posterior end of the animal, and also by the large radula with claw-shaped teeth; its relationship with the zonitids is hardly to be doubted. The same is to be assumed of the American systrophiids. In a different direction, the vitrinids have developed from zonitids by a reduction in the size of the shell, having more or less large mantle lobes over the shell; in the genus *Vitrina*, a variously strong glandula amatoria appears in or on the vagina.

Even more advanced is the reduction of the shell in *Plutonia* and the arionids, among which only *Binneya* still retains a *Vitrina*-like shell; in Ariolimacinae and Arioninae it is completely enclosed by the mantle and in *Oopelta* it has completely disappeared. The philomycids have developed differently; they do not have such a mantle field as arionids, so that their body form attains some resemblance with vaginulids; they have a wide, empty shell pouch; their genitalia have acquired a different structure. Next to vitrinids may be placed also the limacids, of which *Parmacella* still has a shell with a spiral initial part, which in young animals is not yet enclosed by the mantle. More doubtful are the affinities of the predatory trigonochlamydids, the mantle of which at times is placed near the center of the dorsum and at times at the end.

1107

The Ariophantacea represent a similar developmental series, in which the marginal plates of the radula as a rule bear dicuspid cutting edges (cf. Fig. 694), their initial forms have shells similar to zonitids and simple gonoducts without special appendages; they still stand close to the endodontids, and like these are small. Near them stand numerous genera, some of which attain more or less considerable size (cf. Figs. 685 and 688), the shell being well developed and able to harbor the entire animal. In contrast, the shell in other series becomes weak and small as in *Vitrina* and is finally enclosed by the mantle and becomes rudimentary as in limacids. On the other hand, in some groups an accessory gland, provided in most cases with a stylet, has developed; among the Helicarioninae and the closely related Urocyclinae this gland occurs only in a part of the genera, in variable development, hence it is to be assumed that in these cases it has not been inherited from common ancestors; but it may be homologous in Macrochlamydinae, Ariophantinae, Xestinae, Sophininae and probably also in Girasiinae and Parmarioninae; it is uncertain in the case of Durgellinae and similarly in *Staffordia*, the gland of which is very peculiar.

The phyletic origin of Acavacea is still quite uncertain; Pilsbry's view that they derive from Polygyrids has little substantiation, because the latter live in America. One may perhaps assume that in "Gondwana-land" under the especially favorable living conditions the endodontids attained a considerable size increase without showing great modifications in their organization; that along with the shell the embryos also became larger, that the lung chamber had little depth and hence there was increased branching of blood vessels and the kidney became shortened without first acquiring a ureter; and that the radular plates still retained inner and outer accessory cusps, and the gonoducts remained simple. While then these animals spread over the lands of the southern hemisphere, · they partly changed considerably under other conditions, which is

already evident in the form of the shell, which became turreted on the one side (*Clavator*, Fig. 702) or very low on the other. The radular plates in most cases lost their accessory cusps and sometimes acquired long, pointed cutting edges. Occasionally a ureter has developed, which reaches the intestine. The genitalia have also become modified, especially in Caryodidae; this Australian group is the most divergent, on the other hand the South African genus *Trigonephrus* seems to be the least modified, with roundish shell, radular plates with accessory cusps, a kidney the anterior end of which is curved toward the intestine—similar to Orthurethra—but without a ureter, and without special appendages on the gonoducts. *Dorcasia*, with a low shell and unicuspid central and lateral radular plates of the radula, stands near *Trigonephrus*. The South American strophochilids are also little different from this, the shell of *Microborus* being only somewhat higher; some species attain considerable size (cf. Fig. 704). The Chilean *Macrocyclis* has a shell form similar to *Dorcasia*, but a direct relationship with it seems doubtful. Very different has been the development of the Acavacea living in Madagascar, which also include the turreted genus *Clavator*.

1108   It will hardly be doubted that closely related to the strophochilids are the Bulimulinae, among which some genera have similar shells, whereas others (cf. Figs. 707–709) have become highly modified. The dentitions also undergo modifications, of which the considerable broadening of the cutting edges (cf. Fig. 710) needs to be highlighted; the condition of the kidney is also different. Because *Partula* has a straight ureter, it has been placed near the achatinellids, however, the genitalia—penis without appendix, short-stalked bursa copulatrix—have little similarity with that family, but much more so with *Placostylus* (cf. Figs. 713 and 715), and the latter subgenus *Diplomorpha* has a shell very similar to that of *Partula*—the anatomy of which is unfortunately still unknown. However Pilsbry also recently declared the similarities of *Partula* with bulimulids to be a mere analogy and not a sign of relationship, which is contradicted by the kidney form and the lung without distinct blood vessels. How these Melanesian genera and the Australian genus *Bothriembryon* are connected with the American ones can hardly be explained otherwise except by migration from South America toward the west across the then-existing land bridges. It is also to be assumed that the Odontostominae and Orthalicinae are closely related with Bulimulinae. Less certain is the relationship of the latter with the Amphibuliminae, because their anatomy is still little known. Pilsbry took them for bulimulids with a more or less reduced shell and supposed that they have developed in 2 lines, in which *Simpulopsis* and *Peltella* are being closer to *Drymaeus*, whereas *Amphibulima* and *Gaeotis* being closer to *Bulimulus*; Odhner, on the

other hand, believed that *Simpulopsis* stands closest to the root of the bulimulids as well as that of the succineids. This view would hardly permit the strophochilids and bulimulids to be designated as related and, contrary to current opinion, would consider the thin and only slightly coiled shell as more primitive than the normally developed one. At all events, *Peltella* and *Gaeotis* are extremely developed forms with a small shell more or less covered by the mantle; the latter genus also with greatly broadened cutting edges of the radular plates.

Also to be derived from bulimulids are the cerionids, with a normal radula and a long blind tube on the stalk of the bursa copulatrix, and the urocoptids, of which the Eucalodiinae have a very high-turreted shell, but originally a similar radula and—except for the missing blind tube of the bursa—have genitalia similar to those of cerionids; in the shell form the nearly disk-shaped *Hendersoniella* differs strikingly from the other Eucalodiinae. The Microceraminae and Urocoptinae have undergone modifications of the dentitions (cf. Figs. 727, 728), in the latter the cutting edges of the more or less numerous lateral plates have become much enlarged and the outer cusps are displaced forward.

If the original home of the Acavacea lay in the Indian region, one can assume that the helicaceans which stand in close relationship to the former, also originated there; this applies mainly to the pleurodontids, which have spread not only across southern and eastern Asia and Australia, but also to northern South America and Central America, becoming more or less modified in their external appearance as well as in their organization; forms such as *Camaena* (cf. Fig. 735) and *Eurycratera* (cf. Fig. 732) may be the most primitive; on the other hand the highly variable *Papuina*, near which stands *Cryptaegis* with a thin shell completely enclosed by mantle, as well as *Amphidromus* and *Calycia*, the radular plates of which have broadened bi- or tri-lobed

1109 cutting edges, seem to be most highly modified. Near the pleurodontids stand the fruticicolids in which a "love dart" has developed in a sack-shaped process of the vagina in association with a gland. Among them, *Helicostyla*, native mainly in the Philippines, with small dart sack and simple gland, branched off early. The others became widely distributed, undergoing various modifications; the Fruticicolinae mainly across Asia, close to which may stand the few East African helicaceans; the Epiphragmophorinae have migrated eastward to America, and the helicids westward, where they have spread across Europe, North Africa, and the Atlantic islands. The some helicaceans the "secondary" ureter is more or less incomplete.

It is also very probable of the Streptaxacea that they originated from endodontids. In the family Haplotrematidae, which according to Baker

belongs to this stirps, the ureter is short and opens at the base of the mantle cavity, the genitalia have no special appendages, the radular plates are strong, claw-shaped, a weak jaw is still present. In what manner this American family is related with paryphantids and streptaxids appears uncertain; Baker also states that they are perhaps polyphyletic, but emphasizes the similarity of the shells of South American *Austroselinites* species, which however have not been studied anatomically, with New Zealand paraphantids. In the last-named family, the anatomically still little-known genus *Priodiscus* stands isolated and its affinities are uncertain. Some of the species placed by Kobelt in *Ouagapia* are rather endodontids, and the similarity of the shells may point to a relationship. The dentitions show differences, which permit one to conclude closer relationships between certain genera; thus the plates of *Delos*, *Ouagapia* and *Diplomphalus* resemble each other (cf. Fig. 766), and a central plate is lacking; of these, the last-mentioned may be the most extreme form. The closer relationship of *Schizoglossa*, which also has no central plate, seems uncertain; on the other hand, *Paryphanta*, *Wainuia* and *Rhytida* have more claw-shaped plates and a central plate (cf. Fig. 768). Highly doubtful is the group *Macrocycloides*, the typical species of which from Borneo has not been anatomically investigated; Kobelt wanted to "insert a series of *Rhytida* species from Melanesia, New Zealand and Australia here," but he also included South African species. One of these (*tarachodes* Conolly) is noticeably distinguished from *Rhytida* by the shape of the radular plates (cf. Fig. 765) and perhaps stands closer to *Delos*; recently H. Watson has erected the genus *Nata* for it.

Among the Streptaxacea, the small, low-spired forms currently living in the Seychelles, may be considered the most primitive. Of the anatomy of *Augustula*, for the unfortunately imperfect anatomical knowledge of which we are obliged to Wiegmann, the following are to be emphasized: the "foot with double broader," a relatively large right "neck lobe" on the mantle margin, the large median radular plates, the arming of the penis, the neck of the uterus, and the short bursa copulatrix with "thorn-shaped stimulatory papillae." Wiegmann regarded this snail as a "transitional form from the hyalinias to the agnathans," however the zonitids probably cannot come into consideration, but rather the endodontids.

The genus *Imperturbatia* has a dentition similar to some streptaxids its embryonic shell is smooth, the other whorls strongly ribbed, the apertural margin reflected, in the interior with 1 or 2 small warts behind the repeatedly invested apertural margin. Because the South American *Martinella* is strikingly similar, one may assume that these two genera in earlier times were connected and then went extinct in the intermediate

1110

lands. *Acanthennea*, living in the Seychelles, agrees with *Imperturbatia* in the strong ribs and the small interior warts and may have arisen from the latter by elevating the shell. There is no doubt that other streptaxids have developed from low-spired forms, because they in part have such shells permanently and in part only in the young stage. At the same time there is also a tendency toward the development of turreted or cylindrical shells, often also a more or less strong development of apertural teeth, especially in Africa.

Looking back, one may assume that the ancestral form of the stylommatophorans had a small, moderately high-spired shell and an organization which was transitional between *Pyramidula*, valloniids and the most primitive endodontids, and that from this, by differentiation of the radula, the kidney and the genitalia, these 3 groups and then the various branches of the stem developed. The lateral furrows of the foot, characteristic of some groups, may at times have become reduced in the course of the phyletic development, as such are developed in the ferussaciids, but are not recognizable in subulinids.

The scaphopods have at times been placed closer to the gastropods, sometimes closer to the bivalves; it is fruitless to quarrel about it. Without doubt they represent a separate class, which is transitional between gastropods and bivalves. From the common stem forms, they have still inherited a snout-like head, which contains a buccal cavity with subradular sense organ, jaw and radula, whereas such has been lost in the bivalves. But like bivalves, they have retained the original symmetry; their nervous system—aside from the buccal ganglia—is very similar to that of bivalves and is very different from that of zeugobranch gastropods. Their foot has no sole, but rather serves for burrowing into the substratum, like in nuculids; it is however to be assumed that this form of the foot has been independently acquired by the scaphopods. Both ctenidia of the stem forms have disappeared and in connection with this, the heart and blood vessels are imperfectly developed. The initially saddle-shaped shell becomes ring-like by fusion of the ventral margins, whereby an anterior opening is separated from the posterior one; the mantle cavity is very different from that of zeugobranchs. As a result of the more or less strong elongation of the animals, certain organs, mainly the gonad, have moved to the back, and the pericardium also lies posterior to the rectum. As in bivalves, no trace of an epipodium is left, but the cirri serving to obtain food, and the shield-shaped folds bearing them, may correspond to the head fold and the cephalic tentacles beset with cirri of zeugobranchs.

Because to date only a few species have been anatomically studied, nothing can be said about interrelationships of the groups that have been

based on external features. However, one may assume that the short forms (*Cadulus*) are more primitive than the very much elongated ones.

Among the bivalves, the nuculaceans are in most cases regarded as the most primitive, mainly because of the form of the gills, which is similar to that of zeugobranch snails, as well as because of the separation of the pleural ganglia; at the same time it must not be overlooked that certain characters of their organization make it impossible to derive other bivalves from them, especially the arcaceans, which are more primitive in some respects. Both stirps have taxodont hinge margin, and hence one can designate that taxodonts as the most primitive bivalves. It is, however, noteworthy that the embryonic shell (prodissoconch) of the taxodonts does not yet show the anlage of the hinge teeth, but that the hinge margin is provided, anteriorly and posteriorly of the small ligament only with transverse grooves, whereas the teeth appear only later below this grooved margin. The question now arises as to the significance of these prodissoconchs for the phyletic development of the bivalves and whether there are mature species which correspond with this ontogenetic stage. The latter question has to be answered affirmatively. The genera *Hockstetterina* and *Adacnarca*, and also the mytilid genera *Idasola* and *Dacrydium*, have such grooved hinge margins without teeth. Can these forms then be considered as the initial forms for the taxodonts? According to Pelseneer, the animal of *Adacnarca* has a completely open mantle, a small anterior and a larger posterior adductor muscle, the foot is posteriorly prolonged lobe-like and contains a byssus, the visceral mass is very small, only the posterior pair of the labial palps is developed, the intestine is short and straight, the gills are broad, composed of filaments, only the outer gill laminae with ascending limbs, they do not reach to the labial palps, the kidneys are simple sacks separated from one another, the gonads are ventrally united with one another, their efferent ducts opening separately from those of the kidneys. Although such an organism shows many primitive characters, there is no mistaking that it is closely related with *Limopsis*, and that the absence of hinge teeth is probably only a consequence of the small size under the severe living conditions in the Antarctic; hence *Adacnarca* can hardly be considered a preserved ancestral form, but as a sexually mature larval form (neoteny). In comparison with the ancestral conchiferans, the mantle margins have become greatly expanded in conjunction with the shell, so that they cover the gills, and, after the shell had divided along the median line, could enclose the entire animal. Consequently, the head along with the pharynx became reduced and ingestion of food had to take place in a different way. In nuculaceans the labial palp appendages were used for this purpose, which may correspond to the cephalic tentacles of snails,

but in most other bivalves food particles were led to the mouth opening by ciliation of the broadened gills and of the labial palps. It cannot be doubted that the hinge margin was originally stretched straight; probably as in gastropods, the body had a considerable width and a moderate height, which would lead one to decide on such a form as *Arca*. The foot had a sole, which could be used for creeping, but in a fashion similar to janthinids produced a glandular secretion (byssus), with which the animals attached themselves to stones, etc.; on the other hand, in nuculaceans the foot was used for burrowing in soft substratum and the byssal gland became reduced. This form of the foot is certainly less primitive than that of arcids. Also apparently correlated with the production of the byssus are the strong muscles, extending from the byssus groove to the shell, and these may be the reason for the urogenital organs remaining widely separated from one another; hence not only the gonads and kidneys were paired, but also the pericardia which originally connected the gonads and kidneys with one another and were parts of the same anlagen. In this respect also the nuculaceans are less primitive. If one assumes that the ancestral forms possessed not only paired auricles of the heart, corresponding to the two ctenidia, but also paired ventricles and aortae, one can easily visualize the posterior aortae which unite below the rectum as branches of the anterior aortae, and because the anterior and posterior aortae enclose the intestinal tract, it is understandable that with approximation and fusion of the two ventricles, as has taken place in most bivalves as well as in zeugobranch snails, the now single ventricle is transversed by the intestine; but at times it may shift above or below the intestine. A connection of the gonads with the pericardium does no longer exist, but occasionally with the kidneys; but in most cases only their openings are close together.

Among the nuculaceans, the 4 families have developed in different ways. Their mantle is originally completely open (*Nucula, Tyndaria*), but has developed more or less long siphons in the genera *Neilonella* and *Malletia* and in the ledids. The hinge teeth are sometimes present only in small numbers, and in *Solenomya* they have completely disappeared. This genus stands close to the nuculaceans because of the form of the foot and of the gills, and also because of the labial palp appendage and the open statocysts; it may be most closely related to *Malletia*.

From such gills as the nuculids possess, arose those of the arcaceans by elongation of the two rows of lamellae into two-limbed filaments; labial palp appendages are lacking. The foot in most cases has a well-developed byssus gland, which produces a simple byssus stem. The kidneys are sack-shaped. Among the arcaceans, the *Arca* species with a long, straight hinge margin and a strong byssus are to be viewed as the

most primitive. *Glycymeris* has lost the byssus and has a foot similar to that of nuculids, on the other hand *Limopsis* has retained the byssus; the shell has a form similar to that in *Glycymeris*, but the anterior adductor muscle has become smaller and lies higher. Close to this stand several small forms, in which the hinge teeth tend toward reduction and disappear completely. Following *Hochstetterina* is *Philobrya*, as a terminal form, in which the umbones have shifted forward and the anterior adductor muscle is completely reduced.

It is noteworthy that those groups of bivalves which are closest to taxodonts are not related to nuculaceans but to arcaceans; like the latter, they have broad gills composed of filaments, a completely open mantle, often a well-developed byssus gland, and sack-shaped kidneys. However, the phyletic development has taken place very differently in 2 main directions. In one direction first come the mytilaceans. They lack taxodont hinge teeth, occasionally only a few small tubercles are developed, the shell form of *Idasola* is *Arca*-like but it is often anteriorly pointed, and the anterior adductor muscle tends toward reduction; the gills are as in *Arca*, the mantle has a closed excurrent opening, the byssus consists of threads. In pteriaceans the straight hinge margin is at times strikingly emphasized (cf. Figs. 799 and 800), the shells are greatly compressed, occasionally inequivalve, the ostracum is made of prisms, the hypostracum nacreous. The umbones have shifted more or less 1113 anteriorly and in *Pinna* they lie entirely at the pointed anterior end. The byssus is sometimes reduced (*Crenatula, Vulsella*), the gill lamellae are at times smooth, at times folded. *Pinna* is the most divergent form of this stirps.

