PART I

MOLLUSCA 1

MOLLUSCA—GENERAL FEATURES
SCAPHOPODA
AMPHINEURA
MONOPLACOPHORA
GASTROPODA—GENERAL FEATURES
ARCHAEOGASTROPODA AND SOME (MAINLY PALEOZOIC) CAENOGASTROPODA AND OPISTHOBRANCHIA

By J. Brookes Knight, L. R. Cox, A. Myra Keen, A. G. Smith, R. L. Batten,
E. L. Yochelson, N. H. Ludbrook, Robert Robertson, C. M. Yonge
and R. C. Moore

CONTENTS

INTRODUCTION

By Raymond C. Moore

This volume of the *Treatise,* introducing invertebrate phylum Mollusca, has been guided in organization by Dr. L. R. Cox, of the British Museum (Natural History), London. He assisted in arranging for the introductory chapter on general characters of Mollusca, contributed by Prof. C. M. Yonge, of the University of Glasgow, making helpful suggestions in connection with paleontological aspects of this subject. Early-made plans called for treatment next of the minor classes, Scaphopoda and Amphineura, the latter at least being recognized as distinctly primitive in various morphological features. The mollusks that now are distinguished as an independent class, termed Monoplacophora, formerly were classified as an archaic group of gastropods characterized by the bilateral symmetry of their low cap-shaped shells and multiple muscle scars on the inner side of the shell for attachment of soft parts. Except for having a single shell, they suggest the amphineurans in structural organization and correspondingly differ from typical snails. The discovery (first reported in 1957) of living forms *(Neopilina)* of the same sort, which demonstrate correspondence to the Amphineura in having multiple pairs of gills along sides of the mantle cavity, as well as in other characters of soft-parts anatomy, supports separation of such mollusks as a group distinct from both gastropods and amphineurans; they have been defined (1952) as a class named Monoplacophora and in this volume are described in a section following that devoted to the Amphineura.

It is not to be understood that the sequence of molluscan classes as arranged in the *Treatise* reflects judgment as to order of their evolutionary differentiation or even as to the relative complexity of their morphological characters, taking account both of hard and soft parts. The present volume, designated as Mollusca 1, contains systematic descriptions of (1) Scaphopoda, (2) Amphineura, (3) Monoplacophora, and (4) the geologically oldest kinds of Gastropoda, which chiefly are classified as Archaeogastropoda; predominantly younger gastropod main groups, comprising the Caenogastropoda (subclass Prosobranchia) and representatives of the subclasses Opisthobranchia and Pulmonata, which together are far more numerous than the archaeogastropods, are assigned to the volume Mollusca 2 (in preparation). Then follow divisions of the Cephalopoda (Mollusca 3-5), of which only the Ammonoidea so far has been completed (1957), and finally the Pelecypoda (Mollusca 6). This surely is not intended to imply that the bivalve mollusks are the most highly developed or "advanced" class of the phylum; on the other hand, as now understood, they are interpreted to include very specialized, rather than prevailingly simple and therefore inferentially "primitive" mollusks. About all that can be said is that the allocated divisions of Mollusca in the *Treatise* are arranged in measurably arbitrary manner, but their respective taxonomic delimitations fairly well reflect utilitarian purposes in studies by paleontologists. Among volumes devoted to the Mollusca, the present one may seem to meet specifications of utility least acceptably, because only a fraction of the Gastropoda is included and this fraction is not defined neatly along taxonomic lines. Opposed to such a view is the advantage from stratigraphic viewpoints of treating together all known groups of Paleozoic gastropods, some being placed in a Supplement for the purpose of republishing them in proper taxonomic position with units belonging to Caenogastropoda and other main divisions assigned to Mollusca 2. This arrangement has been adopted as result of strong recommendations to the director-editor of the *Treatise* by Dr. J. BROOKES KNIGHT.

The oldest known mollusks are monoplacophorans and helcionellacean gastropods from Lower Cambrian deposits. At least two genera *(Helcionella, Coreospira)* are firmly identified as representatives of the gastropods having this age, whereas the supposed monoplacophorans from the Lower Cambrian *(Scenella, Cambridium, Stenothecoides)* are as yet somewhat doubtfully included in this class. Thus, the Gastropoda have slightly the better claim to rank as the most ancient molluscan class recorded by fossil remains. Upper Cambrian strata contain at least three unquestioned members of the Monoplacophora *(Palaeacmaea, Proplina, Hypseloconus)*. These are numerically much outweighed by at least 16 known genera of gastropods classified in 9 families and representing three suborders (Bellerophontina, Macluritina, Pleurotomariina) (Fig. 88,*1*). The purpose of making these observations is to point out features of the early fossil record that distinguish monoplacophorans and gastropods from other mollusks, none of which are recognized without question in rocks older than Lower Ordovician (Tremadocian), even though all (excepting doubtful occurrence of scaphopods below the Devonian) appear to have become well established and strongly differentiated in Ordovician time.

GENERAL CHARACTERS OF MOLLUSCA

By C. M. YONGE[1]

CONTENTS

DEFINITION OF MOLLUSCA

The Mollusca, or "soft-bodied" animals, constitute a large and most important group of invertebrates which occupy many habitats in the sea, in fresh water, and on land. Although conforming to the criterion of a phylum in the possession of a highly characteristic common structural plan, mollusks are exceptionally diverse in outward appearance and in habits. Apart from the recently discovered monoplacophoran, *Neopilina galatheae* (LEMCHE, 1957), they are not segmented and include, in the Cephalopoda, the most highly organized nonsegmented animals. Except in *Neopilina,* the coelom is small, consisting of the pericardium and the cavity of the gonads with paired ducts to the exterior.

The animal is divisible into four regions, (1) a usually well-developed **head** with tentacles and eyes, although in the bivalves it is lost, (2) a ventral and muscular **foot,** probably provided primitively with a broad "sole" on which the animal crawled on hard surfaces, but capable of very great modification and seldom lost, (3) a dorsal **visceral mass** (coiled in Gastropoda), in which the internal organs are concentrated, (4) an overgrowing sheet of tissue, the **mantle** (or **pallium**), which secretes a calcareous shell with an organic matrix. The shell assumes many forms, is usually in one piece (including most bivalves where the two valves and the connecting ligament together form the shell), although consisting of eight plates in the Polyplacophora. It may become enclosed by the mantle, reduced, or lost.

A space, usually at the posterior end of the visceral mass between the mantle and underlying tissues and known as the **mantle cavity,** constitutes the respiratory chamber. In it lie the highly characteristic paired molluscan **gills** (or **ctenidia**) By means of cilia they create an inhalant current of water ventrally and an exhalant current that leaves the cavity dorsally. Except in certain Gastropoda and Aplacophora where the primitive condition is lost, the anus and the excretory and reproductive systems all open into this cavity where their products are removed with the outgoing, exhalant current. The **mouth,** commonly with jaws, leads into a buccal cavity that usually contains the characteristic **radula** (or **lingual ribbon**), a horny structure bearing teeth and capable of wide modification. Both jaws and radula are absent in the bivalves. Into the stomach open blind-ended tubules or digestive diverticula. Most recent evidence (1959) indicates that these may have been primitively concerned with extracellular digestion.