The pectinaceans, of which only *Dimya* has still retained an anterior adductor muscle, may stand close to ancient pteriaceans, the umbones of which were still close to the middle. Near this genus of only a few still-living species stands *Plicatula*, in which a pair of strong teeth have developed, as also in the fossil genus *Dimyodon*. The gills consist of identical filaments, as also in Amussiinae, which in most cases have thin, inequivalve shells, sometimes with dissimilar structure of the two valves, in *Propeamussium* with a deep notch in the right valve for the byssus, this notch being reduced in *Amussium* and *Adamussium*. This group lives on the substratum and is not able to swim as some Pectininae do; mantle margin eyes are rarely present in small numbers. *Amussium* species are hermaphroditic. The Pectininae have undergone a considerably higher development through the stronger formation of eyes at the mantle margins and the associated high development of the nervous system, through the ability of some species to swim by the opening and closing of the valves, and through the higher differentiation of the gills.

Spondylus differs mainly by the hinge teeth, which are similar to those of *Plicatula* but are probably not homologous.

It is probable that limids are related to the Pectininae, because, like the latter, they possess pleated gill lamellae and in part have retained the ability to swim, but it appears possible that they have acquired these characters independently. They differ from the Pectininae by the always-equivalve shell, the absence of similar eyes, the unique rotation of the foot and the approach of the cerebral and visceral ganglia to one another. The *Mantellum*-group is most highly developed. It hardly appears doubtful that the anomiids stand close to *Propeamussium*, but they have developed uniquely because of the strong asymmetry; the calcified byssus is overgrown by the right shell valve, but in some groups it is lost and the hole in the shell closed. Most remarkable is the fact that the heart without closed pericardium projects into the mantle cavity. Like the kidneys, the gonads are highly asymmetrical, the right one being largely forced into the mantle; it would be wrong to conclude that because of this circumstance there exists a relationship with mytilids. Of the ostreids one can assume that they stand closest to the pteriaceans; as a result of the cementation of the left valve to the substratum, the foot has become reduced; the gill lamellae are pleated as in *Pteria*.

A separate developmental series is represented by the schizodonts which already differ from others by the characteristic structure of the shell. The marine trigoniids have a recognizable relationship with arcids: both adductor muscles are well developed, the mantle completely open, the gills each formed of a rachis and identical filaments fused with one another only at the margin; the kidneys are sack-shaped. The byssus gland is rudimentary, the foot is large, suited for burrowing. Various opinions have been expressed about the hinge of trigoniids; recently it has been regarded similar to the heterodont condition: the right valve has the central tooth, and the posterior tooth represents a union of a main and a lateral tooth; the posterior part of the large left main tooth is divided by an indentation on the underside. There is also some debate about the relationship between trigoniaceans and unionaceans, though generally such a relationship is admitted. The similar shell structure supports this view, and paleontologists especially emphasized the similarity of arrangement of the hinge teeth; but in this respect sight should not be lost of the significant modifications that the hinge in the series of the unionaceans underwent, where it can not only disappear completely but can also be replaced by altogether different teeth, the genus *Iridina* even simulating a taxodont hinge (cf. Fig. 810). The mantle margins can fuse with one another and with the gills, the latter having formed perforated lamellae from partially fused filaments; the gills have undergone more

or less extensive modifications as brood chambers. The kidneys are unique, but according to Odhner the most similar ones are found in trigoniids; the adaptation of most of the larvae to a parasitic mode of life on fishes is also very characteristic. Accordingly, one may assume that the unionaceans represent a separate branch of the stem, which among recent bivalves stands closest to trigoniids and after transition into freshwater has enjoyed a rich development. The oyster-like aertheriids, with reduced foot, are the most modified.

If one can relate the hinge of trigoniids to that of heterodonts, one will be able to assume a relationship with the latter, bridged by extinct probably non-nacreous forms. Among the true heterodonts, in which the left main teeth do not have the characteristic form as in trigoniids, the marine families Astartidae, Crassatellidae and Carditidae are considered the most primitive. Besides the normal main teeth, lateral teeth are occasionally more or less distinctly developed, but are in most cases lacking. The mantle is in most cases open except for the separated excurrent opening; the gills are as a rule smooth and not fused with the visceral sack and mantle; a byssus is sometimes well developed, sometimes lost; the kidneys are sack-shaped, interconnected, with short proximal limb; not seldom brood care takes place. Pelseneer derives the gaimardiids from carditids, with which they agree in the anterior position of the umbones nevertheless such a relationship seems rather doubtful; they perhaps stand closer to the cyamiids.

In some families, in addition to the excurrent opening, an opening below it is also separated from the anterior opening for the incoming current and both posterior openings can be extended into short tubes. In the freshwater, stirps Sphaeriacea, the hinge of the corbiculids shows well-developed teeth, whereas those in sphaeriids are often weakly developed; lateral teeth are as a rule present. The foot has no byssus and is used for creeping. The kidneys of corbiculids differ from the normal condition only by the arch-shaped curvature of the two limbs, whereas in sphaeriids a characteristic convoluted form has developed from the simple loop as a result of several bends of the two limbs. Different opinions have been expressed about the relationship of the stirps while Neumayr and Douvillé derive it from *Cyprina*, Odhner assumes that first the genus *Corbicula* developed from the extinct genus *Myophoriopsis*, which leads him to conclude "a common phylogenetic origin of the 1115 unionids and cyrenids from *Trigonia*-like ancestors." At all events one can assume that the small sphaeriids are less primitive than the larger corbiculids.

Opinions differ as to whether the lateral teeth in heterodonts are to be considered as primitive or as secondary, and hence opinions also

differ as to the interrelationships of some families, for even the body often provides little indication for this. In the family Kellyellidae the animals are not only of very different size but the mantle is also sometimes completely open, sometimes provided with distinct siphons, and presumably more detailed knowledge would reveal other differences. To this group of deep-sea inhabitants the isocardiids may be related. Pelseneer wants to derive them from cyprinids, from which they differ in the form of the main teeth. The libitinids, more or less elongated as a consequence of their life in cavities are also placed near the cyprinids. The small, mainly Antarctic cyamiids with internal ligament appear to be related here. Completely uncertain appears the systematic position of Dreissenidae, which are widely distributed in freshwater; they were earlier included in mytilids because of the similarity of the shells; in the structure of the kidneys they show some resemblance with gaimardiids, but a closer relationship with them seems doubtful.

It is possible that, as assumed by Pelseneer, there exists a closed relationship between Lucinacea and Erycinacea but perhaps the two stirps can only be traced back to common ancestors, which perhaps stood close to the astartids. Of the Lucinacea, the Ungulininae may be the most primitive, having 2 main teeth in each valve, but no lateral teeth, and the gills of which on either side consist of 2 lamellae; the long, thin digging foot is unique. In the Thyasirinae the hinge teeth are reduced, a small incurrent opening, such as possessed by Diplodontinae, is not yet present; as in lucinids, strong bulges on either side of the visceral mass have developed. In the family Lucinidae also, the hinge teeth representing the main and lateral teeth may become reduced; of the 2 posterior openings, the upper one can sometimes become extended into a distinct siphon which however has no retractors; the main difference from the Ungulinidae is the reduction of the outer gill lamellae. The development of accessory gills on the inner side of the mantle of *Codokia* is unique.

The Erycinacea are a peculiar group of mostly small animals the mantle of which posteriorly has only an excurrent opening, while the inflow happens through an anterior opening, the ventral margins are more or less fused together leaving an opening for the in most cases large foot. The erycinids possess 2 gill laminae on either side, of which the montacutids have lost the outer one. The mantle margins of the former sometimes bear papillae, sometimes longer tentacles, in Galeommatinae one each in front and behind; this group, the mantle margins in most cases become broadened and place themselves upon the surface of the shell. Completely covering it in *Chlamydoconcha* as well as in *Entovalva* and *Scioberetia*, which live commensally on or in holothurians or spatangids. The gonads of montacutids are hermaphroditics. Pelseneer

wants to derive them directly from lucinids, and the erycinids from ungulinids, but this appears doubtful.

1116   The chamids are to be derived from Cardiacea, and are characterized by cementation of one shell valve; in most cases this is the left, more seldom the right valve. According to Odhner, the ones attached by the right valve, for which he erected the genus *Pseudochama*, differ not only in the condition of the hinge teeth, but also anatomically, lacking an anterior blind sack on the stomach, whereas it is present in *Chama*, and the pericardinal limbs of the kidneys lying freely on the inner side, while being completely enclosed by the outer sacks in *Chama*; Pelseneer states that species attached by the right valve show a situs inversus in the position of the intestine and the anterior aorta compared to the ones attached by the left valve (the investigated species is undetermined). Based on the nature of the gills, the chamids are placed by Ridewood in a suborder Cardiacea and Pelseneer too derives them like the tridacnids from cardiids. In the form of the hinge teeth and the mantle opening, they have some similarity with tridacnids, which however are modified in a different way and have lost the anterior adductor muscle. The more primitive cardiids perhaps not yet possessed an incurrent opening separated from the anterior opening and the siphons are elongated only in *Adacna*, the foot originally will not have had the size which is so apparent in most of the cardiids.

    The venerids are placed next to the cyprinids. The hinge teeth are well developed and show little variation except for the left anterior lateral tooth, which is often rudimentary or absent; a mantle sinus is occasionally absent and hence has first developed in the family. The gill folds are also sometimes indistinct, sometimes greatly developed. The siphons are originally completely or largely united with one another, in other genera they are more separated, standing close to the venerids are the petricolids, among which *Petricolaria* is the most divergent.

    The mactrids are characterized by their ligamental cartilage, which has failed its way behind the main teeth, of which the right central tooth seems to be absent, but it is probably more correct to assume that the angular tooth consists of the central tooth, and the anterior limb of the anterior main tooth, whereas its posterior limb has disappeared as a result of the penetration of the ligamental cartilage; the in most cases cleft left main tooth then corresponds only to the anterior limb, the posterior limb being more or less clearly indicated. Lateral teeth are present. Here again a mantle sinus is sometimes not yet developed, the siphons are more or less united with one another; the gill laminae are sometimes smooth, sometimes more or less strongly folded, the foot without byssus. With the indicated concept of the hinge teeth, their derivation from those of

the cyprinids, corbiculids, etc. would be less difficult and would permit the placement of *Rangia* in the mactrids, the former having been placed by Fischer in a separate family related with corbiculids. If *Anatinella* is also related with mactrids, then this relationship seems to be based only on common precursors, which still have no mantle sinus; an animal called *Anatinella* by Pelseneer, about which he made some statements, was probably incorrectly identified. Even more doubtful is the relationship between mactridae and *Cardilia*.

Based on the gills, Ridewood has placed the mactrids in a suborder Tellinacea, and Pelseneer wanted to derive from them not only the Tellinacea, here combined as a stirps, but also the Adapedont; however the donacids, psammobiids, and tellinids with external ligament cannot have descended from forms with internal ligament, and the semelids may have acquired their cartilage independently. *Hemidonax*, earlier grouped with the cardiids, has no siphons, the posterior mantle opening being divided only by the terminations of the gills, the foot is short, the gill laminae are distinctly folded; it is perhaps most correct to assume a separate family or subfamily for them, as Fischer has done. The gills of most of the Tellinacea are smooth but in some *Donax* species, in psammobiids and in *Semele*, they are more or less strongly folded. The lateral teeth are sometimes weak or absent; the mantle sinus is often not separated from the ventral mantle line. The foot in most cases has no byssus.

The psammobiids were in most cases grouped together with the solenids; Ridewood has united them with others in a suborder Myacea, which includes the Adapedonta without the Adesmacea. Here again occur smooth as well as folded gills, and it is to be assumed that the modification has taken place in the individual stirps; thus the rather small *Saxicava* species have smooth, the large *Panopea* and *Cyrtodaria* folded laminae, in gastrochaenids and the Adesmacea they are not or scarcely folded; among the solendids, Novaculininae and the genera *Siliqua* and *Pharus* have smooth, the others folded laminae. The ligament is sometimes external, sometimes internal, the hinge margin narrow, sometimes with main teeth always without lateral teeth. In the Solenacea the shell is considerably elongated, more often it is roundish or moderately long, the siphons too are variously long. The initial forms of the Adapedonta may have stood close to the Tellinacea; the Solenacea have developed in a direction different from the others, among which the saxicavids still possess an external ligament and more or less distinct hinge teeth, the aloidids an internal asymmetrical cartilage and a right hinge tooth, while the gastrochaenids have an external ligament and a tooth-less hinge margin, their shell gaping widely in the anterior portion of the underside.

Near them may be placed the pholadids, the shell of which gapes anteriorly and posteriorly and has completely lost the ligament, while the anterior part of the dorsal margin is reflected outward and the anterior adductor muscle is attached to it, which thus acts antagonistically to the posterior muscle, so that the shell can perform rasping movements with the teeth developed on the anterior part, enabling the animal to bore into wood of other solid bodies. As a protection for the parts not covered by the shell various accessory calcareous plates have developed in the pholadids, whereas the teredinids, like *Fistulana*, produce a calcareous tube which encloses the entire animal, the shell of which covering like a head only the small anteriormost part. The teredinids have developed most uniquely in this respect and in some anatomical characters, as well as in having "pallets" at the ends of the very long siphons.

New the Adapedonta stand the Anomalodesmata which as a rule have no hinge teeth and an internal ligamental cartilage, often with a lithodesma; siphons and mantle sinus are sometimes still little developed, the gonads with the exception of the cuspidariids are hermaphroditic. The gills are variably developed, in Pandoracea and Clavagellacea the inner laminae are still well developed and folded, whereas the outer ones are in most cases represented each by a single, upwardly directed lamella; but in verticordiids they are narrow, net-shaped, and more or less fused with the septum, which becomes perfected in poromyids, whereas the gills are reduced to 2 or 3 small sieves or rows of holes; in cuspidariids the strong septum on either side contains 4 or 5 holes and the gills are completely reduced. The tooth-shaped elevations of the hinge margin sometimes occurring here are probably not homologous with the teeth of heterodonts; the structure and form of the shells are variable, in clavagellids, as in *Fistulana*, a tube enclosing the animal along with the long siphons has developed, and in *Clavagella* this tube has fused with one of the shell valves in *Brechites* with the entire shell, so that it can no longer be moved and the adductor muscles disappear.

The class of the cephalopods has developed independently from the ancestral conchiferans and has by far attained the highest stage. Like scaphopods and bivalves, they have retained the original bilateral symmetry, and have not undergone a torting of the visceral sack against the foot as have the snails; accordingly they have paired ctenidia and kidneys, originally also paired gonoducts, although the gonad is always single. Similar to that in some opisthobranchs, the foot has become transformed into the "funnel" by broadening of the lateral margins; in the dibranchs, by fusion of the free margins, the funnel has become a closed tube which is open anteriorly and posteriorly and is largely covered by the mantle, and serves as the swimming organ. As in zeuogobranchs, the

head originally has open eyes, but in dibranchs they are in most cases developed into highly efficient visual organs. One can also assume that the cephalic tentacles and an epipodium were originally present, as in zeugobranchs, and have become transformed into the arms of the cephalopods. The pharynx, with radula and jaw as well as a subradular sense organ, has also been inherited from the ancestral conchiferans, but here a lower jaw is also developed, which together with the upper jaw forms a powerful biting organs resembling a parrot's beak. The radular plates are simple, with projecting, more or less long cutting edges, originally without differentiation. The nervous system—with exception of the buccal ganglia—shows little resemblance to that of zeugobranchs, more to that of bivalves, because an anterior and a posterior ventral cord, corresponding to the pedal and the visceral ganglia, issue from a cord corresponding to the cerebral ganglia overlying the pharynx; but in dibranchs these are united with one another and the innervation centers of the arms have become detached and form special arm ganglia which are connected with the pedal, cerebral and buccal ganglia. The parts are originally not separated from one another by connectives, so that a sharp delimitation between cerebral and pedal ganglia is not recognizable; special pleural ganglia are also absent.

The shell of the cephalopods is originally external and, as in the zeugobranchs, it is internally nacreous, externally colored. Very early it became elongated and chambered internally by numerous septa pierced by a "siphuncle" which· is sometimes wide, sometimes narrow; the animal inhabited the last chamber, but in most cases remained in contact with the other chambers by a process lying within the siphuncle. Of the numerous cephalopods with an external shell, which have lived a very

1119 long time ago and were probably very diverse, only the genus *Nautilus* has survived to the present day, so that we know the nature of the body only from this form. It consists of a very large head with the hood and numerous cirri and a massive body lying in the last chamber, the underside of which anteriorly showing the large bilobed funnel and posteriorly 2 pairs of gills in the mantle cavity. This body form had to be changed considerably when the animals clasped their elongated shell with lobe-shaped processes and gradually completely enclosed it, as it is the case in the belemnites. Because of this the body underwent a considerable elongation and the shell turned from an external protective organ to an internal support. The oldest ancestors of the currently living dibranchs have to be visualized in this way.

The nautilids also seem to have originated from the same ancestral forms from which the belemnites arose. Because the belemnites had in all probability only one pair of ctenidia, corresponding on the one hand

to those of the zeugobranchs and the primitive bivalves, and on the other hand to those of the decapods and octopods, it is to be assumed that one pair of gills of the nautilids represents a special acquisition. The origin of the anterior pair of gills will have to be visualized in such a way that each ctenidium continued anteriorly from the base of the process bearing the two rows of leaflets, similar to the case in primitive bivalves, and that these anterior portions detached lobe-like from the body; later the rows of lamellae between the two processes became interrupted, so that on each side 2 separated gills arose. As a result of such a division of each ctenidium, the gill vessels had to divide as well as the excretory glands developed on them (pericardial glands and kidneys), so that the anterior pair of kidneys developed in association with the anterior pair of gills.

An additional acquisition of the cephalopods is the more or less large body cavity, which represents a widening of the pericardium and has entered into connection with the gonad. It cannot be doubted that this state is a further development compared to that of the other mollusks. In some snails the pericardium has undergone a usual extension (*Septaria*) and similarly one can assume that in cephalopods it has enlarged somewhat more and has penetrated between the gonad and its effecient ducts. Accordingly, the germ cells must pass the body cavity, but they are immediately taken up by the gonoducts lying opposite to the gonad. These conditions at all events arose as an adaptation to the very large and yolk-rich eggs or to the mass production of sperm and the large spermatophores. The phyletic relationship of nautilids to the dibranchs may thus be so visualized that the former are more primitive because of their external, chambered shell, as well as because of the bilobed funnel, the open eye cups, and probably also because of the form of the nervous system; it may be uncertain what shape of head and arms the initial forms of the dibranch had, and they probably would not have possessed such a cephalic hood as in *Nautilus*. These initial forms still had an elongated and chambered shell. Its considerable length was gradually 1120 found to be useless and obstructive, and a shortening occurred, which produced various results. In *Spirula* the shell curved in towards the ventral side, still retaining its distinct chambering and, because of the incurving, had no anterior process; in *Sepia* it assumed the form of a dorsal shield, on the underside of which the fine septa became obliquely placed in a highly characteristic way. Only in these two families is the shell still calcified, in all other decapods which still possess a shell, it is horny, and not chambered; it corresponds to the "proostracum", whereas, along with the "phragmoconus" the equivalent of the original external shell has completely disappeared.

While *Spirula* has most clearly retained the remains of such a calcareous shell, the body shows in part primitive characters like the open eye chamber, and in part special modifications, such as the absence of a radula. It seems uncertain whether *Idiosepius* is directly related with *Spirula* because of the similar body form and the two hectocotylized ventral arms, in spite of the absence of a shell. The sepiadariids and sepiolids also have no or only rudimentary shells. The loliginids have eyes resembling those of *Sepia*, but a horny "gladius" as in the Architeuthacea. The latter represent a separate developmental series, differing from the Sepiacea—with the exception of *Spirula*—and from the Loliginacea by the open eye chamber; in addition they lost the accessory nidamental glands. They advanced phyletically in different ways, so that their interrelationships are difficult to ascertain. The following may be regarded as primitive characters: an elongated body, a buccal membrane with eight lobes, and paired gonoducts; although these are not found together in one group that could be considered as a little modified initial form. Some are probably to be regarded as divergent, such as *Histioteuthis* (Fig. 877) with short body and the large velum, but especially the cranchiids with their greatly enlarged body and mantle cavity and the fusion of the mantle to the funnel, and among the *Bathothauma* is the most peculiar (Fig. 882).

The phyletic relationships of the octopods with the decapods are not very clear; the phylogenesis of the former has been discussed in detail by Robson. He felt he could assume that they stand close to decapods with 10 identical arms, of which the 4th pair later developed into tentacles, whereas the 2nd pair would correspond to the thread-shaped process of some vampyroteuthids. At all events such ancestors of both orders still possessed separate kidneys and paired oviducts, their arms were beset with one row of suckers. On the whole, the most primitive octopods are the vampyroteuthids with well-developed radula, the plates of which are simply pointed, with a distinct internal shell, the form of which in *Vampyrotheuthis* is comparable to the gladius of Architeuthacea, with fins on the widely open mantle, with a funnel valve, and perhaps also other characters, such as the moderately long arms with one row of small suckers; on the other hand the cirri and the broad velar membrane are to be considered as special acquisitions. Near them stand the Cirroteuthacea, primarily the stauroteuthids, the mantle of which has a narrowed opening and in *Chunioteuthis* fuses with the funnel, and the radula of which is reduced. *Cirrothauma* is peculiarly modified, with a completely gelatinous body, attached to which are a pair of large fins, and the eyes are rudimentary, without lens and ganglion; of the suckers, only the 6 innermost ones of each arm are normally developed, the others

are spindle-shaped, without distal depression, in the proximal portion contain a whitish body consisting of a spherical cell mass and a cartilage-like shell, and has a certain similarity with light organs. *Opisthoteuthis* is highly modified in a different way, in which the shortening of the long axis of the body (distance of the mouth from the posterior end) has reached the highest degree, so that the posterior of the body forms only a flat hump, attached to which are a pair of small fins; the mantle opening narrowly encloses the funnel; the suckers are normally developed, sometimes fairly large and crowded together.

Another developmental series of the octopods, which again divides into 3 large branches, is represented by the Incirrata, in which the mantle bears no fins and contains no or a very rudimentary shell; the more or less long arms bear 1 or 2 rows of suckers, but no cirri and in most cases no broad velar membrane. Of the 3 branches, the bolitaenids show a primitive condition because of their open eye chamber and their rather short arms; it seems doubtful whether the soft body without distinct cartilage and the soft jaws can be considered as primitive, but there is no doubt that the strongly broadened intermediate plates of the radula are a special acquisition. The amphitretids are more modified with long arms connected by a broad membrane, with the eyes approaching each other on the dorsal side, and with the funnel fused to the mantle; here too may be placed the vitreledonellids, the arms of which are long and connected by a membrane and their radula having undergone a certain reduction presumably associated with the small size of the viscera. The hectocotylus formation in this stirps is little developed and differs from that of the Octopodacea, in which at the end of one of the 3rd arms a more or less large spoon-shaped structure (cf. Fig. 890) is developed. The arms of the octopodids sometimes reach considerable length and strength, the sucker rows occasionally appearing doubled because of their being compressed. The radular plates have relatively broad bases and mainly the median ones have often small accessory cusps, the inner intermediate plate is small. The ink sack is sometimes reduced (Bathypolypodinae). Because of the difference between the sexes and the detaching, greatly modified hectocotylus, the Argonautacea reach the highest stage of peculiar developement, and at the end of this series stands *Argonauta*, in which the females possess the unique spiral shell, which, as a product of the lobe-shaped broadened dorsal arms, has perhaps developed because such arms initially only received the eggs and only gradually secreted a firm shell for them. The similarity of the radular plates, especially of *Ocythoe*, with that of some decapods, can hardly be considered as an indication of relationship.

Thus the octopods are because of several different traits such as the fusion of the mantle margin to the body, which at times underwent the most extreme shortening, the rudimentary or completely lost shell, the highly organized eyes, the short gills, and the reduction of the pericardium, the most highly and uniquely developed mollusks.

Paleontology and Phylogeny

This is not the place to go into the details of the relationship between paleontology and systematics of Recent mollusks, that being a subject for paleontologists, but certain aspects of significance for the phylogeny and the system will be highlighted.

The rare finds of fossil loricates agree well with the conception of the phyletic development of the class. The most primitive forms are put in their own order Helminthochitonida which still lacked apophyses; hence they do not yet seem to have developed an articulamentum nor perhaps a differentiation of shell layers, but the perinotum surrounding the elongated body was already beset with spines. The shells found in the Palaeozoic belong to Lepidopleurida because of the absent insertion margins, and only from the Liassic are some known with incised insertion margins.

Ashby described the genus *Protochiton* from the Australian Oligocene, in which the terminal valves still have no insertion plate, whereas the apophyses are large and extend posteriorly on the sides. Ashby believes he can bring this form into a phyletic relationship to the acanthochitones which he placed as a separate phylum in contrast to the remaining chitonids. This, however, cannot be accepted, because, apart from the fact that this *Protochiton* is far too young, there is no reason to exclude it from the lepidopleurids, for the shape of the apophyses is quite similar to those in *Hanleya*, as also the surface sculpture, and the absence of an anterior insertion margin is the only important difference.

In other respects, the fossil finds can hardly be taken into consideration for the classification of the interrelationships of chitonids. Even if in ancient times a shortening and broadening took place, it cannot be concluded from this that among Recent forms the elongated ones are more primitive than the shorter ones; but rather such animals as *Cryptoplax*, *Stenochiton* and *Schizochiton* are undoubtedly individually adapted forms. The more or less distinct sculpture is also probably of small phyletic importance, because it occurs in various groups.

Much better preserved are the shells of marine snails from as early as the Cambrian period and these can be taken into consideration for the recognition of the phylogeny, but at the same time it should be born in

mind that certain shell forms can appear in various groups and some are so little characteristic that one can say nothing definite about their systematic position without a knowledge of the animals; for this reason some uncertainties persist in the paleontological system. Such a system has been worked out by Cossmann, and a brief review of it may serve to highlight some deficiencies in comparison to a system of the Recent snails.

The fact that pleurotomariids have been preserved since the Cambrian seems to allow the conclusion that they have lived in protected places or in quiet waters, whereas the haliotids, which stand very close to them in their organization, have adapted to life on the seashore and are known only from much more recent times, partly perhaps because the shells were easily ground up by the surf.

1123   The species allocated by Cossmann to *Subemarginula* and *Scutum* from the Eocene of Paris seem to include members of cocculinids. The family Trochidae is divided into a number of subfamilies; Trochinae, Polyodontinae, Monodontinae, Umboniinae, Gibbulinae, Margaritinae and Conulinae. The last of these corresponds mainly to Calliostomatinae, but *Jujubinus* and *Strigosella* belong to *Cantharidus*, *Lischkia* (= *Lischkeia*) and *Euchelus* to Margaritinae, which are essentially acceptable except *Minolia* and *Conotrochus*; *Monilea* is to be placed in Umboniinae, but *Chrysostoma* does not belong there. The remaining subfamilies are not very different. The stirps—called cénacle by Cossmann—Astylacea, cannot be accepted; they are trochaceans with ear- or cup-shaped shell, which in part (*Stomatella*) stand near *Euchelus*, in part near *Gibbula*, whereas *Phaneta* presumably does not belong here. A subfamily Eucyclinae is placed by Cossmann under the littorinids, although the shells are nacreous, for which reason the group perhaps properly was placed by Fischer in the trochaceans, *Littorinopsis* which does not have a nacreous shell has evidently to be excluded. The Trochonematidae, Cyclonematidae and Paraturbindiae also may belong to the trochaceans rather than to the littorinaceans, at all events this is supported by the tightly coiled, externally cone-shaped operculum of *Trochonema*, which, like that of the Horiostomatidae, compares best with that of *Leptothyra*. Near the Liotidae, in which *Lippistes* and *Mecoliotia* were erroneously placed, Cossmann puts the extinct families Peristomatidae, Ataphridae and Colloniidae, but also the Cyclostrematidae with the subfamilies Cyclostrematinae and Tinostomatinae, whose genera were taken mostly from the Skeneinae and the Adeorbidae; this last group is also included here. The turbinids and phasinellids are essentially correct. Near the Littorinacea, in addition to Littorinidae and Lacunidae stand the Fossaridae, among which *Phasianema* and *Jsapis* which actually are pyramidellids

are placed. Of the rissoids, Cossmann believes that the rissoas derive from Palaeozoic littorinaceans, the rissoinas from entirely different forms, which however is unlikely in view of the great similarity of the dentitions; among the rissoas, genera are named which belong to the Barleeinae, whereas *Barleeia* stands near the litiopids, which are also regarded as Rissoacea; *Fenella* and *Scaliola* are also no rissoids. *Micromelania* and *Baicalia* are called hydrobiids.

The cénacle Euomphalacea contains a very peculiar assortment of differing groups; next to the Euomphalidae, among which the Recent genus *Pseudomalaxis* is named, and the Solariidae, stand the Raphistomidae, which Fischer counted among the pleurotomariids, as well as the xenophorids, the extinct Cirridae, and the delphinulids.

Cossmann believes that the loxonematids, even though they do not possess a slit, are to be derived from murchisoniids, which belong to the pleurotomariids because of the slit in the apertural margin. He recognizes a cénacle Loxonematacea, in which, aside from the extinct families Loxonomatidae, Coelostylinidae, Spirostylinidae, Pseudomelaniidae, Subulitidae, he also wants to place the Mathildidae, Scalidae, Turritellidae, Vermetidae and Caecidae. That the genus *Vanesia* A. Adams, 1861, from the littoral of Manchuria is related to pseudomelaniids appears to be just as uncertain as the relationship of *Abyssochrysos*. Koken wanted to view the loxonematids as the common root not only of siphonostomous taenioglossans, the rhachi- and toxoglossans, but also of pyramidellids and opisthobranchs, but this is of not much use for our zoological system, because the organization of these forms is completely unknown. Probably they will essentially have belonged to the Cerithiacea, and perhaps some of the Recent groups of this stirps are descended from them. In the cénacle Cerithiacea the following families are distinguished: Eustomidae — according to Fischer perhaps related to *Terebralia*, but according to Cossmann intermediate (?) between the Alatacea (= Strombacea) and Cerithiacea; Brachytremidae, which hardly belong here; Procerithidae, without a siphon, with the subfamilies Procerithinae, Paracerithinae and Metacerithinae, all of which are extinct; in addition the Cerithidae with the subfamilies Cerithinae, Potamidinae and Bittiinae; Cerithiopsidae, Triforidae, Diastomidae with an apertural sinus, but without canal, which perhaps correspond to the Finellidae; also the Trichotropididae, of which he states that in the shell form they show some affinities with purpurinids, which are also placed here; and finally the Planaxidae and Modulidae.

Strangely, the naticid genus *Acrybia* is placed in the Janthinids; with the vanikoroids are named *Micreschara* (= *Couthouyia*) and *Macromphalina* (= *Megalomphalus*), but not *Fossarus*. Among the

Alatacea, the struthiolariids are declared as reduced aporrhaids; besides the strombids, the fossil columbellinids are also placed with this stirps. It cannot be accepted that the strombid genus *Terebellum* is connected to *Simnia* through the extinct *Diameza*. Cossmann separates a family Euspiridae from the naticids and maintains that it would be a great error to place them together, because the latter are derived from Loxonematacea, whereas the former had a capuloid origin. Among the Euspiridae he names the Recent genus *Cernina* = *Globularia*, the anatomy of which is not known, and also the pyramidellid genus *Amaura*. However, his view can hardly be accepted, because a closer relationship between naticids and capulids does not exist. He also seems to assume closer relationships of the naticids with naticopsids and neritopsids. The Cypraeacea form a cénacle Involvacea, and to the Doliacea corresponds a cénacle Tritonacea. The Muricacea are divided into Muricidae with the subfamilies Muricinae, Ocenebrinae, Trophoninae, Typhinae and Rapaninae, into Purpuridae and Coralliophilidae; the Buccinacea into Nassidae with the subfamilies Nassinae, Dorsanine and Truncariinae, Buccinidae with the subfamilies Buccininae, Cominellinae, Photinae, Pisaniinae and † Anochetinae, into Chrysodomidae, Pyramimitridae (including *Nassarina*), and Strepturidae (including *Melapium*); also the Fusacea into the families Fusidae with the subfamilies Fusinae, † Streptochetinae, Fasciolariinae and Ptychatractinae, and Turbinellidae with the subfamilies Turbinellinae, Tudiculinae, Fulgurinae and Melongeninae. The cénacle Plicacea comprises the families Mitridae with the subfamilies Orthomitrinae, Plesiomitrinae, Semimitrinae, Pseudomitrinae and Cylindromitrinae, Volutidae with the subfamilies † Pholidotominae, Loxoplocinae, Volutinae, Cymbinae, Zidoninae and Homoeplocinae, Cancellariidae with the subfamilies Cancellinae, Trigonostominae and Admetinae, Olividae with Olivinae and Ancillinae, and finally Harpidae and Marginellidae. The named subfamilies are probably partly superfluous, and partly they do not correspond to the actual interrelationships.

1125   Cossmann erected a separate suborder Entomotaeniata for a group of fossil snails of the Mesozoic, with the families Tubiferidae, Itieriidae and Nerineidae; he assumes that this group is to be placed near the tectibranchs or the pyramidellids; some (*Itieria*) resemble these somewhat, others have greater similarity with cerithiids.

Of the Cambrian forms, the bellerophontids were probably not at all gastropods, and for this reason they are placed in a separate class, the Amphigastropoda, the animals of which were still bilaterally symmetrical and probably led a swimming mode of life like that of the nautilids. Their symmetrically inrolled shell as a rule had a slit with an adjacent band similar to that in zeugobranch snails. It is altogether impossible to

regard these, especially *Porcellia*, as ancestral heteropods (Koken). As a matter of fact it appears highly doubtful whether Cambrian snails are related to recent one, with the exception of the pleurotomariids, but. even in this family the shell has forms so diverse that it may be assumed that, like the trochids, the animals would have shown considerable differences; of the developmental series one then led to the haliotids, another to the scissurellids, still another series to fissurellids, to trochids, as well as to extinct groups like the euomphalids. It is impossible to relate the latter with solariids. In the same way one will not be able to assume that capulids already lived in the Cambrian, and a direct descent of the loxonematids from *Murchisonia* or of the xenophorids from trochaceans is likewise excluded. **One will have to assume that only from one group of archaeogastropods, of which only the trochaceans can be considered, the ancestral form of the mesogastropods developed, to which among the marine families the lacunids probably stand closest; and likewise that only from one group of mesogastropods (Doliacea) the stenoglossans derived, and that from still another, which was most closely related with pyramidellids, descended the ancestral form of the opisthobranchs.** Because of the great uncertainty about the affinities of Palaeozoic snails to recent ones, the first appearance of certain groups often remains highly doubtful, such as the occurrence of true docoglossans and pteropods in the Cambrian, and of scalids and pyramidellids in the Silurian. But up to the Carboniferous, the phyletic development had made significant progress, and it is very noteworthy that during this period not only actaeonids but even pulmonates had already made their appearance: *Zonites* (*Conulus*) *priscus* Carpenter, which probably was closely related to *Pyramidula*, *Anthracopupa ohioensis* Whitfield, *Maturipupa vermilionensis* (Bradley) and *Dendropupa vetusta* (Dawson); it seems inconceivable that such forms already lived in the Devonian, especially because otherwise the ellobiids are known only since the Jurassic, just as most groups of the more highly developed snails have originated during the Mesozoic.