The **nervous system** consists of nerve centers in connection with the head, where

---

[1] Professor of Zoology, University of Glasgow, Glasgow, Scotland.

there is a loop around the anterior end of the gut, viscera, foot, and mantle. Where, as in most modern mollusks, the nerve cells are locally concentrated, these are known respectively as the cerebral, visceral, pedal, and pleural (or pallial) ganglia. They are united by way of commissures.

The **circulatory system** consists of a heart, usually with two auricles which receive blood from the ctenidia, together with a median and more muscular ventricle (elongated and double in *Neopilina*), from which blood is forced anteriorly and posteriorly through arteries opening into large blood sinuses or haemocoels. Only the highly evolved Cephalopoda possess capillaries. The blood may be colorless or contain haemocyanin.

The **excretory system** consists of kidneys, which are mesodermal tubes opening from the pericardium into the mantle cavity. Pericardial glands having an excretory function may also occur.

The **reproductive system** consists of gonads, primitively paired, discharging their products by way of the kidneys. Secondary gonoducts have usually been acquired. Although most often separate in sexes, the Mollusca exhibit a widespread tendency to hermaphroditism, particularly protandry. Development, except where secondarily it has become direct, is by way of a trochophore followed by a veliger larva.

AFFINITIES

The discovery in deep water in the eastern Pacific of the living monoplacophoran, *Neopilina galatheae* Lemche (13), has profoundly affected understanding of the relationship of the Mollusca to other phyla. It is no longer true to declare that in adult structure the Mollusca show no obvious affinities with other phyla. In general it may be said that their bilateral symmetry (lost in the Gastropoda) places them in the Bilateria, and the presence of a coelom, which arises by splitting of the mesoderm, indicates relationship with other schizocoelous phyla. Moreover, the fertilized egg develops by spiral cleavage in very much the same manner as in the polyclad Turbellaria, Nemertina, and Annelida. Particular association with the last named had been indicated by the presence in both of a trochophore larva, suggesting common descent from the Radiata. Although previously separation of these phyla, now clearly very widely separated, had been regarded as having preceded the appearance of segmentation, preliminary accounts of the structure of *Neopilina* show that this undoubted mollusk *is* segmented. In addition to the shell muscles, previously known to have consisted of a series of pairs in the fossil Monoplacophora, it is now established that the auricles, the kidneys, and possibly the gonads are serially repeated. There is also a series of pallial outgrowths, which appear to be segmentally arranged. Now, no doubt remains that the Mollusca must have separated from the Annelida *after* the appearance of segmentation; the affinities between the two phyla are much closer than was previously suspected.

GENERAL FEATURES

The following account of the Mollusca aims only at consideration of some aspects of structure from the functional standpoint; few papers are cited, but these carry extensive reference lists. Classification is taken from Thiele (22), although emendations to this are occasionally suggested. Demonstration of the common structural plan behind the diversity of appearance and habits in the Mollusca represents a major achievement of comparative anatomy, but those who made this analysis of structure did not appreciate all reasons for the great plasticity of the molluscan form. Much light is thrown on this problem when it is realized that primitively a mollusk is divisible into (1) the body consisting of the head and (behind this) the ventral foot with the visceral mass concentrated in a hump dorsal to it, and (2) the shell-secreting mantle, which represents an overlying cap upon the visceral hump. Of these, the body is bilaterally symmetrical, with an anteroposterior axis of growth, but the mantle-and-shell, which grows by marginal increment around a central dorsoventral axis, is radially or, more correctly, owing to the influence of the body, biradially symmetrical. Taking the foot as the one fixed point, mid-ventral, the mantle-and-shell with the visceral mass may revolve through an angle of 180 degrees in the horizontal plane (Gastropoda), or the mantle-and-shell alone may revolve through a similar angle in the vertical plane (Pelecypoda: Tridacnidae). These are but two instances of the independence of regions of the body and of the mantle-and-shell.

Although now liable to revision when the full account of the segmented Monoplacophora becomes available, fundamental aspects of the structure of the type of primitive mollusks, from which members of all other existing classes probably arose, may be noted briefly by reference to Figure 1, representing the views of GOODRICH (9). The presence of ectodermal excretory organs in the form of a pair of protonephridia in larval stages of prosobranch and pulmonate Gastropoda and of Pelecypoda furnishes indication of the presence of similar organs in the primitive mollusk. But in addition, there were paired coelomic cavities opening to the exterior by coelomoducts. The cavities separated into anterior genital and posterior pericardial chambers and the ducts, originally serving solely as genital ducts, acquired an excretory function, their inner openings becoming the renopericardial funnels while the ducts dilated, forming renal chambers. Meanwhile, the nephridia were lost in the adult, although retained in the larvae. The two pericardial chambers fused to form a single pericardium, the contained heart consisting of a single ventricle with an auricle opening into it on either side. This primitive arrangement, with gonads opening into the pericardium and the coelomoducts serving the dual function of gonoducts and excretory organs, becomes modified in the course of evolution within the Mollusca, with notable effects upon both habit and habitat, especially within the Gastropoda.

GOODRICH indicates a straight gut running the length of the body, with radular sac and associated salivary (mucous) glands and paired masses of digestive diverticula opening into the stomach. To this should be added (Fig. 2) the probability of glandular esophageal pouches secreting carbohydrate-splitting enzymes, digestion of protein and fats being carried out intracellularly in the tubules of the digestive diverticula, possibly also in blood phagocytes that migrated into the lumen of the gut. The stomach itself probably early contained a ciliated sorting region, an area of cuticle forming a gastric shield, and a "style-sac" region initially concerned with the consolidation of fecal material—a matter of prime importance when the gut opened into the respiratory (i.e., mantle) cavity. Lengthening of the gut posterior to the stomach was also associated with the formation of firm fecal pellets.

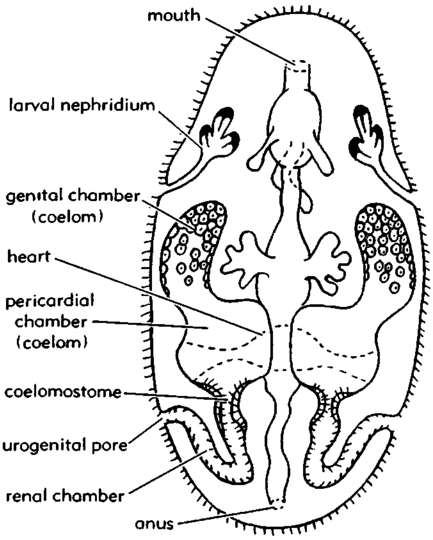

FIG. 1. Diagram of a primitive mollusk, dorsal view (9). Each of the paired coelomic sacs has a genital and a pericardial chamber and a coelomoduct with coelomostome and renal chamber.

As indicated in Figure 2, the foot in primitive Mollusca is envisaged as having a broad muscular sole, the original habit being one of creeping on a hard substratum (the habit of *Neopilina galatheae,* which lives on abyssal ooze, being certainly secondary) and feeding by scraping with a broad multiseriate radula. It was attached to the shell by a series of paired pedal or shell muscles, as in existing and extinct Monoplacophora, e.g., *Neopilina* (13), and fossil Tryblidiacea (12). Such a condition could be regarded as ancestral to that in both the Polyplacophora and the Pelecypoda and, following torsion which involves previous reduction to one pair of shell muscles, to that in the Gastropoda.