Fossil bivalve shells are not known from the older Cambrian, and from this fact it may be concluded that the bivalve form developed only during the course of this period, and hence is younger than the snail form. The bivalves occurring in the uppermost Cambrian or lowermost Silurian belong to the taxodonts and modiolopsids. The genus *Ctenodonta* Salter can be included in the nuculaceans and *Glyptarca* Hicks in the arcaceans; it is remarkable that the latter, with its long posterior hinge teeth parallel to the margin, can be considered as a secondarily modified arcid form, if it is assumed that species with normal teeth have preceded

them, and were not preserved because they were firmly attached to stones by their byssus and were destroyed by the surf. *Glyptarca* has pointed umbones approaching the anterior end and only few anterior hinge teeth; in *Modiolopsis* Hall the umbones are terminal and the hinge margin has 1–4 short, oblique, and 1 or 2 long teeth, *Cyrtodonta* Billings has nearly terminal umbones and 2–8 small and a few very oblique posterior hinge teeth; the latter group can probably still be allocated to the arcids or at least be derived from it, but its affinity to gaimardiaceans and dreissenaceans seems more than doubtful. Judging by the shape of the area, the cardiolids also belong to arcaceans, but without relationship with cardiids. The hinge in the ancestors of the anisomyarians is in most cases edentate—like *Philobrya, Ambonychia* Hall is perhaps also to be included in arcaceans, but allied to *Glyptarca*—and the umbones lie close to the center of the hinge margin as in *Posidonomya* Bronn; they retain the median position in the pectinaceans—*Aviculopecten* Mac Coy may be considered a transitional form—whereas in mytilaceans and pteriaceans they have shifted more or less far forward, as in *Pterinaea* Goldfuss. The Silurian genus *Lyrodesma* Conrad, with 5–9 transversely grooved teeth radiating out from the umbones, is considered as the initial form of the trigoniids. The latter at all events acquired the unique structure of the shell, whereas the cardiniids, to which belongs the genus *Trigonodus* Sandberger mentioned by Odhner, do not possess a nacreous shell, because of which they are allied to the stirps Astartacea and Carditacea. *Anodontopsis* Mac Coy has been recently placed with the Cyprinacea. The Silurian grammysids and praecardiids are thin-shelled bivalves without hinge teeth which have been called "desmodonts," but a direct relationship with pholadomyids will probably have to be excluded. It is emphasized that the known Silurian bivalves have been found predominantly in deposits of deeper seas, those from parts close to the seashore were thus probably largely destroyed, whereas such forms appear ever more richly in the Devonian and Carboniferous. Most of the extant groups developed in the Mesozoic in place of some Paleozoic groups; among them the anisomyarians gradually decline in comparison with the eulamellibranchs which have also invaded freshwater.

As far as the cephalopods are concerned it is now generally assumed that the oldest forms, among which Spath calls the endoceratids not only the ancestors of orthoceratids but also of the nautiloids and the ammonoids had elongated shells. This latter series alone seems to have acquired a second pair of gills, whereas the first series, near which belemnoids of the Triassic are placed, possessed only the two ctenidia. Naef divided the fossil decapods into: 1. Belemnoidea, with the families Aulacoceratidae, Phragmoteuthidae, Belemnitidae, Belemnoteuthidae, Xiphoteuthidae and

Vasseuriidaae; 2. Teuthoidea—a) Prototeuthoidea, with the families Belopeltidae, Geoteuthidae, Leptoteuthidae and Plesioteuthidae,—b) Mesoteuthoidea, with the families Trachyteuthidae, Beloteuthidae, Palaeololiginidae and Kelaenidae,—c) Metateuthoidea, with the Recent
1127 Myopsida (= Loliginacea) and Oegopsida (= Architeuthacea); 3. Sepioidea, with the families Belemnosidae, Belopteridae, Belosepiellidae, Spirulirostridae, Spirulirostrinidae and the Recent Sepiidae, Spirulidae, Idiosepiidae and Sepiolidae.

Among fossil octopods, *Palaeoctopus* Woodward is important, for which Naef erected a subroder Palaeoctopoda; the impression in the upper Cretaceous shows an egg-shaped body with triangular fins, containing a shell rudiment and an ink sack and a narrower head with variously long arms, each bearing one row of suckers; cirri and a velar membrane seem to be absent.

Geographical Distribution of the Mollusks

Because of the great age of the lepidopleurids and their present distribution in all seas it is understandable that the place of their first development is not recognizable. The extant species of the genus *Lepidopleurus* in the south [*L. kerguelensis* (Haddon)] reach the Metantarctic, but not the Holantarctic; in the north [*L. asellus* (Chemnitz) and *cancellatus* (Sowerby)] they reach Greenland, the former also Spitzbergen but without being confined to the cold sea; others have been found at considerable depths; *L. belknapi* Dall 1800 m, *opacus* Dall 3650 m, *simplex* Nierstrasz and *setiger* Nierstrasz 1300 m. *planus* Nierstrasz 2050 m, *giganteus* Nierstrasz 2800 m and *benthus* Haddon 4200 m; the localities are situated in the Pacific and Indian oceans. Most species however live in shallow depths. The subgroups, proposed for somewhat divergent species, in most cases have little phyletic significance; *Parachiton*, the typical species of which lives near New Guinea, has also been found by Sulc in the Miocene of Central Europe. The sole *Oldroydia* species from California has no close relative, and the few *Hanleya* species as well as the Australian *Protochiton* (cf. p. 1651) have no connections to higher loricates. But, on the contrary, such a connection may be assumed for *Hemiarthrum*, which extends from the Kerguelen to the Magellanic region. Evidently, the most closely related genus *Tonicella* is restricted to the northern hemisphere, with 2 circumpolar species [*T. rubra* (Linné) and *marmorea* (Fabricius)], although the latter extends in the south to the Gulf of Mexico. The distribution of *Lepidochiton* is similar, whose southernmost species *canariensis* (Thiele) and *liozonis* (Dall & Simpson) live near the Canaries and the West Indies; it is

doubtful whether *solidior* (Carpenter) from the Philippines belongs here. The only known *Mopaliella* species from Peru differs from *Lepidochiton* only by groups of rather large needles on the perinotum; the closely related *Middendorffia* is restricted to the warm parts of the Atlantic Ocean (Canaries, Azores) and the Mediterranean Sea, on the other hand *Nuttallina* lives near California and Japan. Of considerable interest are *Notochiton* and *Nuttalochiton*, the former of which lives in the Holantarctic, the latter near Tierra del Fuego on the one hand of the paired gonads, found only in these cases, and on the other for the multiple connections with other groups of loricates. The most primitive group of Callochitoninae: *Icoplax,* the median shell pieces on either side possess only one incision and the radulae of which have a cutting edge on the lateral plate, lives in the Antarctic Ocean, *Trachyradsia* near South Africa and Tasmania, *Eudoxochiton* near New Zealand and the Kermadek 1128 Islands, only few species have extended into the tropics and only one [*laevis* (Montagu)] into the northern Atlantic. But of the mopaliids only the genus *Plaxiphora* and 2 *Mopalia* species [*M. australis* Suter from the Snares Islands and *M. (Semimopalia) grisea* Dall from Cape Horn] are known from the southern seas, most of them living in the northern Pacific Ocean, *Symmetrogephyrus* (= *Amicula*) having arrived in the Arctic Ocean. The situation is similar in the Acanthochitoninae; few species of the genera *Cryptoconchus* and *Acanthochiton* live near New Zealand and in the Magellanic region, others have spread more or less far northward, but are lacking in the cold seas; *Craspedochiton* too inhabits the warm seas, especially the Indian Ocean; the large *Cryptochiton* extends in the Pacific to the Aleutians and Alaska. Of the Cryptoplacinae, *Choneplax*, which is indigenous to the West Indies, is widely separated from the *Cryptoplax* species living at present in the Indo-Pacific Ocean, but the frequently occurring *C. Winlandi* Sulc in the European Miocene proves that such species earlier lived also at other places. Of *Chaetopleura* species, some live in the Magellanic region, partly however in more or less wide distribution, *C. fulva* (Wood) for instance also occurring near Portugal; other species live partly in southern areas, near South Africa and Australia, partly in the tropics; only *C. livida* (Middendorff) is stated to be found near Sitka. The very species-rich subfamily Ischnochitoninae is also absent from the Holantarctic; few *Ischnochiton* species living in the Magellanic and Aucklandic region, the subgenus *Stenoplax* predominantly in warm part of America, only few species *I. (St.) alatus* (Sowerby) and *lindholmi* (Schrenck) near eastern Asia and *I. (St.) madagassicus* Thiele near Madagascar. The subgenus *Ischnochiton*, with several species, inhabits the Australian coasts, but is also otherwise widely distributed, only one species [*I. rissoi* (Payraudeau)] being

indigenous to the Mediterranean Sea. The species of the subgenus *Chondropleura* are scattered in the southern seas; *I.* (*C.*) *exaratus* G. O. Sars being found in the Magellanic region, but has spread to Norway without being found on the east coast of South America, occurring however near North America. The only Arctic species, extending southward to England and California, is *I.* (*Stenosemus*) *albus* (Linné). Of the subgenera of *Lorica*, *Lorica* s. s. and *Loricella* as well as some *Callistochiton* species are represented near Australia, one species (*L. haurakiensis* Mestayer) also near New Zealand; the majority of the species mainly of *Lepidozona* are distributed on both shores of the northern Pacific. Of the two subgenera of the genus *Chiton*, some species of the subgenus *Chiton*, which is otherwise almost completely restricted to America, occur near New Zealand and Tasmania to eastern Australia: *C.* (*Poeciloplax*) *glaucus* Gray, *C.* (*Sypharochiton*) *pellisserpentis* Quoy and Gaimard, *sinclairi* Gray, *torri* Suter, *mayi* (Pilsbry), *maugeanus* Iredale & May and *septentriones* Ashby; only *C. connectens* Thiele, which is said to be found near West Africa, still belongs to *Chiton* s. s. The subgenus *Rhyssoplax* has spread over all coasts of the Old World but is most abundant in the Indo-Australian region, the Mediterranean Sea containing only 3 species: *C. olivaceus* Spengler *rubicundus* O.G. Costa, and *phaseolinus* Monterosato, none having reached England. Most species of Acanthopleurinae live in the southern hemisphere; *Squamopleura* and *Acanthopleura* mostly near Australia; only one species near Japan, and one in the West Indies; *Enoplochiton* and *Mesotomura* on the west coast of Sourth America. The *Tonicia* species inhabit the same coasts, but in considerably greater extent, because they reach Patagonia and the Auckland and Campbell Islands in the south, and California and Japan in the north. The peculiar genus *Schizochiton* is known from the Philippines, Moluccas, Maldives and eastern Australia. On the whole, it seems that the distribution of loricates has taken place from south to north; very striking is the paucity of species on the European coasts in comparison with Australia, but also with California.

1129

The few *Pleurotomaria* species, which have survived to the present, have been found in the West Indies, near Japan, and near the Moluccas, at depths of ca. 130–400 m; the considerable size of most species indicates favorable conditions for existence, they appear to subsist mainly on sponges. The Moluccan species *P. rumphii* Schepman is most similar to the West Indian *P. adansoniana* Crosse & P. Fischer. The distribution of the scissurellids is quite different; these small animals inhabit all seas, a few species (*Scissurella euglypta* Pelseneer and *amoena* Thiele) the Holantarctic, a few the Kerguelena and the Patagonian region, others have extended more or less far northward, one (*S. crispata*

Fleming) into the Arctic Ocean, but without being confined to it. The genus *Schismope* is less widely distributed, 3 species of which live near the Snares Islands, whereas it has reached northward only to Japan; *Incisura* has been found only near New Zealand and the Snares Islands. The haliotids are shore dwellers; according to Pilsbry, Australia and the neighboring parts of the earth are to be considered as the center of distribution, because here the largest number of species and diversity of form is noticeable. They have probably reached the west coast of North America (Alaska—California) by way of eastern Asia; south of California only one species is known and one (*H. tuberculata* Linné) from Europe, none from the east coast of America.

The fissurellids as a whole inhabit especially the warmer seas, *Zeidora* mostly the Pacific Ocean, one species the West Indies, partly at considerable depth; *Emarginula*, with 2 species of the subgenus *Tugalia*, extends into the Magellanic region, *E. striatula* Quoy & Gaimard to the Snares and Bounty Islands, 2 species occur near Norway. *Scutus* inhabits the coasts of Australia, New Zealand in the south, Japan in the north, and Africa in the west. *Hemitoma* and *Clypidina* appear to be originally indigenous in the Indian Ocean, from where they have spread eastward into the Pacific, and—probably westward—to the West Indies. The few species of the genus *Rimula* live in most cases in the western Pacific Ocean, one near Mazatlan and one in the West Indies to the Atlantic Ocean, but *Cranopsis* occurs predominantly in the Atlantic; *Puncturella* lives mostly in cold or deep seas, *P. noachina* (Linné) appears to live not only in the Arctic Ocean but also in the Magellanic region and near Kerguelen, *P. spirigera* Thiele is holantarctic. The species of the genus *Diodora* are distributed over the warm and temperate seas. *Lucapina* is restricted to America, except *Cosmetalepas*, which is perhaps not closely related. Of the sole species of the subgenera *Fissurellidea* and *Pupillaea*, one inhabits Patagonia, the other South Africa. *Fissurella* s. s. lives on the west coast of South America washed by the cold current, on the other hand *Cremides* is distributed over the warmer seas; *Amblychilepas* is known from Africa and Australia, *Macroschisma* from Australia to Japan and Suez.

Scutellastra, the most primitive group of the patellids, seems to have originated from the Indian Ocean, because the species live mainly on the coasts of Australia and South Africa, only the larage *P. (S.) mexicana* Broderip & Sowerby having reached America (from Peru to California). The coast of southeastern Africa harbors the greatest abundance of forms of various sections, on the other hand, the subgenus *Patella* is confined to the Atlantic coasts. *Nacella* inhabits the southern cold seas from Kerguelen to Chile, but *Cellana* the warm parts of the

1130

Indian and Pacific oceans, only few species have reached New Zealand and neighboring islands, one each Juan Fernandez and Chile, none the Atlantic Ocean. of the Acmaeids, *Lottia* inhabits only the American west coast, on the other hand *Acmaea* with several species is widely distributed, but more predominantly in the Pacific Ocean; *A. rubella* (Fabricius), and *testudinalis* (Müller) have advanced into the Arctic and also into the northern Atlantic, and similarly *A. virginea* (Müller). Only few species of *Pectinodonta* are known from the deep sea of the West Indies and the Moluccas. The few species of the lepetids live partly in cold seas (*Lepeta*), partly in the deep sea (*Propilidium*).

Among the trochids the genus *Margarites* lives in the Arctic as well as the Antarctic Ocean, in the latter mainly the subgenera *Margarella* and *Submargarita*, but some species of *Margarites* s. s. have also been reported; it is uncertain whether the genus also occurs in warm seas. The related genera inhabit the warmer parts of the Indian and Pacific oceans, only *Solariella* extending with 3 species into the Arctic Ocean and being also represented in the Atlantic; *Calliotropis*, *Basilissa*, *Seguenzia* and *Guttula*, as well as *Gaza* have been found at considerable depths. *Calliostoma* is a genus living in all seas and depths, represented in the south by a few species in the Magellanic and New Zealand region, and by *C. occidentale* (Mighels & Adams) in the boreal Atlantic. *Gibbula* has a wide distribution but only on the coasts of the Old World, similarly *Cantharidus*, *Clanculus* and *Trochus*, as also the Umboniinae, except *Halistylus*, the Stomatiinae—except for one species, [*Stomatia coccinea* (A. Adams)] in the West Indies—and the Angariinae; *Monodonta* also has only a few species on the west coast of South America, but *Tegula* inhabits mainly the American coasts, with few species also Japan, the single *Cittarium* species inhabits the West Indies and *Norrisia* California. The few known species of the Skeneinae are scattered across all seas, represented in the Arctic Ocean by the group *Lissopira*, in the Antarctic Ocean by *Cirsonella*; this group and that of the Cyclostrematidae are still insufficiently known. Of the Liotiinae, *Liotia* inhabits the warm seas, *Cynisca* South Africa, *Leptothyra* with one species (*L. innocens* Thiele) reaches the holantarctic; on the other hand *Mölleria* the Arctic Ocean. *Bothropoma* is known only from the Red Sea and from western Australia; the Turbininae live in the warm seas, mainly in the Pacific and Indian oceans, only one species [*Astraea* (*Bolma*) *rugosa* (Linné)] in the Mediterranean Sea. Of the Phasianellinae, *Tricolia* has extended into the Mediterranean Sea.

Of the neritids, only the genera *Nerita*, *Magadis*, *Smaragdia* and *Pisulina* are entirely indigenous to the sea, and that only in the warm zones; other groups, such as *Vittoclithon*, *Neritoclithon*, *Pseudonerita*

and *Dostia* live mainly in brackish water, and several, especially *Theodoxus*, *Clithon*, *Neritina* and *Septaria* in freshwater; of these only the first has reached Europe. *Neritilia* also inhabits the freshwater in warm countries. The neritopsids, phenacolepadids and titiscaniids live in the warm seas. *Neritodryas* species leave the water and stay on neighboring bushes. The hydrocenids have completely adapted to aerial life and have lost the gill; they are found partly still on the seashore, partly in greater distance from the water; they have their main distribution on the coasts of Asia and the islands in the Indian and Pacific oceans; one *Hydrocena* species is found in Dalmatia and one on Tenerife and the Azores; they are absent from America. However the related helicinids have reached their richest development in the warmer parts of America, because such peculiar groups as *Pseudhelicina*, *Ceratodiscus* and the nonperculate Proserpininae are entirely limited to America, whereas others are more closely related to the forms living in Asia and on the Pacific islands; they are absent in Africa.