The mantle-and-shell must originally have formed a domelike cap over the visceral mass, although the animal could not have been withdrawn inside it. The limpet form (found also in *Neopilina*), in which the mantle-and-shell are pulled down over the body, secured by the sucker-like foot, appears

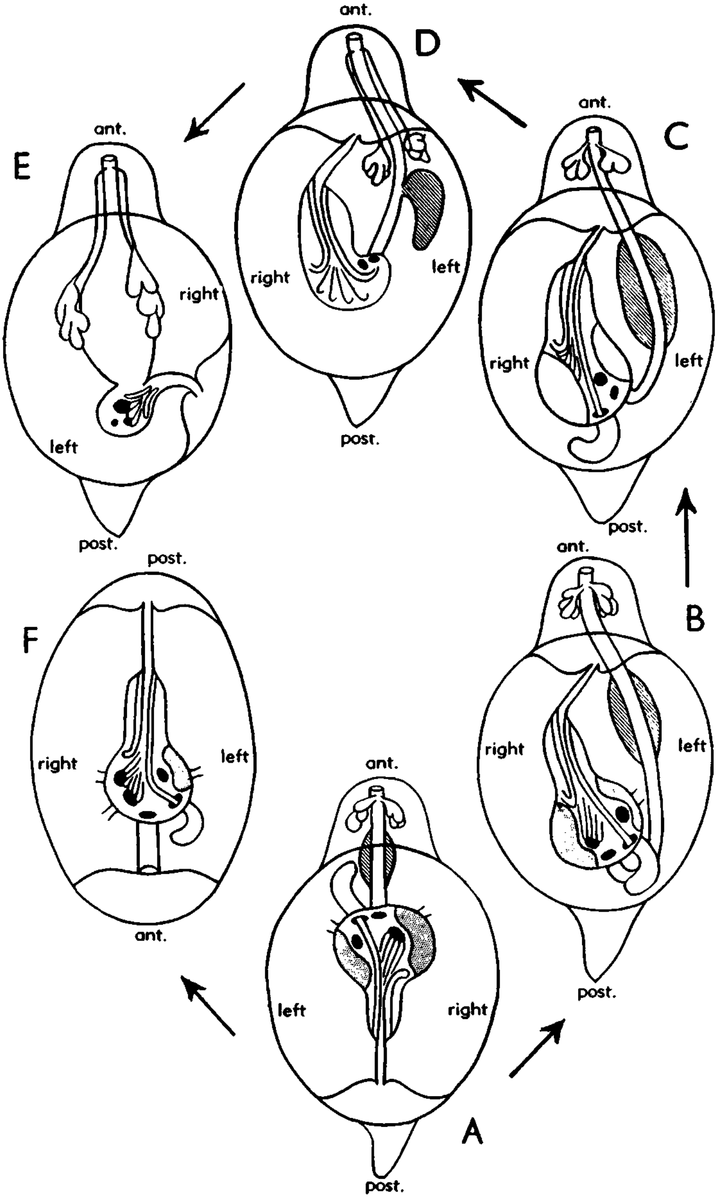

FIG. 2. Possible evolutionary scheme of molluscan gut (11).——*A*. Hypothetical primitive condition showing salivary glands, esophageal glands (hatched), stomach with right and left ducts from digestive diverticula, coiled caecum to left of esophageal opening, into which passes major typhlosole, ciliary sorting region between this and minor typhlosole, cuticular gastric shield covering much of stomach wall.——*B*. Gastropod, esophagus now opens posteriorly into stomach.——*C*. Archaeogastropod such as *Monodonta*, esophagus migrating anteriorly.——*D*. Neogastropod such as *Nucella*, greater simplification of stomach.——*E*. Tectibranch or pulmonate, stomach reduced to caecal appendage, esophagus dilated forming crop, esophageal glands lost.——*F*. Pelecypod (posterior end at top), salivary and esophageal glands lost but stomach retaining primitive features.

too specialized to be primitive. It has been evolved many times independently in the Gastropoda (more than once each in Archaeogastropoda, Mesogastropoda [Caenogastropoda, *partim*], and Pulmonata) but certainly in these cases without subsequent evolutionary advance.

Special interest attaches to the mantle cavity, primitively a respiratory chamber and so remaining throughout the Mollusca (except in the relatively few instances where it has been lost), despite its added functions as a feeding organ in some Gastropoda and almost all Pelecypoda and an organ of jet propulsion in most Cephalopoda and a few Pelecypoda. Although consisting in *Neopilina* (but not necessarily in all Monoplacophora) of narrow pallial grooves with a series of ctenidia or ctenidia-like outgrowths, it is here considered to have been reduced to a relatively deep posterior cavity with a single pair of ctenidia before the other molluscan classes (including the Polyplacophora with multiplied and certainly true ctenidia) were evolved. It is therefore necessary to consider in some detail the organization and functioning of the pallial complex enclosed within this posterior cavity. In this matter deductions from conditions in modern representatives of these classes appear of greater significance than those from conditions in *Neopilina,* although future study of the mantle cavity of this animal in life should prove of great interest.

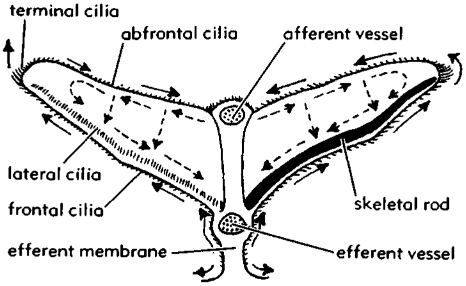

FIG. 3. Lateral view of two filaments with the axis shown in section of *Haliotis tuberculata* and indicating the probable primitive structure of the molluscan ctenidium (29). Lateral cilia shown on left filament only, skeletal rod on right only. Arrows show direction of respiratory current created by lateral cilia and of cleansing currents, dotted arrows course of blood flow within filaments.

The pallial complex of ctenidia, osphradia, and hypobranchial glands may be considered in that order. Apart from *Neopilina,* where the precise status of the pallial outgrowths awaits detailed description, the characteristic molluscan gills, or ctenidia, persist in all classes except the Scaphopoda. It would appear that primitively each consisted of a central axis with filaments disposed alternately on the two sides. The condition now found in *Haliotis* (Fig. 3) probably indicates the primitive state. Down the axis run muscles, nerves, and blood vessels. Each filament bears four sets of cilia. The current-producing lateral cilia on the two sides of the filaments create a current of water that moves upward between adjacent filaments. Particles borne in suspension are caught in the currents created by the frontal cilia and so carried to the tip of the filaments and thence, by the agency of long terminal cilia, either on to the hypobranchial gland on the roof of the mantle cavity, or else, by way of the abfrontal cilia, to the upper surface of the axis, where they are conveyed to the distal end of the ctenidium and there expelled from the mantle cavity. Buckling of the soft filament is prevented by chitinous supporting rods, which extend within the filaments beneath the zone of lateral cilia. Internally, blood enters by an afferent vessel that runs the length of the axis on the "upper" or "abfrontal" surface and flows from this into each filament, circulating there in the opposite direction to the flow of water created by the beat of the lateral cilia. Respiratory efficiency is thus insured. Blood is re-collected in the efferent vessel that runs along the other surface of the axis and dilates terminally to form the auricle. Throughout the Mollusca the relations of the afferent and efferent vessels are constant and it is advisable to refer to the afferent (abfrontal or dorsal) and efferent (frontal or ventral) surfaces of the ctenidia. For varying distances from their point of origin, the ctenidia are attached to the pallial wall by afferent and efferent membranes. Primitively, as in existing zygobranchous Gastropoda, the efferent membrane was probably the greater, but in some the afferent membrane may be as long (e.g., Gastropoda: Trochacea), or it may entirely replace the efferent membrane (Pelecypoda). So organized, the paired ctenidia constitute a functional partition dividing the mantle cavity into ventral inhalant and dorsal exhalant cavities.

Certain consequences follow from this (Fig. 4). The sensory osphradium associated with each ctenidium lies in the inhalant cavity in the path of the incoming current where larger particles tend to fall out of suspension. This fact, together with the histology of these receptors in modern Gastropoda, gives strength to the view that they are tactile organs concerned with the estimation of sediment carried in the respiratory current and not, at any rate exclusively, chemoreceptors as they are usually considered. The third component of the pallial complex, the hypobranchial mucous glands, are situated in the roof of the mantle cavity. By the secretory action of these glands particles of sediment are consolidated before being removed, by ciliary action, from the mantle cavity. Fouling with sediment represents the major danger to the efficiency of the respiratory chamber and the activities of osphradia, hypobranchial glands, and all cilia (apart from the lateral tracts) on both ctenidia and mantle surface are concerned with cleansing. Moreover, both the alimentary and the reno-reproductive systems open into the exhalant chamber, so that their products are carried out in the exhalant current without fouling the ctenidia. These facts are fundamental to the understanding of future developments in the form and functioning of the mantle cavity and the contained pallial complex throughout the Mollusca.

The circulatory system is simple, the two auricles (more in *Neopilina* and duplicated in Polyplacophora and in *Nautilus*) and the single ventricle (double in *Neopilina*) into which they open lie in the pericardium. Blood flows into anterior and posterior aortas and so into the haemocoels. Apart from circulation, these play an essential role in Mollusca, notably Gastropoda and Pelecypoda, in which foot and head are protruded, as a result of hydrostatic pressure.

Conditions in *Neopilina* and in the Polyplacophora give the best indication of the primitive condition of the nervous system, there being little accumulation of nerve cells in ganglia. But there was probably an early tendency for such accumulations in centers within the head, foot, mantle, and viscera, with production respectively of cerebral, pedal, pleural, and visceral ganglia connected by way of commissures. Apart from the striking crossing of the visceral loop (streptoneury) in prosobranch Gastropoda, the major changes are the loss (or

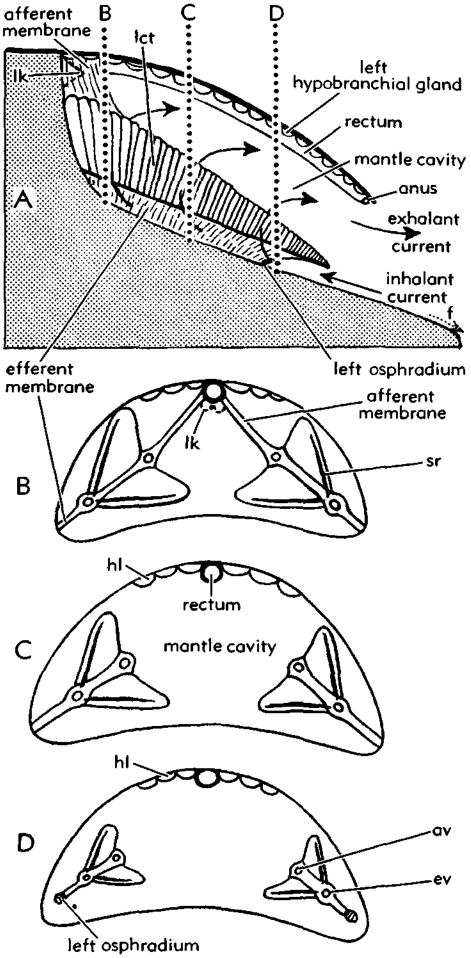

Fig. 4. Diagrams showing probable arrangement of the pallial organs in the pretorsional ancestors of Gastropoda. Mantle cavity viewed from the left side, the dotted lines *(B, C, D)* indicating the position of the three similarly lettered sections, each drawn as viewed from the posterior. (Explanation: *av,* afferent blood vessel; *ev,* efferent blood vessel; *f,* surface of foot with backward directed ciliary currents; *hl,* left hypobranchial gland; *lct,* left ctenidium; *lk,* left kidney aperture; *sr,* skeletal rod in ctenidial filament.)

great reduction) of the cerebral ganglia (and the head itself) in Pelecypoda and the tendency for concentration of all ganglia in the head in pulmonate Gastropoda and especially Cephalopoda.

From a bilaterally symmetrical primitive mollusk with uncoiled univalve shell and posterior mantle cavity, the evolution of all existing molluscan classes, except the Monoplacophora, may be deduced. The differences between them are to a large extent due to whether the body or the mantle-and-shell has the dominant influence on form.

Class MONOPLACOPHORA

Until the discovery of *Neopilina galatheae,* this recently erected class consisted solely of extinct Paleozoic mollusks characterized by the presence of a series of pairs of muscle scars. Quoting from the only existing account to date of the one modern species[1] so far discovered (13), the class may be defined as follows: "Almost bilaterally symmetrical mollusks with internal metamerism. A single piece of shell covers the pallium which extends all over the dorsum. Anus posteromedian. Coelomic cavities well developed. The metamerically arranged, paired auricles deliver the blood to the two symmetrical, long ventricles, each on either side of the intestine. Metamerically arranged nephridia arise from the coelomic sacs to open on the surface in the pallial furrow. Gonads symmetrically arranged, possibly metameric, opening through the nephridia. Nervous system primitively orthoneurous."

Neopilina galatheae was taken by the *Galathea* expedition west of Central America at Station 716 (9° 23′ N, 89° 32′ W) on May 6, 1952, at a depth of 3,590 meters on a dark muddy clay bottom. LEMCHE suggests that it lives with the almost circular limpet shell undermost and that it is a filter feeder. However, this posture seems inherently unlikely (36), and the animal would seem more probably a deposit feeder (the gut contains radiolarians). Possibly it collects organic debris from the bottom by means of frilled organs, which may be ciliated, situated at the margins of the mouth and which could be analogous, possibly even homologous, with the palp proboscides in the Nuculidae and Nuculanidae (protobranchiate Pelecypoda).

Class POLYPLACOPHORA

[Subclass Polyplacophora of class Amphineura]

In the chitons, which comprise this class Polyplacophora, also known as the Loricata, the mantle-and-shell may be said to dominate the much-flattened body over which, including the head, devoid of tentacles and eyes, it extends. Receptors are confined to the subradular organ, a chemoreceptor that "tests" the ground over which the mouth slowly moves, megalaesthetes (probably receptors of light) on the surface of the shell plates and sensory streaks, homologous or analogous to osphradia, in the mantle cavity. The characteristic subdivision of the shell into eight articulating plates is foreshadowed by the monoplacophoran *Archaeophiala* (12) with six (or ?eight) pairs of muscle scars. Lengthening of the body, together with subdivision of the shell into the linear series of articulating plates, permits these animals to conform to irregular hard surfaces and, if torn off by heavy seas, to curl up with the underside of the body, including the important pallial grooves, protected so that the animals can be rolled about without damage. They are typically inhabitants of rocky, surf-beaten shores and have retained, and indeed developed, the primitive habit of attachment by a broad foot to a hard substratum; in form and habit they are essentially elongated limpets.