The species of the cocculinaceans have been found in most cases in great depth of various seas.

The distribution of the cyclophorids has some similarity with that of the helicinids, but the Asian forms and those of the Indo-Pacific islands considerably outweigh over the American Poteriinae; in Africa only a few species of the groups *Maizania*, *Chondrocyclus*, *Cyathopoma* and *Ditropis* (?) are native, in the Mediterranean region the genus *Cochlostoma*, and on the Canaries and Azores *Craspedopoma*, which is related neither to *Maizania* nor to *Cochlostoma*.

The viviparids inhabit freshwater, and from Asia, where they have by far the largest number of species, they have spread to Australia, Europe, Africa and North America. *Margarya*, living in Tali Lake, has a sculpture similar to that of the American *Tulotoma* as well as some southeastern European Tertiary species; *Rivularia*, found mainly in mountain streams of Hunan, is somewhat similar in the shape of the shell, as well as certain *Campeloma* species, but this is not to be interpreted as a sign of closer relationship. *Neothauma* is a form from Lake Tanganyika. The origin of the ampullariids is less clear; their most primitive forms may be the west African *Afropomus* and *Saulea*, perhaps also the South American *Asolene*; they have reached the largest number of species in South America; the sinistrally coiled group *Lanistes* is restricted to Africa, whereas *Pila* is distributed from there to the Philippines. *Lavigeria* is one of the "thalassoid" snails of Lake Tanganyiaka.

The valvatids inhabit the freshwater of the northern hemisphere, in the south reaching to North Africa and Central America (Mexico and Guatemala).

The land-snail group of the Pomatiasids inhabits 2 separated regions: the Pomatiasinae mainly the Indo-African region, but with a few species of the genera *Pomatisas*, *Tudorella* and *Leonia* they reach into the Mediterranean region together with the Canaries; on the other hand, the Chondropomatinae extend to the West Indies and the neighboring parts of the continent.

Of the Littorinacea, *Lacuna* seems to be confined to the northern seas, the only *Mainwaringia* species is known from the Indian coast; it is uncertain whether *Benthonella*, living in the deep sea, is related to *Lacuna*. *Laevilittorina*, which resembles *Lacuna* in the shape of the shell, inhabits the cold southern seas, likewise *Pellilittorina*; but *Haloconcha* is known from the northern Pacific (near Alaska and the Pribilof Islands) as well as from the South Sea (near South Georgia and Macquarie Island). The genus *Littorina* is widely distributed in the littoral zone, with few species extending into the Arctic Ocean; the subgenus 1132 *Littorinopsis* and the genus *Tectarius* prefer the tropics. Species of the genus *Cremnoconchus* have left the shore and have climbed into the coastal mountains of India.

The small group of acmids is confined to Europe and North Africa. The hydrobiids, however, which with the exception of *Hydrobia* inhabit freshwater, are very widely distributed. Of the European genera *Paladilhia* and *Plagigeyeria* most species occur in springs or caves, *Pseudamnicola* lives mainly in the Mediterranean region, *Sadleriana* in southeastern Europe and similarly *Horatia*. *Lyogyrus* is found not only in North America but also in New Caledonia. The Littoridineae inhabit mainly the southern hemisphere (South and Central America, Australia, New Zealand and a few islands), the Amnicoleae North and Central America, the Benedictieae Lake Baikal, the *Lithoglypheae* East Asia, and only *Lithoglyphus* also Europe. The Truncatellinae are widely scattered, some of them leave the water and stay on the shore, *Geomelania* has climbed into the mountains of the Greater Antilles. *Hydrococcus*, known only from the Swan River in Australia, was previously probably more widely distributed and stands close to the Stenothyrinae, which extend from Australia to South and East Asia. Of the Bithyniinae, the subgenus *Gabbia* occurs from Australia, by way of India to Africa and southern Europe, *Bithynia* being more western in Europe and Asia Minor.

The micromelaniids were originally distributed over the largest part of Asia from Lake Baikal to southeastern Europe (Ohrid Lake), and hence the Recent species live mainly in these lakes and in the Caspian Sea; probably the genus *Emmericia* also will have to be placed here, but hardly the Mexican *Emmericiella*.

The rissoids inhabit all seas, generally in shallow water, often on seagrass; *Cingula* reaches the Holantarctic and the Arctic Ocean — the relationship of *Assiminopsis* found in the deep sea is uncertain. *Alvania* and *Rissoa* are found mainly in northern seas, *Merelina* near New Zealand, *Zebina* and *Rissoina* in the warmer zones. Of the Barleeinae, *Barleeia* and *Eatoniella* species have been found in various seas, the former more in the northen, the latter in the south (Kerguelen to South Georgia), likewise *Boogina* and *Skenella*; *Eatoniopsis* is holantarctic. The hemistomiinae live in brackish water of the Australian region. The Assimineinae, which have lost their grlls, are found in most cases in or near brackish water of the higher littoral zones, and are widely distributed; on the other hand, the Omphalotropidinae have entirely climbed on land and are confined to the islands in the Pacific and Indian oceans. The groups united in the family Adeorbidae, which in part are somewhat doubtful, are scattered over all seas, one species in the Holantarctic. The northern *Skeneopsis* is represented in the south by *Microdiscula*; *Homalogyra* and *Rissoella* also occur in the north and in the south; *Trochaclis* is known only from the Holantarctic.

Of the turritellids, *Tachyrhynchus* inhabits the northern parts of the Atlantic and Pacific oceans to the Arctic Ocean, in the south mainly the Kerguelen, *Turritellopsis* the Holantarctic and the northern Atlantic, *Turritella* the warm and temperate zones, and similarly the few species of the Mathildidae, of which one species occurs near New Zealand; the solariids, vermetids and caecids also live in the warm seas.

The melaniids inhabit the freshwater of warm and temperate zones. In America we find 3 groups: *Pachychilus* (Melanatriinae) and *Hemisinus* in Central America and in the northern part of South America, but the Pleurocerinae in North America; the remaining Melantriinae in southeastern Asia and on the islands, in Madagascar and in western Africa. The distribution of the Melanopsinae is peculiar; of them *Faunus* lives in Indochina and a few islands, *Fagotia* in the lower reaches of the Danube and *Melanopsis* not only in the Mediterranean region but also on New Calendonia and New Zealand. The genus *Semisculcospira*, which is most closely related to Pleurocerinae, inhabits eastern Asia. *Amphimelania* is a southern European group. Of the Paludominae, *Paludomus* is distributed in South Asia, the Sunda Islands, and the Philippines, *Cleopatra* in Africa and Madagascar; near these stand the "thalassoid" Paramelanieae of Lake Tanganyika. The numerous species of Melaniinae are to be found from Oceania to Africa, the West African genus *Pachymelania* being most closely related to the American genus *Hemisinus*.

The planaxids are shore dwellers of tropical or subtropical lands, in most cases on stones in the vicinity of tide pools or on mangrove roots;

Quadrasia, found in freshwater in the Philippines, probably belongs to the Melanopsinae. The Potamidinae live in brackish water of warmer lands, mainly in the Indo-Australian region, *Tympanotonus* in West Africa similarly the Batillariinae, of which *Lampanella* is found in the West Indies, *Rhinocoryne* on the west coast of South America. Of the Finellidae, *Cerithidium pusillum* (Jeffreys) lives in the Mediterranean Sea, most species in the Indo-Pacific Ocean. *Litiopa*, because of its life on floating algae is distributed over all warm seas. The numerous species of the Cerithiinae are indigenous to the warm and temperate seas, the only *Campanile* species living near Australia. Of the cerithiopsids, *Cerithiopsilla*, *Cerithiella* and *Eumetula* reach the Holantarctic, one species each of the two latter ones also the Arctic Ocean; the only *Laeocochlis* species lives in the North Sea. Of the triphorids, only one species occurs near Europe, one in the Holantarctic, numerous species in the warmer seas. The distribution of the scalids is similar, of which a couple of species [*Acirsa borealis* (Beack) and *Scala (Boreoscala) groenlandica* (Chemnitz)] were found in the Arctic Ocean and a few in the Antarctic Ocean as well as in the deep sea. Entirely different is the distribution of the janthinids which are able to lead a pelagic mode of life because of their foam raft and have thus reached across all warmer seas. Of aclidids some species are known from the northern Atlantic Ocean and a few, some of which are doubtful, from other seas. The melanellid genus *Niso*, the shell of which is similar on the one hand with *Hemiaclis* and on the other hand with certain pyramidellids, is restricted to warm seas, whereas the other genera with numerous species are distributed over all seas, a few reaching the Holantarctic and one (*Liostraca stenostoma* Jeffreys) Greenland. The parasites related to the melanellids are, like their hosts, generally scattered in warmer zones, only *Entocolax* having been found in the Arctic Ocean and near Southern Chile. Of a few small pyramidellids (*Odostomia* and *Angustispira*) it has been demonstrated that they live ectopasitically on certain bilvalves; it is not known whether it is true of all species of the family, especially also the larger ones. Most of them are found in the warmer seas, a few —mainly *Odostomia*—in the cold Antarctic Ocean (Tierra del Fuego– Kerguelen) and (*Odostomia* and *Menestho*) in the Arctic Ocean. *Kleinella* lives in most cases in the Pacific Ocean—the Atlantic *Euparthenia* does not seem to be closely related to it.

Of the fossarids, only few species are known from various, in most cases warm seas, one *Couthouyia* from New Zealand and the Snares Islands; just where a few species from that area which have been called *Fossarus* belong, is uncertain without a knowledge of the animals. *Vanikoro* is native in the Indo-Pacific Ocean, except for a few somewhat

doubtful West Indian species. In contrast to the amaltheids living in the warm seas, the trichotropidae are found mainly in the cold seas, *Neoconcha*, *Trichoconcha* which is similar to be northern *Torellia*[1] and a couple of *Trichotropsis* species are holantarctic. *Capulus* extends from the tropics into the Antarctic Ocean (*C. subcompressus* Pelseneer). Of the calyptraeids, only one *Crepidula* species has been found in the Arctic Ocean, most live in warmer seas, the only *Neojanacus* species near New Zealand. The Strombacea also inhabit mainly the warm seas, but the struthiolariids are restricted to the southern regions from Australia to Kerguelen and South Georgia, and a couple of *Aporrhais* species reach Greenland.

The heteropods are the only prosobranchs which are completely adapted to active swimming and have shifted to a pelagic mode of life, this adaptation has reached its highest degree in the pterotracheids. The species are partly distributed over all warmer seas, in part are known only from limited areas.

Of the naticids, *Globularia* and *Sigaretus* are native in warm seas, and largely also the genus *Natica* which is provided with a calcareous operculum, but 2 species [*N. bathybii* Friele and *N.* (*Cryptonatica*) *clausa* Broderip & Sowerb] extend into the Arctic Ocean. The groups with a horny operculum are met with partly in the warm and temperate seas, and partly entirely or predominantly in cold water, also in the deep sea, *Friginatica* in the south near Kerguelen and in the Magellanic region, the related *Lunatia* extends into the Arctic Ocean, *Amauropsis* in the south as well as in the north, *Frovina* in the Holantarctic. The lamellariids are inhabitants of cold seas to a still greater extent of with *Capulacmaea*, *Velutina*, *Onchidiopsis* and *Marsenina* in the. north, *Marseniopsis* and *Lamellariopsis* in the south, only *Caledoniella* and *Lamellaria* avoiding the cold water. This is also true of all cypraeids, which in most cases are found in warm seas, a couple of *Trivia* species have extended farthest into the cooler regions (Norway, New Zealand)— likewise the Doliacea, of which *Oocorys* inhabits the deep sea.

Like these most highly developed taenioglossans, many stenoglossans live on coral reefs. Of the muricids, the genus *Columbarium* inhabits generally the deep sea; *Trophon* not only reaches the Magallanic region with several species, but also the Holantarctic, the deep sea, in the north the Arctic Ocean, in which a few *Nucella* species are also found. The columbellids predominantly inhabit the warm seas and live in shallow water on sand or stones, but a few species more alo found at considerable

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[1] *Torellia* is the correct spelling; *Torella* on original p. 132 is apparently an unnoticed error —Editors.

depths; some species have been found in the south near the Snares Islands and Bounty Islands, one [*Pyrene* (*Alcira*) *transitans* (Murdoch)] also near the Campbell Island and few species near Patagonia, only one [*Pyrene* (*Astyris*) *rosacea* (Gould)] extends into the Arctic Ocean. *Buccinum undatum* Linné is stated to live on every kind of substratum, from the coast to considerable depths, and hence the family also seems to have easily adapted to the most diverse conditions and can be encountered in a considerable number of species not only in warm but also in cold seas; represented in the north are the genera *Buccinum*, *Liomesus*, *Mohnia*, *Beringius*, *Volutopsis*, *Plicifusus*, *Sipho* and *Neptunea*, in the south *Prosipho*, *Pareuthria*, *Chlanidota*, *Neobuccinum*, the groups *Chlanidotella*, *Proneptunea* and *Meteuthria*, also *Glypteuthria*, *Savatieria*, *Antistreptus* and *Fusinella* —the northern forms are in most cases much larger than the southern. The Galeodidae, which in most cases have large and strong shells, are absent from the cold seas, the same is true of the small Nassidae, of which only a couple of species live in the deep sea, and the Fasciolariidae. The Pseudolivinae are at present native near West and South Africa, except for the less closely related *Zemira* from East Australia; the Olivinae are restricted to the tropics, as also the Harpidae and as a whole also the Mitridae, of which only individual species occur at greater depth, and the Vasidae, the genera of which are perhaps not closely related to one another. *Metzgeria* and *Ptychatractus* live in the North Atlantic Ocean. The volutids largely live near the coasts of warm lands and burrow into sand at low tide but some groups (*Volutocorbis*, *Fusivoluta*, *Phenacoptygma*, *Neptuneopsis*, *Harpovoluta*, *Guivillea* and *Tractolira*) in the deep sea, some of them in the Antarctic Ocean; *Volutomitra* is represented with a few species in the Antarctic Ocean between South Georgia, Australia and Kerguelen, and one species [*V. grönlandica* (Möller)] in the North Atlantic Ocean. *Cancellaria* species are in most cases found in shallow depths of warm seas, the few *Admete* species are on the other hand mainly in the polar seas, one in the deep sea near Mexico and one near East Africa; *Benthobia* seems to occur in the deep sea not only on the American side but also on the African side of the Atlantic Ocean (cf. "*Lacuna*" *cossmanni* Locard). The marginellids are found not only in the tropics but also in cool seas, numerous species near South and West Africa and in the West Indies, partly at considerable depth, in the Mediterranean Sea and near the Iberian coast, one small species in the Holantarctic. Among the numerous species of the Turridae, of which in most cases is known only the shell, providing little information for classification into the genera, many have been encountered in warm and shallow water, but many also at more or less considerable depth and in few an the polar seas. In the Arctic Ocean almost

exclusively species of the genus *Lora* are present (in addition to one *Mangelia* and one *Taranis* species), in the Antarctic Ocean a few species which are perhaps rightly placed in *Lora*, besides there are a few species of *Thesbia*, *Drillia*, *Pleurotomella* and probably *Leucosyrinx*. Almost all of these genera have also been found in the deep sea, and with them especially *Pontiothauma*, *Gemmula*, *Ptychosyrinx*, *Gymnobela*, *Typhlosyrinx*, *Eubela*, *Gymnobela*, *Borsonia*, *Bellardiella* and *Mangelia*. The Coninae live mainly in tropical seas, living in holes and cracks of reefs, rarely at considerable depth; the distribution of the terebrids is similar.

Of the actaenoids, species from great depth and from the Antarctic Ocean have been placed in the genus *Actaeon*, but without knowledge of the animals and it is very doubtful if this is correct; the true species appear to live near the coast, mostly in warm regions, but *A. tornatilis* (Linné) extends to the Lofotens. *Solidula* inhabits the Indo-Pacific region, southward to New Zealand, but is missing near America, likewise *Bullina*; *Neactaeonina* appears to be restricted to the Antarctic Ocean. The ringiculids and hydatinids are native in warm seas, the diaphanids on the other hand mainly in cold seas, *Toledonia* except for one northern species and *Newnesia* in the Antarctic. The bullariids are plant eaters and are encountered mostly on sand banks at the river mouths or in brackish water pools, in deep water of warmer seas; the atyids have similar habits, *Cylichnium* appears to occur only in the deep sea. *Acera* feeds mainly on seagrass and it is widely distributed with few species which are mostly found on muddy substratum of the coast. The small Retusidae inhabit the ocean floor to considerable depth and feed in most cases on foraminiferans, similarly the Scaphandridae, large *Scaphander* species also overpower much larger prey, such as *Dentalium*; these groups are in part also represented in the cold seas, in the Arctic Ocean *Retusa*, *Cylichna* and *Scaphander*, in the Antarctic Ocean only *Cylichna*. Species of *Philine* also occur in both polar seas.

Broad lateral margins of the foot are used for swimming by some cephalaspideans, such as *Cryptophthalmus* (cf. Fig. 488), *Acera*, *Gastropteron*, but the animals mostly stay on the plants, which perhaps in addition to small animals, also serve as their food; *Gastropteron sinense* A. Adams seems to be best adapted for a pelagic mode of life. The Aglajidae swallow animals which they can overpower, and in most cases are native in shallow depths of warmer seas. The aplysiids are plant eaters, living in shallow water of tropical and temperate zones, only one species (*Dolabriffera holbölli* Bergh) near Greenland; some of them are able to swim, *Notarchus* by contractions of the fused parapodia which expels water from the respiratory opening, so that the animal is driven

forward like the cephalopods. A completely pelagic mode of life has been adopted by the pteropods which are found partly in all seas, partly only in warm regions; in the Arctic Ocean *Spiratella helicina* (Phipps) and *Clione limacina* (Phipps) are especially common; the thecosomes feed mainly on microscopic plankton, the cymbuliids also on copepods and sagittae, the pterotans not only on various small animals but also on larger thecosomes.

The sacoglossans live in shallow water on seagrass and other plants which serve as their food, only *Elysia viridis* (Montagu) and *Limapontia capitata* (Müller) reach Finnmark and the Murman coast; the group is not represented in the cold southern seas. The notaspideans, which swallow all available prey with their large buccal mass, occur in warmer seas, partly on the shore, partly at greater depth; one species [*Bouvieria platei* (Bergh)] was found near Chile and on the Burdwood Bank in the Antarctic Ocean.

Odhner observes in connection with the naked opisthobranchs, that the possession of homogeneous jaws is common to the Doridoxidae and Bathydorididae along with the Arminacea and Dendronotacea, to which the Duvauceliidae and Dotonidae are allocated, and that this group which as Gnathodoridacea may be placed opposite the jaw-less Eudoridacea, is represented only in the northern and southern colder seas and in the deep sea, whereas the Eudoridacea have a cosmopolitan distribution. The genera *Cadlina* and *Aegirus* are native mainly to the cold seas, and similarly *Cuthona*, the Antarctic *Prodoridunculus* is related to the northern *Doridunculus*, corresponding to the northern *Goniaeolis* in the south are the Charcotiidae with the genera *Charcotia*, *Pseudotritonia* and *Telarma* Odhner 1934, *Notaeolidia* is known only from the Antarctic Ocean. The fish-shaped phyllirrhoids lead an entirely pelagic life in warm seas, the tethyids from time to time; *Scyllaea pelagica* Linné, *Spurilla sargassicola* (Kroyer), *Glaucus* and one *Corambella* species live on sargassum.

The ellobiids, which are phyletically considered the oldest nonoperculate pulmonates, are in most cases shore dwellers but *Pythia* is found in forests near the coast, and *Carychium* is to be encountered far from water under decaying wood and fallen leaves; other groups in most cases live in water or in the tidal zone, their reproduction is also correspondingly different. The oldest forms may have developed during the Carboniferous along the Indian Ocean and were distributed over the accessible coasts; most of them are still native to warm zones, *Carychium* species being found from East Asia (Japan, Philippines, Java) through the entire Palaearctic region as well as in the United States to Mexico; the closely related *Zopeum* occurs in Karst caves; species of *Pseudomelampus*,

Ovatella and *Alexia* have reached the European coasts, as also *Otina*. Whereas the few species of the amphibolids are restricted to coasts of the Indo-Australian area, the siphonariids are widely distributed, especially in warm zones of the southern hemisphere, but one species is found in the cold southern sea to Kerguelen and Patagonia.

Among the freshwater pulmonates, the chilinids are restricted to the more southern parts of South America, the latiids to New Zealand, the other families however have spread over all parts of the world, some genera and subgroups occur only in certain regions; the very peculiar *Lanx* only in North America, *Isidora* from New Zealand and Australia to Africa and southern Europe, *Planorbula* in America and northeastern Africa. *Anisus* is widely distributed, especially the subgenus *Gyraulus*; *Segmentina* is absent from America; *Choanomphalus* lives only in Lake Baikal, as also *Pseudancylastrum*; *Acroloxus* in Europe; of the ancylines, *Ferrissia* has the widest distribution, but is absent from Europe, where it is replaced by *Ancylus*; *Amphigyra* and *Rhodacmea* are North American groups.

The oncidiids are shore dwellers, presumably having arisen from a shell-bearing southern littoral form (Actophila); of the genera, *Oncidiella* has the widest distribution, extending in the south to Campbell Island and Patagonia, in the north to Alaska and southern England; *Oncis* is limited to the Indo-Australian region, similar but extending somewhat farther is *Oncidium*. Of the two families of the soleoliferans, the Rathouisiids are found only in Southeast Asia, on the nearby islands and in eastern Australia, on the other hand the vaginulids are much more widely distributed and inhabit Ethiopia and the warm parts of America in the palm zone, a few species found in Australia may have been introduced.

The genus *Succinea* is found in all continents and on many islands, one species in Greenland, it is absent in New Zealand; the related genera are restricted, *Homalonyx* to South and Central America, *Hyalimax* to some islands in the Indian Ocean and Indochina; the athoracophorids, which probably are related here, inhabit the Admiralty Islands, New Caledonia, the New Hebrides, Australia and New Zealand.

The home of the Achatinellacea are the islands of the Pacific, few species having reached westward to Mauritius, others have spread eastward and have reached the Galapagos and Juan Fernandez, few have reached New Zealand; the amastrids and partulids also live only on Pacific islands. The distribution of *Cochlicopa* is quite different; the northern part of Asia and North America, the whole of Europe to North Africa, Madeira and the Azores, the related *Azeca* lives in the Mediterranean region and Central Europe to England. The small vertiginids have spread mainly over the lands of the northern hemisphere, especially

1138

Eurasia, but in part have also extended more or less far southward; Pilsbry considers the following as endemic; *Gibbulina* is South America, *Fauxulus* in South Africa, *Campolaemus* in St. Helena, *Costigo* on Indo-Malayan and Melanesian Islands, *Cylindrovertilla* in tropical Australia and Melanesia, *Lyropupa* on the Hawaiian Islands, *Pronesopupa* and *Pupoidopsis* on the latter and Polynesia. The valloniids also inhabit mostly the northern hemisphere, only *Pupisoma* and *Strobilops* have also extended into the southern continents. The Enidae are completely absent from America and almost entirely from Australia; the Ethiopian forms belong to the Napaeinae without spermatophore sack. The clausiliids perhaps also spread out from eastern Asia, only the small group of *Nenia*, *Peruinia*, *Temesa* has reached South America, and *Macroptychia* with few species has reached Ethiopia; the great majority of species are found in Asia and Europe, some of the genus *Boettgeria* on the Canary Islands.

Of the ferussaciids, the genera *Hohenwartiana*, *Ferussacia*, *Cryptazeca* and *Calaxis* are indigenous entirely or predominantly to the Mediterranean region, *Caecilioides* being considerably more widely distributed not only on the East African islands, in southern Africa, in India, on the Philippines, and perhaps introduced on New Caledonia and the Hawaiian Islands, but also in the West Indies; *Coelostele* is also found outside the Mediterranean region in Mexico and India. According to Pilsbry, a species found in the Eocene of Italy proves that the genus probably developed in the European Mesozoic, but its point of origin may have been further south, hence in Africa, where according to Pilsbry's assumption the subulindis also developed. There the latter have achieved their richest development, and have spread with some groups westward and eastward across the warm zones; probably the ancestral forms of the Megaspiridae also arose in Africa, but became extinct as in Europe (*Palaeostoa* Andreae), so that at present they are found only in Brazil, as well as in Australia (*Coelocion*) New Guinea, and Obi (*Perrieria*). On the other hand, the achatinids are completely confined to Africa. The most primitive forms of the Oleacinidae live only in tropical America, from which one may conclude that it was their original home, but European species are known from the Cretaceous on, and Pilsbry therefore considers it probable that they have originated from the Archhelenis. Perhaps the testacellids of the Mediterranean countries are also to be derived from such ancient oleacinids.

Because the very ancient endodontids are distributed over all continents, their origin is uncertain, although the great richness of forms of the Indo-Australian region may indicate that they arose there; at any rate the Discinae, indigenous to Europe and North America, are probably

not very primitive. They are strongly represented in New Zealand, the southernmost form being *Notodiscus hookeri* (Reeve) on Kerguelen.

1139   The polygyrids, placed by Pilsbry in the Helicacea, live in North America to Mexico and Honduras and on some islands, the Sagdidae mainly on the Antilles and in Central America; their origin in Asia seems to be out of the question. On the other hand, *Sculptaria* is indigenous only in South Africa, *Corilla* in India, and *Plectopylis* in India and China; Degner has emphasized the similarity of the mantle organs and the reproductive apparatus of these genera; the presence of lateral furrows on the foot in the first of these alone would hardly contradict their relationship. The zonitids are almost entirely limited to the northern hemisphere, aside from a few introduced species and perhaps *Zonitoides* species in Brazil. The home of the systrophiids is in South America, beyond whose borders only a few species extended. The vitrinids have probably spread from East Asia and have extended mainly westward, so that they have advanced through Arabia to East Africa and through Europe to the Canary Islands and the Azores, only few species have migrated eastward to North America, and one species related to the Philippine *Vitrinoidea* southward to New Zealand. The situation with the arionids is similar, the most primitive form of which (*Binneya*) having a shell similar to *Vitrina* and living in California and Mexico; the genera extended partly somewhat more toward the east, partly more or less toward the west, so that they are found not only in Asia (*Anadenus*), but also in western Europe and in North Africa. *Oopelta* may be considered a branch of the arionids, which has migrated into West and South Africa. The distribution of the philomycids is considerably different, proceeding perhaps from western North America, having spread across the United States and Central America, and on the other hand (*Meghimatium*) to East Asia and the nearby islands, but did not extend further to the west. The original home of the limacids seems to be Asia, from where they have spread mainly toward the west across Europe and North Africa to the Canaries; *Agriolimax* has the greatest distribution, in the south occurring in Abyssinia, a few species also occurring in North America— in addition some species of the genus *Milax* also have become widely introduced. The trigonochlamydids are restricted to Asia Minor.

    The most primitive group of the ariophantids is very widely distributed; *Kaliella* in the Indo-Pacific region, *Guppya* and *Habroconus* in tropical America, and *Euconulus* in different parts of the northern hemisphere. Related groups inhabit more or less narrowly delimited areas, and none of them has reached Europe and America; the family is most strongly represented in Africa, South and East Asia and on the islands in the Indian and western Pacific Ocean.

The acavaceans, proceeding from the ancient "Gondwanaland," spread over the lands of the southern hemisphere, having become more or less modified, the South African *Trigonephrus* is to be seen as the most primitive form; the Madagascan and Australian groups show considerable differences, the South American strophochilids are related to the dorcasiids, but whether the Chilean *Macrocyclis*, the shell form of which is similar to that of *Dorcasia*, is uncertain.

According to Pilsbry, the bulimulids have developed in South America, where they are most richly diversified, and have probably migrated across Antarctica (?) toward the east, where *Bothriembryon* lives in Australia and Tasmania, *Placostylus* from New Zealand to New Guinea, Solomon and Fiji Islands; but the South and West African genera *Prestonella* and *Aillya*, recently placed in bulimulids, must have come across the Archhelenis. However, the family has also advanced northward across Central America and the Antilles into the southern United States; in this region the cerionids and urocoptids have originated. Because the helicaceans undoubtedly arose from the same root as the acavaceans, they would also have had the same original home, from where they migrated further northward and then gradually toward the east and west, so that they reached all continents with various groups; they are most sparsely represented in tropical Africa, mainly in the mountains of Abyssinia and further south.

The affinities assumed by Baker of the haplotrematids, which are native in North America and the West Indies, with the paryphantids, are still unclear; the latter are mostly distributed in southern lands, a few genera in New Zealand, others in Australia and the islands of the Pacific as well as in South Africa, where the aperids have originated. The great resemblance of the South American *Martinella* with *Imperturbatia*, which is known only from the Seychelles indicates that both groups have originated from a common ancestor, which presumably lived in Africa and is now extinct; the latter also may have stood close to the *Helix*-shaped genera *Tayloria* and *Scolodonta*. The streptaxids currently live not only in Africa, where they have produced a very large variety of forms, and in South America, but also in South and East Asia to the Philippines.

The scapophods are exclusively inhabitants of the sea and burrow into the substratum. According to Pilsbry, the genera are as a whole distributed in all seas, the subgroups are more or less localized. Of these *Siphonodentalium, Fissidentalium, Heteroschima, Bathoxiphus, Rhabdus, Episiphon* and *Compressidens* are almost entirely deep-sea forms; *Dentalium* s. s., *Antalis* and *Graptacme* are found in most cases on the shore. Few species occur in the Arctic Ocean, others in the Holantarctic.

Of. the very ancient taxodonts, the nuculaceans are burrowing animals and hence live in sand or mud; because they find such substratum at the most varied depths, they are correspondingly distributed, but, as in the case of the scapophods, some genera and subgroups occur in limited regions. A few *Nucula* species extend into the North Atlantic Ocean to Greenland, *N. tenuis* (Montagu) is circumpolar, only one small deep-sea species is known from the Holantarctic. Most of the malletiids have been found in deep or cold water, as also *Ledella* and *Yoldiella*; *Portlandia isonota* (Martens) from Kerguelen is very similar to *P. arctica* (Gray) from the Arctic Ocean. *Yoldia* and *Leda* are widely distributed like *Nucula*, likewise *Solenomya*. Most of the arcids have a well-developed byssus, with which they attach themselves to stones and rocks, so that they are mostly found in not very deep water, but some groups, especially *Acar* and *Bathyarca*, have more or less rudimentary byssus, in adaptation to life at considerable depth; only the small *Scaphula* species have migrated into rivers of India. Of the limopsids, *Limopsis* is mainly distributed in the deep seas and extends into the cold seas, the *Pleurodon* species in most cases in shallow depth; the remaining groups are almost exclusively inhabitants of the southern seas between Antarctica and Australia, South Africa and Patagonia, one species of *Philobrya* has been found near Juan Fernandez and one species near California. The *Glycymeris* species have completely lost their byssus and have acquired a burrowing foot similar to that of nuculids, they live in most cases in warm seas at shallow depth.

The distribution of the mytilids is similar to that of the arcids, the *Dacrydium* species being native to the cold and deep seas, most groups live in warmer and shallower water, a few *Musculus* and *Crenella* species extending into the Arctic Ocean; only a few small species are found in the freshwater of Southeast Asia. The Pteriacea are inhabitants mainly of the warm parts of the Indian and Pacific oceans, only few species have reached the West Indies and Europe.

The genus *Dimya* also lives in the Pacific Ocean from Australia to Japan, one species in the West Indies. The Amussiinae are mostly indigenous to cold and deep seas in contrast to the Pectininae and Spondylinae, which are almost completely lacking in cold seas, only *Pecten* (*Chlamys*) *islandicus* (Müller) living in the Arctic Ocean. The limids live in the warm and temperate seas, a few large *Acesta* species in the Pacific deep sea, only the *Limatula* group extending into the polar seas. Species of the genus *Anomia* are scattered over all seas, *Placenta* is restricted to the Indo-Pacific region. The ostreids live on the coasts of the warm and temperate zones.

The trigoniids, which were widely distributed in the Mesozoic, are

at present restricted to few species of the genus *Neotrigonia* near Australia. As far as the freshwater unionaceans are concerned Pilsbry has expressed the opinion that the original group split into 2 branches, one of which, the mutelids, developed in the south on the Gondwana-Archhelenis continent, and the other, the unionids, in North America and Asia. The genus *Diplodon* probably originated in South America and has—perhaps across Antarctica (?)—spread to New Zealand, Australia and New Guinea, on the other hand the Mutelinae with species of the genus *Anodontites* have reached Mexico and with other groups, across the Archhelenis, have reached the east and distributed in tropical Africa. The distribution of the aetheriids is similar, of which one species, *Pseudomulleria dalyi* (E. Smith) has reached to India. Like the margaritanidae, the Unionidae essentially inhabit the northern hemisphere, but some groups have extended southward, especially into Africa, where they have arrived from Asia; they reached their greatest richness of forms in North America, East Asia, and the Sunda Islands.

The astartids are native mainly in the North Atlantic into the Arctic Ocean, one *Digitaria* species has been found near Port Alfred and one *Astarte* in the Holantarctic; *Crassatella* inhabits the warmer seas. The small genus *Cuna*, the systematic position of which is not clear, occurs near Australia, New Zealand and South Africa (Port Alfred). The carditids live in most cases in warm seas not far from the coast, only the group *Cyclocardia* having advanced into the Arctic and Antarctic regions; the distribution of the condylocardiids is predominantly southern.

Only few species of the Sphaeriacea live in brackish water of the coasts, most of them have wholly migrated into freshwater. The more or less large, thick-shelled corbiculids have spread across the tropics, radiating presumably from South Asia; the group *Cyanocyclas* is South American, and the American groups of the genus *Polymesoda* extend into the southern United States; the smaller sphaeriids have reached all continents, especially with the genus *Pisidium*; *Byssanodonta* = *Eupera* is known alive only from Africa and South to Central America; *Sphaerium* is absent in the Indo-Australian region, but one species has been described from New Zealand.

The very variously sized Kellyellidae inhabit the deep sea, the few species of the isocardiids the warm seas in shallow depth. The cyprinids are at present represented only by one species in the northern Atlantic to Greenland and the Murman coast, on the other hand the libitinids live in rocky and coral reefs of warm seas. The cyamiids are a group of small species in the southern seas from the Holantarctic to Australia, most of the neoleptonids also occur in the south, but some also on the European coasts. The gaimardiids are also completely southern, and are probably closely related to the cyamiids.

The Dreissenidae live in freshwater of Africa, Europe to East Asia and the central parts of America, their fossils are known from the European Miocene; their origin is unknown.