The body retains primitive characters in the absence of accumulations of nerve cells forming conspicuous ganglia and in the symmetrical arrangement of the renal and reproductive systems and the general character of the gut. But the gonads have lost connection with the pericardium and are usually fused, although with paired ducts opening into the pallial grooves anterior to the renal pores. Sexes are separate and fertilization is usually external, but one case of viviparity is known. Lunar periodicity in spawning occurs. The kidneys extend forward, although their external openings, almost on a line with the renopericardial pores, are posterior. The heart is unusual in possessing two pairs of auricles opening into

---

[1] Subsequent to the preparation of Professor YONGE's typescript on general characters of Mollusca for the *Treatise,* A. H. CLARK, JR., & R. J. MENZIES, of the Lamont Geological Laboratory, Columbia University, in New York have reported (*Science,* 17 April 1959) the discovery of another monoplacophoran described as a new subgenus and species named *Neopilina (Vema) ewingi.* It was dredged from the sea bottom about 140 miles west of Chicama, Peru, at a depth of 3,200 fathoms.—ED.

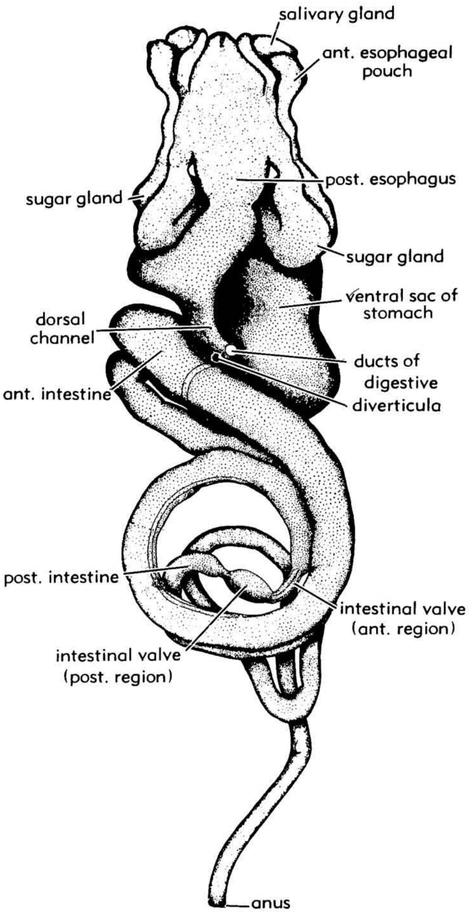

FIG. 5. Alimentary canal of *Lepidochitona cinereus* (6).

the invariably single ventricle. The gut (Fig. 5), described in detail by FRETTER (6), has many primitive features. In keeping with the habit of browsing (primarily on plant material) on hard substrata, there is a long and broad radula, each tooth row possessing 17 teeth, lubricated by mucus from salivary glands. The primitive esophageal glands are here represented by small anterior and large posterior pouches, the latter being sugar glands that secrete amylase. Cilia in the stomach, more restricted than in most Gastropoda and essentially all Pelecypoda, are confined to tracts in a dorsal channel, into the posterior end of which open the ducts of the bilobed digestive diverticula that secrete protease. Phagocytes are numerous in the epithelium and lumen of both stomach and intestine, but there is apparently no intracellular digestion, only absorption, in the digestive diverticula. The intestine is divisible into four parts, (1) an anterior intestine, from which fluid products of digestion are squeezed into the ducts of the digestive diverticula, (2) a valve, controlling passage of material into the very long and glandular (3) posterior intestine, which is followed by (4) a short, nonglandular rectum. Regions (3) and (4) are concerned exclusively with elaboration and consolidation of fecal pellets. The anus opens into the posterior end of the mantle cavity.

This cavity and its contained organs are profoundly influenced by the complete overgrowth of the body by the mantle-and-shell and the general flattening of the entire animal. Between the foot and the encircling pallial girdle, also normally in contact with the substratum and a structure of great sig-

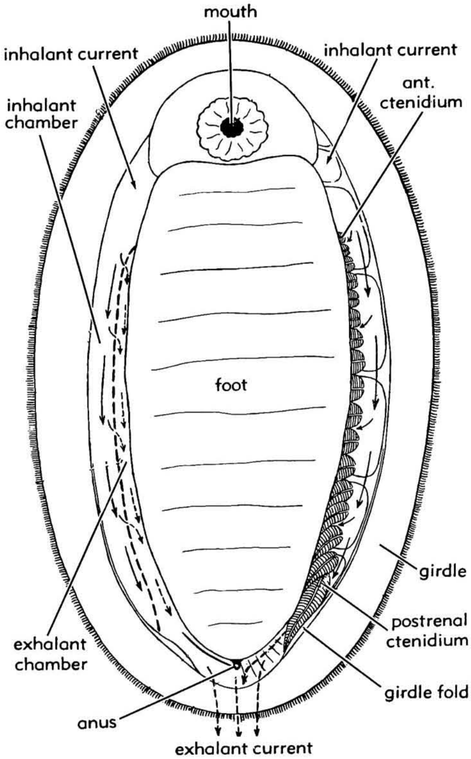

FIG. 6. *Lepidochitona cinereus,* ventral aspect, drawn from life; ctenidia and boundaries of shell plate shown in left pallial groove, division between inhalant and exhalant chambers (denoted by broken line) in right pallial groove (27).

nificance, extend the narrow pallial grooves representing the anterior extension of the much-reduced posterior mantle cavity (Fig. 6). The problem presented by this change in form of the respiratory chamber is met by multiplication of the ctenidia, which continue to divide the mantle cavity into inhalant and exhalant chambers. The ctenidia vary greatly in number (4 to 80 pairs), and the series may be holobranch or merobranch according to whether they occupy all or only part of the pallial grooves. Each one (Fig. 7) has the structure already outlined, but the filaments are characteristically short and deep, with a very broad band of lateral cilia. The unique feature is the presence of a broad band of long cilia on the sides of the filaments (corresponding to the tip of the more characteristic filaments shown in Fig. 3); these cilia interlock with those of the filaments of adjacent ctenidia so as to form the functional division between inhalant and exhalant chambers.

The ctenidia are attached to the roof of the pallial grooves and hang down with the efferent (or frontal) surface facing outward. Hence the respiratory current is drawn inward against the side of the foot. Separation of the outer (ventral) inhalant chamber and the inner (dorsal) exhalant chamber is completed posteriorly by the bridging of the pallial grooves in the region of the girdle folds (Fig. 6), by the last (postrenal) ctenidia in the Chitonida and by the adanal ctenidia in the Lepidopleurida (27).