Of the Lucinacea, in most cases small Thyasirinae are found mainly in cold and deep oceans, the Ungulininae mostly in warm seas, but 2 *Diplodonta* species live in the Arctic Ocean; the same is true of Lucinidae, only few of which occur in deep or cold water. Some genera of the Erycinacea are widely distributed, some of them extending to the polar seas, others are known only from limited areas. The chamids are absent in the cold seas. Of the cardiids, *Serripes* is native in the Arctic Ocean and the boreal parts of both oceans, few *Cardium* species also extend into the Arctic Ocean, but most of the species live in the warm seas, the tridacnids only in the Indo-Pacific region. The species-rich stirps Veneracea inhabits the oceans of warm and temperate zones, mostly at shallow depth, only a couple of *Liocyma* species extend into the Arctic Ocean—similarly the Mactracea, of which only one *Spisula* species is known from the Arctic Ocean. Most of the Tellinacea live close to the coasts of warmer lands, *Iphigenia* and *Egeria* in brackish water of America and West Africa, *Profischeria* in rivers; some *Macoma* species are native in the Arctic Ocean. Most of the solenids live in sand in the tidal zone of warm and temperate lands, only one species *Siligua media* (Gray)] is reported from the Arctic Ocean; *Novaculina* and the glaucomyids have penetrated into South and East Asian rivers. The saxicavids live partly only in the Arctic Ocean, but the genus *Saxicava* is distributed in all seas, in the south to Kerguelen, and *Panopea* inhabits deep waters of various seas. The Myacea are found in shallow depth, *Aloidis* predominantly in warmer seas, *Anticorbula* and *Erodona* in South American rivers, the few *Mya* species in the arctic and boreal sea. The Gastrochaenacea and Adesmacea, which in most cases bore into solid bodies, extend from the tropics to temperate zones, one *Teredo* species to the Murman coast. The Anomalodesmata are in most cases inhabitants of the deep sea or cold seas, but a few species of some genera occur in shallower and warm water, as also some genera, such as *Myochama*, ·*Chamostrea*, *Parilimya* and the clavagellids.

The primitive shell-bearing cephalopods certainly lead a mode of life similar to that of the few *Nautilus* species presently living in the Indo-Pacific region. These generally live in shallow depth near the bottom, being moderately capable of swimming movement with the help of their cone-shaped funnel, and of crawling on their arms. At the same time the orthoceratites may have lived more pelagically; at all events they did 1143 not stick in the substratum with the end of the shell. All cephalopods live on animal foods, especially on crustaceans. *Spirula* lives bathypelagically

in the warm seas, in the south to New Zealand; it can swim forward and backward with the fins and the funnel. The sepiids are littoral animals, which are absent only from the polar seas, on the other hand *Rossia* species occur not only in the Arctic Ocean, but also in the deep sea, the pelagic Heteroteuthinae are distributed in the warmer seas. The Loliginacea and Architeuthacea also lead a pelagic mode of life, some of them at considerable depth and are then not seldom provided with light organs; some of them have achieved considerable ability to swim and thus a very wide distribution, especially in the warm and temperate zones. Only few are known exclusively or predominantly from cold seas, *Psychroteuthis* and *Alluroteuthis* from the Antarctic Ocean, *Crystalloteuthis* from the Antarctic and the northern Pacific; *Gonatus*, *Moroteuthis* and *Ommatostrephes* occur in the cool seas of the north and south.

Of the octopods, the Vampyroteuthacea and Cirroteuthacea are inhabitants of the deep sea; the *Opisthoteuthis* species may generally live on the bottom, others lead a more pelagic life. The Bolitaenacea and Argonautacea also lead a pelagic life, the former at considerable depth. Among the Octopodacea, the Ozaeninae and Octopodinae differ from the Bathypolypodinae, which in most cases occur in the deep sea and in cold oceans, because they live in the vicinity of the shore.

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It is to be assumed that the ancestral metazoans lead a pelagic existence, their movement being performed solely by epithelial cilia, as is shown by the ctenophorans, whereas the ancestral bilateral animals became bottom dwellers with creeping locomotion. From such animals, probably now entirely extinct, which presumably had a body form resembling that of the turbellarians, the ancestral forms of the mollusks have developed, and the formation of a dorsal shell may have served at first as a protection from the wave action at the surface, hence it is likely that the animals lived near the coast. The muscular, sucker-like foot indicates that the animals were mostly attached to solid bodies, such as rocks and rubble, and scraped off encrusting plants by means of their radula. Their mobility was very slight, and therefore, in order to ensure a certain possibility of dispersal, they retained a ciliated larval stage in their ontogenetic development.

Many primitive mollusks, such as the loricates, haliotids, patellids, have permanently retained this life style and the coast as habitat. The arcids also do not seem to have left this habitat; in order to maintain themselves in one place for a longer period of time, they fasten themselves to the substratum with their byssus, and nourish themselves on small organic particles which are directed toward the mouth by the ciliations of the gills and labial palps. Because plant life is possible only

to a depth of about 400 m, numerous species are confined to the continental shelf. Some of them have left the solid substratum and have moved to sand or mud; the foot soon acquired the capability, especially by expansion of the lateral margins, of moving on the surface of the loose substratum at times burrowing into it, as it is done not only by 1144 many snails, but also the scaphopods and many bivalves. Certain snails that live on *Zostera* and algae have acquired a characteristic adaptation; among these the species that stay on the pelagic *Sargassum*, and whose relatives are native in most cases to the coastal regions, are worthy of special note. Many gastropods, especially the higher prosobranchs, are also part of the rich animal life of the coral banks.

These different coastal habitats are in most cases very extensive without being interrupted by others, and there by granting even the not very motile snails the possibility of wide dispersal, which is effected mainly by the ciliated larvae. Only few have acquired the capability in the adult stage to proceed further and more rapidly by swimming than is possible by creeping, these are some olivids and opisthobranchs (Cryptophthalminae, Acerinae, Gastropteridae, Aplysiidae, *Lobiger*, Pleurobranchidae, Tethyidae) and among bivalves some Pectinidae and Limidae; all of these however have not given up their benthic mode of life, but use their swimming ability only temporarily for the purpose of a change of location.

The species living on loose substratum are in part little dependent on whether they live at lesser or greater depth, because everywhere they find sufficient nutrition, consisting mainly of organisms that have sunken from the surface, and accordingly they occur at times at very different depths. Differences of the water temperature are of little importance to them, and climatic conditions generally exert only a slight direct influence on the distribution of many molusks, even if indirectly they are of more or less great importance (breakers, currents, ice, effect on food organisms). From such groups, which can descend into considerable depths, have come those that have completely adapted to life in the deep sea; they are sometimes only individual species, sometimes entire genera, such as *Pectinodonta, Calliotropis, Basilissa, Sequenzia, Guttula, Gaza, Callumbonella, Chunula, Cocculinacea, Benthonella, Oocorys, Columbarium, Volutocorbis, Fusivoluta, Phenacoptygma, Neptuneopsis, Guivillea, Marginellona, Leucosyrinx, Ptychosyrinx, Cryptogemma, Typhlosyrinx, Pontiothauma, Bathyclionella, Benthomangelia, Pleurotomella*; some scaphopods (cf. p. 1140); *Tyndaria, Neilonella, Malletia, Bathyarca, Idasola, Kellyella, Mytilimeria, Myodora, Pholadomya, Panacca* and most of the Poromyacea, are completely or predominantly found in the deep sea.

Only few groups of gastropods have assumed an entirely pelagic mode of life. This has happened in a very peculiar way in the case of jathinids, which have acquired a passive swimming ability by means of a foam raft attached to the foot. The fin of the heteropods has certainly originated from the propodium of related snails, perhaps through transitional forms that could execute jumps by means of their foot. The pteropods stand close to opisthobranchs with strongly broadened lateral margins of the foot, which correspond to the fins. The completely pelagic phyllirrhoids are also unique. The entire class of the cephalopods has acquired swimming ability, and most of them lead a pelagic life, at times near the surface, at times at considerable depth, but some of them have assumed a predominantly benthic mode of life (cf. p. 1677).

1145   Coastal inhabitants, that lived near river mouths, found their way into brackish water and under certain conditions into the rivers, adapting themselves to life in freshwater; this has happened in some groups of gastropods (*Theodoxus*, *Neritina*, *Septaria*, *Neritilia*, Viviparidae, Ampullariidae, Valvatidae, Hydrobiidae, Melaniidae, *Clea*; Chilinidae, Latiidae, Physidae, Lymnaeidae, Planorbidae and Ancylidae) and bivalves *Scaphula*, *Sinomytilus*, Unionacea, Sphaeriacea, Dreissenidae, *Iphigenia*, Glaucomyidae, *Novaculina*, *Anticorbula* and *Erodona*, in part they have reached completely isolated bodies of water.

Other coastal inhabitants reached the tidal zone, where the shore was from time to time deprived of water; some protected themselves from desiccation of the gills by burrowing into the wet sand, others have more or less adapted themselves to life in the air. Among these littoral snails some have retained their gill, although at times somewhat reduced; others have completely lost it (*Hydrocena*, *Assiminea*, Ellobiidae, Oncidiidae), and near these stand those that have fully migrated to dry land (*Georissa*, Helicinidae, Cyclophoridae, Pomatiasidae, Acmidae, *Carychium*, Soleolifera and Stylommatophora).

The littoral habitat thus plays the most important role in the geographic distribution of the mollusks. It essentially corresponds to the coasts of the continents together with the neighboring island groups. Based on climatic conditions, 3 zones are distinguished; an Arctic, a tropic, and an Antarctic. In the Arctic zone, the ocean basin is enclosed by the northern coasts of the continents and of the island groups, and these coasts directly continue into the southward running coasts of the Atlantic and Pacific making it possible for the animals to spread from the warmer regions into the Arctic Ocean. Hence, the coasts of Norway, the east coast of North America and the coasts of the Bering Sea represent transitional areas, and only a few species are completely restricted to the Arctic Ocean, while most extend into the boreal region.

The situation of the Antarctic zone is very different, which not only includes the coast of the Antarctic continent (Holantarctic) but also the more or less distant islands and Tierra del Fuego. This zone is mostly taken to include also a part of New Zealand, the south coast of Australia, South Africa and a considerable part of South America, but their fauna is considerably different from the Antarctic one. The islands from Kerguelen to South Georgia may be distinguished as Metantarctic, the Magellanic and Aucklandic regions, which contain a mixed fauna, as Parantarctic.

The shells of the mollusks living in the cold seas are in most cases colorless and of little strength, sometimes with ribs or rings; because of this the Arctic shells have some similarity with Antarctic ones, and close affinities between the two areas have been inferred, which however more information did not always confirm; nevertheless, several genera were found to be essentially bipolar; *Lepeta, Margarites, Torellia, Laskeya, Cerithiella, Turritellopsis, Volutomitra, Admete, Lora, Thesbia, Diaphana, Toledonia, Cylichna, Philine, Cadlina; Limatula, Astarte, Cyclocardia, Thyasira*; evidently some of them are also known from other zones, especially from the deep sea. This circumstance allows the conclusion 1146 that a migration between the cold regions has taken place through the deep sea, although certain groups may have used the meridional coasts for this purpose. Regarding the direction of such migrations, the assumption has to be rejected that they have taken place southward from the Arctic Ocean; rather they started from intermediate regions, which however often lay far to the south. Groups such as the buccinids, which are strongly represented in the Arctic Ocean, probably first descended to greater depths, from where they reached the Arctic Ocean; the Antarctic buccinids are not closely related to the Arctic ones, *Neobuccinum* having a radula different from that of *Buccinum*, whereas the latter genus has a dentition like that of the South African genus *Burnupena*.

Numerous genera are native to only the Antarctic region, they largely reach the Magellanic region, seldom South Australia: *Hemiarthrum, Nuttalochiton, Notochiton, Icoplax, Tonicina; Nacella, Margarella, Submargarita, Trochaclis, Eatoniella, Boogina, Skenella, Laevilittorina, Pellilittorina, Frovina, Microdiscula, Lamellariopsis, Marseniopsis, Perissodonta, Chlanidota, Neobuccinum, Thalassoplanes, Glypteuthria, Savatieria, Antistreptus, Prosipho, Pareuthria, Fusinella, Harpovoluta, Guivillea, Provocator; Newnesia, Neactaeonina, Tritoniella, Bathydoris, Holoplocamus, Prodoridunculus, Austrodoris, Gargamella, Notaeolidia, Pseudotritonia, Charcotia, Telarma, Galvinella, Guyvalvoria; Adamussium, Adacnarca, Lissarca, Philobrya* (except for a few species), *Gaimardia, Cyamiomactra, Perrierina, Cyamium, Pseudokellya,*

Ptychocardia. Because a few species and several genera live near the Kerguelen and in the Magellanic region it is to be assumed that earlier a connection existed between them; probably the Holantarctic was also colonized from this region, while it mediated the migration of more northern forms mainly from South American coasts. Genera that extend only into the Magellanic region, but are absent from the Antarctic proper, are: *Plaxiphora, Notoplax, Acanthochiton, Chaetopleura, Ischnochiton, Chiton, Tonicia; Fissurella, Acmaea, Calliostoma, Photinula, Chlorostoma, Fusitriton, Calyptraea, Crepidula, Lamellaria, Columbella, Buccinanops, Cymbiola; Mytilus, Carditella, Carditopsis, Chione, Mulinia, Barnea.* Some of these groups also occur in the Aucklandic region, whereas others are lacking; the following are not found in Magellanic region and in the Antarctic: *Cellana, Haliotis, Cantharidus, Monodonta, Trochus, Turbo (Modelia), Littorina (Littorinopsis), Couthouyia, Nucella, Euthria, Cominella, Mitromorpha, Daphnella,* etc.

On the other hand the following may be designated as characteristically Arctic forms, generally also living in the Boreal region, but absent from the Antarctic: *Tonicella, Stenosemus, Symmetrogephyrus; Mölleria, Lacuna, Capulacmaea, Velutina, Marsenina, Onchidiopsis, Liomesus, Beringius, Volutopsis, Mohnia, Sipho, Plicifusus, Ancistrolepis, Sulcosinus, Neptunea, Buccinum, Doridoxa, Dendronotus, Goniaeolis, Coryphella, Chlamylla, Egalvina, Cumanotus, Cuthonella, Precuthona; Cyprina, Serripes, Panomya, Cyrtodaria, Mya.* When some of these groups occur only in the northern Atlantic Ocean or in the Pacific Ocean together with the neighboring parts of the Arctic Ocean, one may assume that the direction of their migration is thus indicated; however, many are circumpolar and are distributed in both oceans so far southward that it is difficult to say where they originated.

1147   If one no longer included the southern parts of South America, Africa and Australia in the tropical zone, their coastal regions are divided into 4 separate subregions: the Indo-Pacific, the western American, the eastern American, and the West African. In spite of this separation, there are in part very striking affinities between these areas; thus the West Indies there live not only many genera but even a few species that also occur in the Indo-Pacific region. This can be explained only by the fact that in earlier times the coasts of both areas were joined in the equatorial direction, the Ethiopian part of Africa being connected with South America; moreover, South and North America were separated from one another. Jhering says about this; "In the early Tertiary there existed between the eastern and western parts of the Tethys Sea a continuous active faunal interchange, which presupposes a free oceanic connection across the Sudan, and secondly: the Eocene migrations of marine Indian

organisms to the West Indies could have taken place only along the coast of long vanished continents of the central and southern Atlantic." Several of these animals lived previously also in the European region, but became extinct as a result of local and climatic changes. The significant difference of the mollusks of this tropical zone in comparison with those of the Antarctic may have as its prime cause that the nature of the northern coast of this large continent with its communities was basically different from that of its south coast, between which and the Antarctic continent extended the ocean known as Nereis.

It is very probable that the Antarctic continent was connected with Patagonia at the beginning of the Tertiary, but it may have also been connected with New Zealand and Australia. On the other hand, Africa seems to have been without a direct connection with the Antarctic. The islands of St. Paul and New Amsterdam in the southern Indian Ocean show certain affinities with South Africa, and probably also to New Zealand. Tristan da Cunha and Gough Island in the southern Atlantic also have no relationship with the Antarctic.

The dispersal capability of those animals that are adapted to life in the ocean depths is very different, encountering certain limits perhaps only through the nature of the substratum, but some deep-sea species have been found in widely separated places. The situation is similar in the case of pelagic animals, especially those that possess a permanent active swimming capability, such as that acquired among mollusks mainly by the cephalopods. The heteropods and pteropods, as well as the phyllirrhoids also lead a permanent pelagic life, although their locomotion is not so effective that they can swim over large distances; the janthinids are completely passive, being moved only by the ocean currents and the winds. These animals live in most cases in the warmer seas, but some pteropods have more or less largely withdrawn from the equatorial regions, partly to the south, but also to the north; completely adapted to both cold-water regions are *Spiratella helicina* (Phipps) and *Clione limacina* (Phipps).

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The freshwater habitat shows highly peculiar conditions. Although the migration of littoral animals into river mouths is possible without much difficulty, it did not occur at all in the case of the loricates, 1148 scaphopods and cephalopods, probably because they did not find the conditions of their existence there; and only a few snails and bivalve groups have succeeded in becoming fully native to freshwater. In many cases it would be misplaced to draw conclusions on the origin of river dwellers on the basis of their present distribution; one may well assume that small groups living in restricted areas, such as *Clea, Scaphula, Sinomytilus, Iphigenia, Glaucomya, Tanysiphon, Novaculina, Anticorbula*

and *Erodona*, have migrated from the sea into the rivers emptying into it, but this cannot be assumed for the others, some of which are very widely distributed. The New Zealand latiids are related to the South American chilinids and indicate an earlier connection between both lands. The situation may be similar in the occurrence of *Planorbula* in tropical America and in African lakes (Lake Tanganyika, Lake Chad) to lower Egypt, especially because other freshwater groups are also native to both continents. The eastern Asian genus *Semisulcospira* is related to the North American Pleurocerinae. The Melantriinae inhabit the Indo-Australian region, Madagascar, the tropical parts of Africa and of America. The occurrence of *Melanopsis* in the Mediterranean region in New Caledonia and New Zealand is very remarkable, whereas *Faunus* lives on Ceylon, in Indochina and the Philippines; *Lyogyrus* is found in North America and New Caledonia. On Opara Island, lying in the middle of the southern Pacific, a few species of the genus *Potamolithus* have been found, which is otherwise native to South America. All these connections as well as the wide distribution of some other freshwater mollusks give proof of former connections of the continents to one another. Even on continuous land masses the river systems and freshwater basins are more or less widely separated from one another, so that at present an exchange of animals is not possible, except for accidental transfer of spawn by water birds, etc. If, in spite of this, the same or closely related species live in them, an earlier connection of shorter or longer duration must have existed, such as through a high water level, especially after extensive glaciation. A particularly striking example is provided by the distribution of the micromelaniids, which extend from the Balkan across the Caspian Sea to Lake Baikal and compel the assumption that this large area was temporarily flooded; it must, however, be emphasized that not only the micromelaniids but also other mollusks, such as the genera *Benedictia* and *Kobeltocochlea* are not of marine origin.