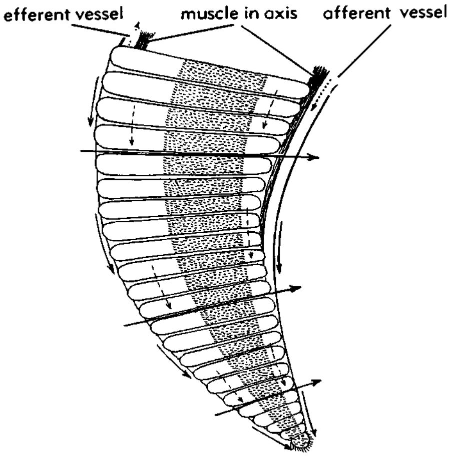

FIG. 7. *Lepidochitona cinereus,* posterior aspect of a ctenidium from the left pallial groove, drawn from life. Stippled area that of long attaching cilia on filaments. Arrows indicate direction of ciliary currents (large arrows respiratory current), dotted arrows showing flow in afferent blood vessel.

The effect of anterior extension of the mantle cavity, together with ctenidial multiplication and changed disposition, has been to displace the inhalant streams from the posterior end. They now have no fixed position. Wherever the girdle is raised, anterior to the girdle fold, water inevitably enters to be carried through the ctenidia. The renal and reproductive pores open into the exhalant chamber between ctenidia and foot, their products being carried posteriorly to leave, together with feces, in the mid-line posteriorly between the last pair of ctenidia (Fig. 6). Strips of mucous and sensory epithelium occur in the pallial grooves or on the ctenidial axes, some being possibly homologous, and all probably analogous, with the hypobranchial glands and osphradia, respectively.

The Polyplacophora constitute a well-defined and homogeneous group in which the primitive molluscan habit of crawling on hard substrata has been developed to permit life on uneven surfaces. Extension and overlap of the body by the mantle-and-shell with dorsoventral flattening and subdivision of the single valve into an articulating linear series, and finally, the modification of the mantle cavity with multiplication of the ctenidia all tend to this end. Since rocky surfaces are intertidal or in shallow depths, it seems reasonable to assume that the Polyplacophora evolved in shallow, possibly intertidal, waters. Of the two existing orders,[1] the Chitonida are almost exclusively shore-dwelling and occur in all seas. They have a more efficient respiratory system and more complex shell plates than the Lepidopleurida, now represented by only four genera, few species of which live intertidally, although extending into deep, even abyssal, seas. They have a poorer respiratory system but consolidate sediment in the inhalant chamber—not, as in the Chitonida, in the exhalant chamber. This doubtless assists them to live in muddier substrata and may explain

---

[1] Living chitons are classified by A. G. SMITH in a later section of this volume as belonging to the order Neoloricata, divided into suborders named Lepidopleurina, Ischnochitonina, Acanthochitonina, and Afossochitonina.—ED.

their survival after the more efficient Chitonida had established themselves on the shore.

Class APLACOPHORA

This small group of wormlike Mollusca can receive only passing reference. It has been included by some authors with the Polyplacophora in the class Amphineura, but appears better treated as a separate class. In many respects the animals are more specialized, although less successful, than the Polyplacophora. In place of a shell, a thick cuticle, in which spicules may be embedded, is secreted by a mantle, which almost or completely surrounds the body. In the former case, a much-reduced foot with associated mucous glands occupies a narrow ventral groove. A reduced radula may be present and the gut is straight, with only salivary glands opening into it. The animals are carnivorous, usually feeding on coelenterates, but the shortened gut is probably associated with lack of danger of fouling the respiratory chamber, which, if present at all, represents a small posterior cloacal chamber. What appear to be ctenidia are present in *Chaetoderma*. The majority are hermaphroditic, at least one protandric, the gonads (or gonad) opening into the pericardium, which communicates with the exterior by paired ducts carrying spermathecae and serving solely as gonoducts. They are not excretory and have been claimed to be ectodermal. There are well-developed ganglia in the nervous system. These sluggish animals extend from shallow water to great depths, usually on muddy substrata.

Class GASTROPODA

GENERAL DESCRIPTION

This class, the most diverse group in the Mollusca, is characterized by having suffered torsion now or in the past. The Gastropoda must have arisen from primitive mollusks in which the mantle-and-shell did not elongate and spread over the flattened body as in the *Amphineura* but deepened to contain the viscera compacted into a rounded mass. The single pair of shell muscles possibly represents reduction from a primitively greater number found in the Monoplacophora for instance, or both conditions could have arisen by the concentration (or splitting up) of a more primitive band of muscles on each side. The mantle cavity deepened as the shell became more conical and instead of the mantle-and-shell spreading over head and foot, these could be withdrawn within the shelter of the deepening shell by contraction of the shell muscles, later extrusion being due to hydrostatic pressure.

Solution to the problem presented by increasing height of the shell was found in coiling, brought about by growth of the mantle-and-shell out of the plane of the generating curve (as it exists at any moment), such growth being greatest around the posterior margin (19) and producing a planispiral shell with the apex directed forward (i.e., exogastric). This enabled the lengthening visceral mass to be disposed in the most compact manner. It is impossible to say to what extent coiling preceded torsion, with which it was certainly *not* connected. Knight (12) thinks that *Latouchella* with the spire of the shell curved only through some 90 degrees, may have been the "first bellerophont and first prosobranch." It seems possible, however, that greater coiling than this did precede torsion, although certainly without asymmetry.

These matters of conjecture are of minor importance; it is agreed that there was no internal asymmetry, although the gonads may have been the exception. In no existing gastropod are they paired, even where the pallial organs, auricles, and kidneys (although asymmetrical) are paired. The solitary gonad, which may represent fusion of the original pair (as occurs in the Polyplacophora), opens primitively by way of the renal duct on the right *(post-torsional)* side. The pretorsional right gonad may have been lost or have become fused with the left gonad, which alone retained communication with the kidney duct (Fig. 8).

The remarkable process of torsion comprises displacement of the mantle-and-shell with the enclosed visceral mass moving in a counter-clockwise direction in the horizontal plane through an angle of 180 degrees in relation to the head and foot. The mantle cavity, in consequence, becomes anterior. Torsion can be observed during larval development in Archaeogastropoda such as *Haliotis, Acmaea, Trochus,* and *Patella,* and in *Viviparus* (5, 29). Initial asymmetry of larval shell muscles causes torsion when they are able to contract, although the time taken in different species to complete torsion varies greatly, judging from available observations. The many hypotheses concerning the possible origin of torsion re-

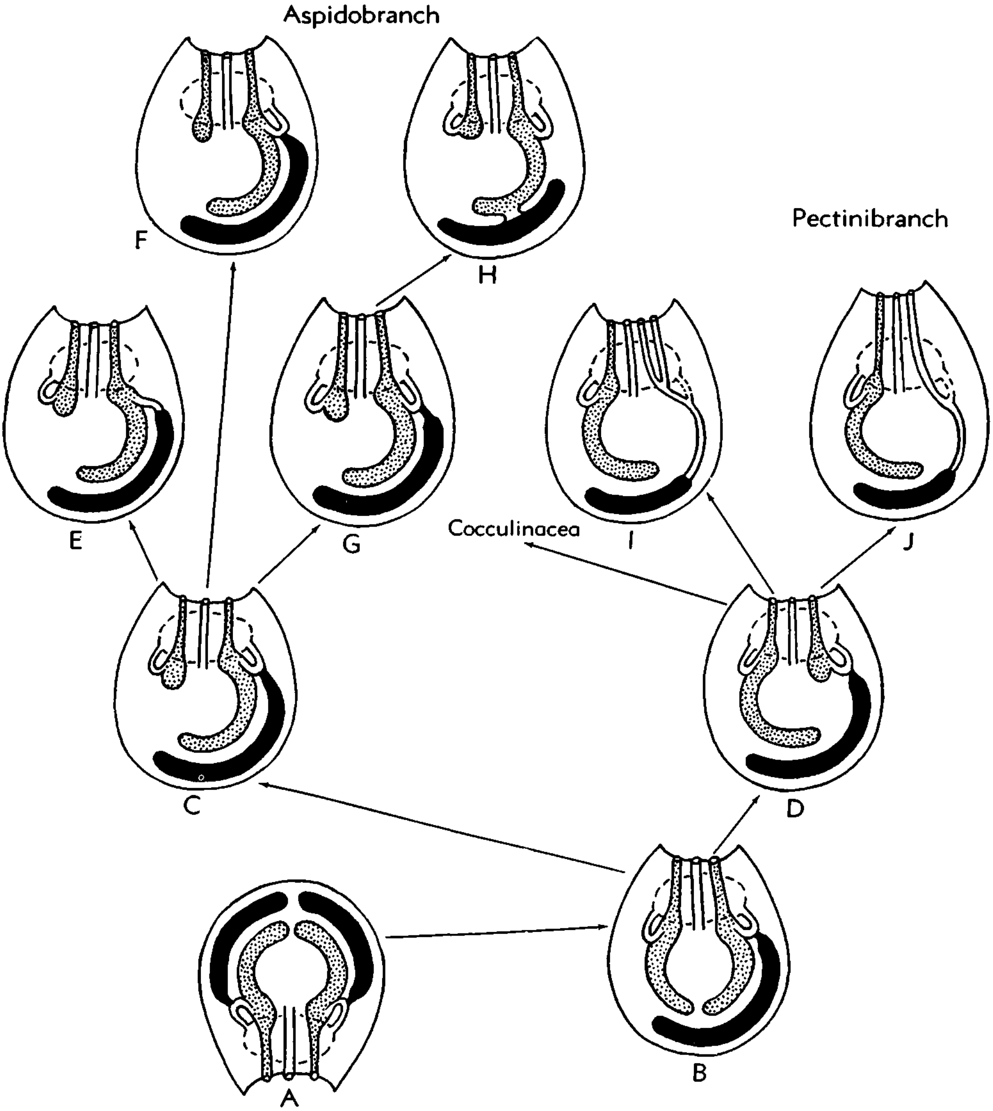

FIG. 8. Diagrams showing arrangement of kidneys and gonads throughout the Prosobranchia (kidneys and ducts stippled, gonad black, pericardium indicated by broken line, anus shown between urinogenital ducts opening into mantle cavity) (29).——*A.* Hypothetical primitive condition.——*B.* Loss of left post-torsional gonad (may have occurred before or after torsion).——*C.* Reduction of left and retention of right kidney, ancestral to conditions in *E, Pleurotomaria* and *Haliotis, F, Diodora* (Fissurellidae), *G, Puncturella* and Trochidae, *H,* Patellacea, i.e., all Archaeogastropoda except Neritacea *(I)* and Cocculinacea.——*D.* Reduction of right and retention of left kidney, ancestral to conditions in Neritacea *(I)* and in all remaining Prosobranchia.

viewed by Naef (17) and Crofts (4) may be summarized (29) in the form of postulates that torsion occurred:

(i) originally by stages in the adult;
(ii) in the embryo due to antagonism between the growth of the foot and that of the shell;
(iii) in the embryo but essentially to meet needs of the adult;
(iv) rapidly in postlarval life to meet the needs of adult life;
(v) rapidly in embryonic life to meet purely embryonic needs.

The last-stated hypothesis, which is associated with the name of Garstang (8), is much the most probable. A larval mutation involving torsion would have survival value because, as shown in Figure 9, before torsion the foot is adjacent to the mantle cavity, so that the delicate and all-important velum—responsible for both locomotion and feeding—cannot be withdrawn. But after torsion the head and velum can be pulled back into the now anterior mantle cavity followed by the foot, the protection of which was enhanced by the appearance, on the dorsal surface posteriorly, of an operculum which closed the opening. It does appear probable that post-torsional veliger larvae would be selected in preference to those in which torsion had not occurred. The other hypotheses (apart from ii, associated with Boutan, which postulates no advantage to either embryo or adult) all assume that the adult benefits by torsion and involve either teleological assumptions or the inheritance of acquired characters. But a larval mutation bringing immediate advantage to the embryo and involving a process still exhibited in the development of Gastropoda with pelagic larvae is much more credible. Moreover, it accounts for the absence of intermediate forms. So far from being of immediate benefit to the adult, torsion raised major problems that only subsequent evolution has solved. With the reduction and final loss of the shell in the Opisthobranchia, detorsion occurs, the mantle cavity moving to the right, the roof then folding back so that the cavity disappears.

The immediate effect of torsion in the adult is to place the mantle cavity behind the head and to twist both gut and nervous system. The anus now opens in the mid-line above the head, while the tube of the gut is twisted to the left in the region of the esophagus. The visceral loop, which connects pleural and visceral ganglia, becomes twisted into the streptoneurous condition. But these asymmetries are internal; so long as the

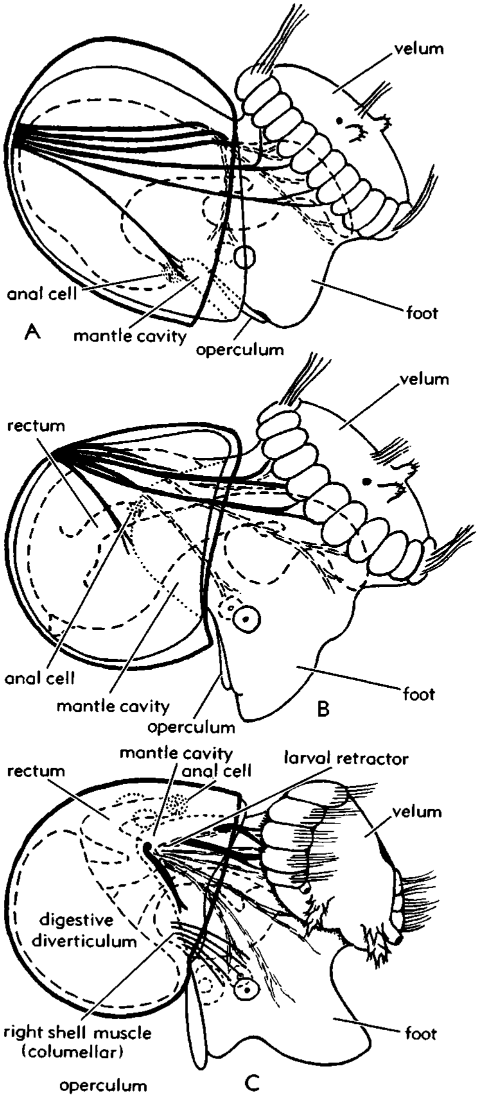

Fig. 9. *Patella vulgata,* reconstruction of veliger larva (5).——*A.* At 70 hours, ready for torsion, viewed from right side, showing lateral retractor cells *(A-F).*——*B.* At 76 hours, with 90 degrees torsion, showing rectum and anal cell with mantle cavity on right side.——*C.* With 180 degrees torsion (3½ to 4 days old), showing final position of rectum, anal cell, and mantle cavity.