In Lake Tanganyika, aside from genera that are undoubtedly typical freshwater inhabitants like *Planorbis, Isidora, Lymnaea, Viviparus, Cleopatra, Corbicula, Pisidium*, a few mutelids and unionids, there live certain snails, which are called thalassoid because of a resemblance to marine forms; these have given some zoologists the occasion to assume that this lake was earlier (in the Mesozoic) connected with the sea. More recently, this assumption has been rejected and these snails are seen as peculiarly modified descendants of freshwater groups which are native in Africa; unfortunately the relationships of all have not been sufficiently clarified, such as those of the Syrnolopsinae and the Lavigeriidae, but it is not to be doubted that *Neothauma* stands close to *Viviparus* and that the Paramelanieae have arisen from the Paludominae; it is uncertain

whether *Bithynia multisulcata* Bourguignat is related to the Indian *Mysorella marginata*, because only the shell is known. The very large lake, over 1000 m deep, with somewhat variable salt content (due to evaporation), has offered the animals conditions similar to those of the ocean, which seems to explain their external appearance.

Within standing bodies of water there is little active dispersal of most of the freshwater mollusks, because they attach their eggs to solid bodies or they are viviparous, without forming a free-living ciliated larva, such as that known for *Dreissena*. The most efficient dispersal capability has been achieved by the unionids through attachment of the glochidium larvae to fishes, by means of which they can be transported over great distances.

The land snails too disperse in part actively, in part passively; passively mainly through human traffic, by which some species, like *Oxychilus cellarium* (Müller), *Opeas gracile* (Hutton), *Agriolimax agrestis* Linné, *Bradybaena similaris* (Férussac), *Helix* (*Cryptomphalus*) *aspersa* Müller, etc., have been transported across various continents; at times flooded rivers may contribute to the dispersal. In spite of their slowness, land snails, in the course of long periods of time, can migrate across wide stretches of land so long as they find favorable local conditions and climate, and the possibility of nourishment. But because even related groups at present live in separate parts of the world and in these parts they are more or less widely distributed and split into subgroups, an earlier connection between the land bodies must have existed. Some such connections are rather generally accepted, for example, a large continent Gondwanaland, which in about the Permian included South America, the largest part of Africa and Australia, and which later split up; according to Jhering, at the time of the Upper Cretaceous, the eastern part of South America (Archibrasil) was connected through the Archhelensis with Ethiopia (Archafrica), the western margin (Archiplata) was connected with Antarctica (Archinotis) and with a northern "Schuchertland" which corresponded to the western part of North America, whereas its eastern part was connected in the north with Europe (Archiboreis). India to Madagascar formed Lemuria. It is assumed that at the time of the Eocene a large land (Archigalenis) connected eastern Asia with the western parts of North America and the northernmost part of South America (Archiguiana). By means of these and some other intermediate lands, such as connections of islands with one another and with continents the present-day distribution of land snails and other animal groups is explained. As far as the Polynesian islands are concerned, Pilsbry has expressed the view that, at the end of the Palaeozoic or during the early Mesozoic they were connected by a large continent, which was inhabited

only by some primitive land snails (including the following nonoperculate pulmonates: Achatinellacea, Vertiginacea, Succineacea, Endodontidae and Ariophantidae) and very soon largely sank into the sea. Although some tornatellinids live on Juan Fernandez, Pilsbry considers a connection of this continent with South America as improbable.

Due to the great changes the surface of the earth has undergone at various times, the dispersal of the land snails would have been considerately different, depending on whether it took place earlier or later and on the starting points of their development. This can hardly be identified with any certainty in the case of some of the oldest groups. In general the individual groups arose from littoral snails, probably mainly in the tropics. If fossil remains of a family were found in areas where it does not live at present, this does not need to be sufficient ground for the assumption that it has originated there; thus some cyclophorids were native in Europe, but at present inhabit mainly Asia and have perhaps also originated there; at any rate, *Craspedopoma* in the Canary Islands and the Azores originated from one such European group. The genus *Palaeostoa* Andreae, found in the western European Tertiary, cannot be considered as the ancestor to the presently living megaspirids, but rather as a lateral branch of this family, which probably arose in Africa, from where it spread to the west (Brazil) and the east (Queenland, New Guinea), but became extinct in its original home.

Related groups, and those coming from common ancestors, may have migrated in various directions from their original home and have developed differently under altered conditions. Thus, some groups are distributed mainly in the northern hemisphere, others in the southern. The original center of the development of the pulmonates may have been on the shore of the Indian Ocean, from where they migrated in all directions. Of the terrestrial groups the oldest are: 1. the soleoliferans, which branched off very early from shelled snails related to ellobiids and are closest to the littoral oncidiids; they are distributed over the equatorial palm zone. 2. the "Orthurethra" with the stirps of the Achatinellacea and Vertiginacea, the first of which as well as the amastrids and partulids have mainly spread eastward, the cochlicopids, vertiginids, valloniids and enids, probably related to which are the clausiliids, have spread more westward and northward but in part have also reached more or less far southward. 3. The endodontids, which are distributed over all continents, whereas the related zonitids, vitrinids, arionids and limacids have become native mostly in the northern hemisphere, the ariophantids more southward; the paryphantids and streptaxids (except for haplotrematids) almost exclusively inhabit the southern lands. 4. The Achatinacea, which attained their main development in Africa. 5. The Acavacea, which

inhabit lands of the southern hemisphere, whereas the Helicacea are distributed mainly in the northern hemisphere; the bulimuldis may have developed from strophochilids in South America and from there have spread in different directions.

Of the Nomenclature of the Mollusks

The naming of the molluscan genera is at present in a thoroughly unsatisfactory condition, thanks to the rules of nomenclature set up a few decades ago, which prescribe the strict application of the law of priority to the names published since 1758, that in part had gone unnoticed, if at the time of publication only one described species was mentioned which can be regarded as the genotype. Among these publications, the greatest damage was done by the "Museum Boltenianum," published in 1798 by P.F. Roding and reprinted in 1906, which contains numerous generic names erected by Bolten for his collection. Whereas these names unfortunately have been accepted by most conchologists, those published in the "Museum Calonnianum" in 1797 are accepted by some, rejected by others because no author was named.

The logical reason behind each naming is that with each name the same object is always designated. We have apparently completely lost sight of this reason, and a contest arose to replace as many customarily used names as possible by others. The result is that for certain genera so many different names have been used in recent publications that nomenclature requires a special study, and this of course is basically completely fruitless. In order to overcome this problem, application was made to allow exceptions to the law of priority for many of the most commonly used names, an effort which nevertheless found little support. With such a division of opinion, it is hardly possible to refer to names which find the approval of all. Some zoologists unconditionally accept the first published name in the form in which it is printed, even if it contains typographical errors or it is grammatically incorrect — which could hardly be considered science any longer.

Like the "Museum Calonnianum," a few other works of the 18th century are accepted by some and rejected by others, because the authors did not use binary names, such as Chemnitz in the "Neues Conchylien-Cabinet" or Geoffroy (Traité sommaire des Coquilles, Paris, 1767). If, for instance, one accepts as the author of *Ancylus* not Geoffroy but Müller, then, one can regard with Beck, *A. fluviatilis* Müller as the genotype. Recently the attempt has been made to validate some old names, which were rather worthless because they included various groups, by designating one species as the genotype; unfortunately,

because of this such monstrosities arose that for instance, *Bulimus*, which was generally considered a land snail genus, is now used for the freshwater genus *Bithynia*. *Pupa* was first published in the Museum Calonnianum in the sense of *Cerion*, but in the Museum Boltenianum as identical with the marine genus *Solidula*, and by Draparnaud it is used in the sense of the small *Pupilla*.

The designation of the typical species is at times debatable, because it is sometimes unclear whether a named species is actually meant as genotype in the present-day sense, especially by older zoologists.

A further difficulty consists in the fact that earlier some names were slightly modified by certain malacologists, without at the same time creating new genera, as for instance *Scalaria* Lamarck for *Scala* (Klein) Bruguière, *Nuculana* Link for *Nucula* Lamarck, *Stomax* Montfort for *Stomatia* Helbling, *Phasianus* Montfort for *Phasianella* Lamarck, *Calyptrus* Montfort for *Calyptraea* Lamarck, *Clavus* Montfort for *Clavatula* Lamarck, *Planorbarius* Froriep for *Planorbis* Müller, etc. If thereby a species was mentioned, this cannot be considered as the genotype of the presumably new genus. The recently established rule, that a species name identical with the genus name is to be regarded as typical, evidently can only have validity if a different species was not previously designated as the genotype.

Should it not be possible to put on end this chaos in nomenclature? !

Literature on Mollusks

It would be understandable if the readers of this handbook wished to find, as far as possible, references to the literature for all the details, but this would go far beyond the available space; and here only a few remarks will be made on the literature on mollusks.

All statements about the erection of genera, subgenera and sections are contained in the alphabetically arranged Nomenclatur Generum Animalium, which of course, has not been quite completed at the present time.

Summaries of all molluscan species for the purpose of identification are impossible because of the enormous, continuously increasing number, of the latter. Such works were of course begun, but have remained incomplete, such as the second edition of the Systematisches Conchylien-Cabinett by Martini & Chemnitz, in which the individual groups were studied by different conchologists in the course of several decades. As a result of this, some of them are already very much outdated, others are rather inferior, but some of recent date, especially those by Kobelt, are very useful.
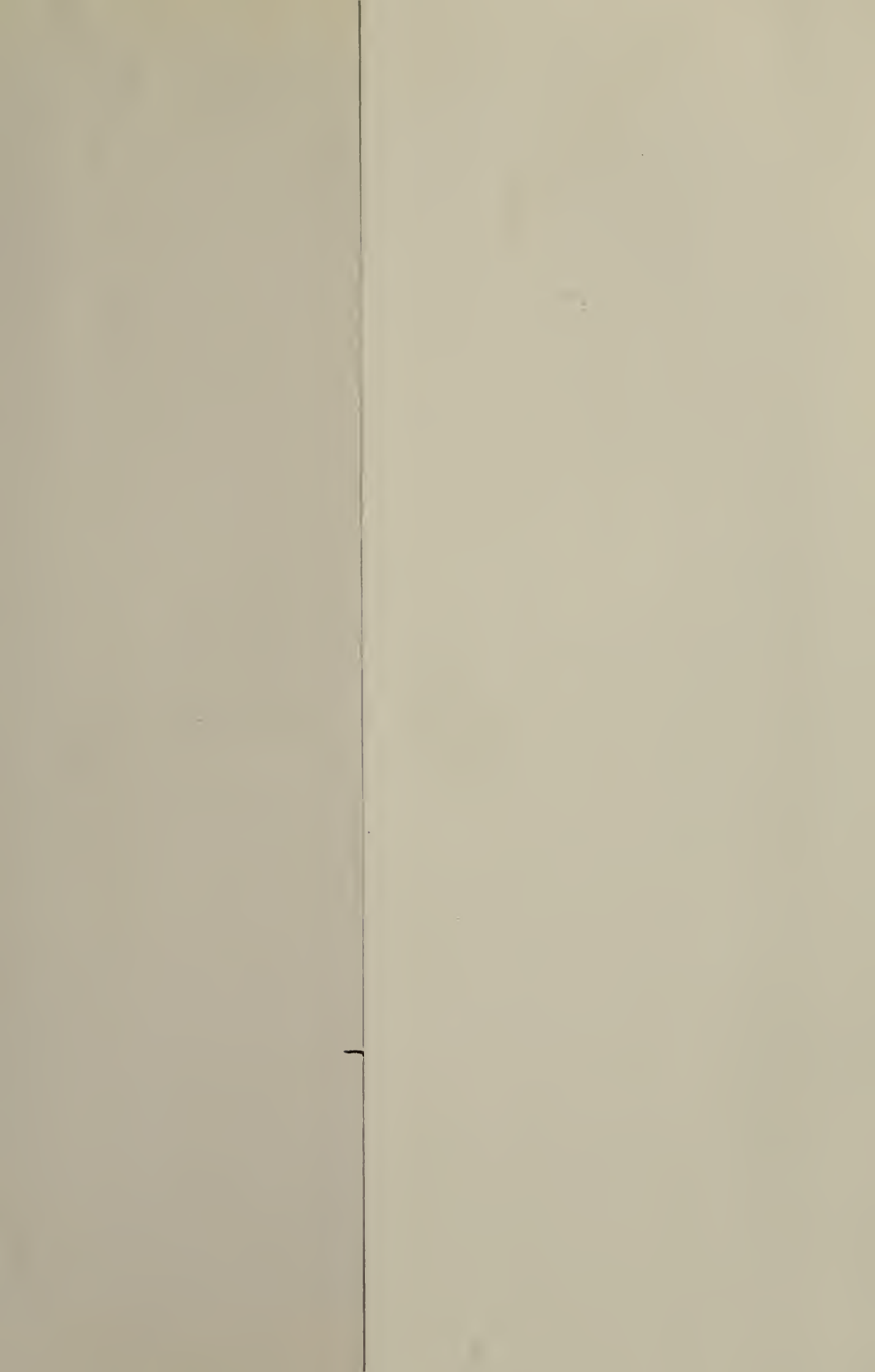
The American Manual of Conchology begun by Tryon and continued by Pilsbry is the most consistent. Studied in it are the cephalopods, the shelled marine gastropods, the loricates (Polyplacophora), and scaphopods in Series 1. Series 2 contains only the land snails, but it is so far incomplete. The monographs of some families (bulimulids, urocoptids, achatinacens, oleacinids, achatinellaceans and vertiginaceans) are the best there are; the enids, clausilids, and a few other families, as well as the freshwater snails and all bivalves are missing.

The Conchologia Iconica by Reeve contains good illustrations in 20 large volumes of most of the species known at the time it appeared in 1843–1878, and thus does not contain many species that have since been described. Innumerable special works appeared in various journals, a few of which are dedicated only to malacology, of which there are in Germany: Zeitschrift für Malakozoologie 1844–1852; Malakozoologische Blätter 1854–1891; Jahrbücher der Deutschen malakozoologischen Gesellschaft 1874–1887 and Nachrichtsblatt of the same society since 1869, which has recently received the title Archiv für Molluskenkunde; in France Journal de Conchyliologie since 1850; in England Proceedings of the Malacological Society of London since 1893 and The Journal of Conchology since 1874; in America; The Nautilus since 1889.

Many marine species are described in the reports of large expeditions, such as the "Astrolabe," the "Challenger," the "Blake," the "Travailleur" and "Talisman," the Plankton Expedition (mainly cephalopods), the Deutschen Tiefsee-Expedition, the Deutschen Südpolar-Expedition etc. Kobelt's Iconographie der europäischen schalentragenden Meer-Conchylien has remained incomplete. Valuable is: G.O. Sars, Mollusca Regionis arcticae Norvegiae, 1878. The English species are described by Forbes & Hanley (History of British Mollusca), by Jeffreys (British Conchology) and by Alder & Hancock (Monograph of the British nudibranchiate Mollusca), the French especially by Bucquoy, Dautzenberg 1153 & Dollfus (Mollusques marins du Roussillon); the Mediterranean species were summarized in the Carus, Prodromus Faunae mediterraneae, the Iberian by Hidalgo and Nobre. Turton in 1932 listed the numerous species found near Port Alfred (South Africa). Dall provided catalogs of species from the southeastern coast of the United States (1889), from Peru (1909) and the northwestern coast of America (1921). Japanese species were studied by Lischke, Dunker (Index Molluscorum Maris Japonici 1882), Pilsbry (Catalogue of the Marine Mollusks of Japan 1895) and recently by Iwakawa (1919) and Sh. Hirase (Collection of Japanese Shells 1934), the cephalopods by M. Sasaki (1929). Robson began a monograph of cephalopods, of which so far the octopods have been completed (1929 and 1932).

The European land and freshwater mollusks are described in Rossmässler's Iconographie, which Kobelt continued, and in addition in several treatments of the faunas of individual countries, such as the German by Ehrmann, the English by Taylor (incomplete), etc. Kobelt in 1909 published the "Verzeichnis der aus Afrika bekannten Binnenconchylien" which however was not very complete and has since been augmented by the description of numerous species; Connolly in 1912 published a list of the South African land and freshwater mollusks and described new African species in several works; the species of the Congo have been studied by Pilsbry 1919 and 1927. Kobelt in 1879 published a "Fauna Molluscorum extramarinorum Japoniae"; Chinese species have been described mainly by Father Heude and O. v. Möllendorff, the latter also· greatly contributed to the investigation of the Philippine species. Valuable is a list of the helicoid land snails of Asia by Gude (1902, 1903). Land and freshwater snails of Celebes were collected and studied by P. & F. Sarasin; the other Sunda Islands as well as the islands lying further to the east to New Guinea have recently had their mollusks thoroughly investigated by several researchers. The study of the land and freshwater mollusks of the United States by Binney and Lea has also been recently greatly supplemented and enriched with several works by Pilsbry, Baker, Walker, etc. Strebel examined the Mexican land and freshwater mollusks, likewise Fischer & Crosse (Mission scientifique au Mexique et dans l'Amérique centrale) and Martens (Biologia Centrali-Americana). Pilsbry has studied the Patagonian inland mollusks (1911).

These few data may give a certain amount of information; it can be supplemented to a certain degree by the annual reports in which new genera and species are listed.

1154   Editors' note:

"Corrections" on this page have been incorporated as footnotes to appropriate text throughout this translation.