]

shell remained symmetrical there would be no asymmetry in the mantle cavity.

The immediate problem, as first stressed by GARSTANG (1928), would be one of sanitation. Renal and reproductive products and feces would be carried forward over the head of the animal in the exhalant current. The marginal slit or shell apertures present in existing pleurotomariids and in other zygobranchous genera (e.g., *Scissurella, Haliotis, Diodora, Emarginula, Puncturella*) enable the exhalant current to be directed dorsally, away from the head. All fossil shells possessing a marginal slit or sinus (e.g., the "bellerophonts") were those of gastropods; before torsion there was no reason for such a slit. As shown by KNIGHT (1947) for *Sinuites* and *Bellerophon,* such animals possessed a single pair of symmetrical shell muscles, each one being "attached to the opposite end of the columella about one-half whorl within the aperture, a position that would enable them to serve effectively as pedal retractors." There is no evidence that they possessed opercula. But the earliest gastropods would have had no marginal slit, and KNIGHT (12) may be correct in considering that the Coreospiridae, which he includes with the Bellerophontacea, were such animals.

With the bellerophonts the effects of torsion were partially offset by the presence of a marginal slit. The mantle-and-shell, and so the organs in the mantle cavity, remained symmetrical; internally there was asymmetry of the gut and nervous system, possibly also of the reproductive system. Asymmetry of the mantle-and-shell came when a turbinate-spiral replaced a planispiral form owing to changes in growth gradients around the margin of the mantle-and-shell (19). The spire of the shell now projected to the right in a dextral shell and to the left in a sinistral one. This change brought about a more compact arrangement of the viscera and a rearrangement of the shell in relation to the foot, on which it came to rest obliquely instead of longitudinally.

The course of this process, outlined by NAEF (17), is shown in Figure 10. The original transverse axis of coiling became directed posteriorly while the apex was turned up so that balance was restored, with the first whorl resting on the dorsal surface of the foot where, then or subsequently, the operculum was formed. The first process NAEF calls "regulatory detorsion," the second "inclination." The effect of this (coiling being dextral) was to compress the right side of the mantle cavity; hence the pallial organs on the left were enlarged, while the marginal slit and anus were moved from the mid-line to the right. Asymmetry of the mantle-and-shell led to asymmetry of the pallial organs, but, as shown in existing pleurotomarians, paired ctenidia, osphradia, and hypobranchial glands persisted and the respiratory circulation in the mantle cavity was unaltered.

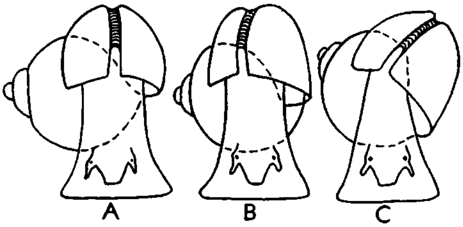

FIG. 10. Diagrams illustrating regulation of position of gastropod shell following asymmetrical coiling (17).——*A*. Shell before regulation.——*B*. Original transverse axis of coiling directed posteriorly ("regulatory detorsion").——*C*. Spire of shell directed upward, so restoring balance, the first whorl resting on the operculum ("inclination").

A fundamental dichotomy arose in connection with the reno-reproductive system. Either the right kidney was enlarged and the left one reduced—as in all aspidobranchiate Gastropoda except the Neritacea and Valvatacea (Fig. 8)—or the left kidney alone remained. While the loss of the right kidney could be associated with that of the right ctenidium and auricle, the loss or reduction of the left kidney in the Archaeogastropoda, where the pallial organs on that side persist, is difficult to understand. But the consequences are clear. Where the right kidney persists, the solitary gonoduct—invariably on the post-torsional right—must open via the ureter. If the left kidney is retained, the right ureter persists to form part of the gonoduct. Important consequences follow. Throughout the Archaeogastropoda, egg and sperm are shed freely; there is no penis and, in the female, no accessory glands, except to a minor extent in certain Trochacea such as *Calliostoma.* Development is larval; in consequence, the Archaeogastropoda are confined to the sea.

In the remaining Prosobranchia, which include the Neritacea and Cocculinacea (contained by THIELE in the Archaeogastropoda), there is no such restriction to internal fertilization and the elaboration of yolky eggs with protective capsules. The male possesses a penis, the female has oviducal glands, which, like the penis, are of pallial origin. With internal fertilization and direct development, leading in some cases to ovoviviparity, these animals were able to invade fresh waters and the land. This is true not only of the higher Prosobranchia (Mesogastropoda and Neogastropoda) but of the Neritacea, which, in the opinion of the author, should be raised to the status of an order. So possibly should the Cocculinacea, where also the right kidney is lost but which, possibly in association with their deep-sea habitat, are hermaphroditic.

The ctenidia may continue to be paired (zygobranchous) or only the left ctenidium may persist (retaining the aspidobranch form with filaments alternating from each side of the axis, or with reduction to the pectinibranch condition having a single row of filaments on the right side and the axis adherent to the pallial wall). Reduction to one ctenidium is accompanied by loss of one osphradium and hypobranchial gland; with the change to the pectinibranch condition the position of the osphradium alters, for it continues to lie in the direct line of the current entering the mantle cavity, suspended matter impinging upon it. In certain cases (e.g., Patellacea, *Caecum*) the osphradium, but never the hypobranchial gland, may persist after the ctenidium is lost.

Subclass PROSOBRANCHIA

Order ARCHAEOGASTROPODA

The aspidobranch condition is retained in all Archaeogastropoda, as well as in the Valvatacea among the Mesogastropoda. It takes the following forms:

(i) Asymmetrical shell with two ctenidia, i.e., zygobranchous Pleurotomariidae, Scissurellidae, and Haliotidae, the last a highly successful and specialized family in which the limpet character has been attained without complete loss of asymmetrical coiling of the shell.

(ii) Secondarily symmetrical shell with two ctenidia, i.e., the zygobranchous Fissurellidae, which form the bulk of living zygobranchs and contain many genera. In these limpets the shell is symmetrical, as are the pallial organs, although not the reno-reproductive system. The exhalant current issues either by way of a marginal slit (e.g., *Emarginula*) or, more usually, through a single apical aperture (e.g., *Diodora, Puncturella, Scutus*).

(iii) Asymmetrical shell with loss of right ctenidium. This condition, accomplished with loss of the shell aperture, has been achieved independently by the Trochacea, Neritacea, and Valvatacea. A left-right respiratory circulation is developed, the anus moving to the right side, one of the major disadvantages of torsion thus being overcome. This becomes apparent when the numerous and widespread Trochacea are compared with the scanty remnants of the Pleurotomariidae, from which they differ essentially only in loss of the right pallial organs and of the slit in the shell. An important point in the mantle cavity of the Trochacea is the enlargement of the solitary left ctenidium supported by the forward extension of the originally short afferent ("dorsal") membrane. While achieving its immediate object, this produces a pocket between the ctenidial membranes and the left wall of the mantle cavity (Fig. 11*C*). This pocket is readily blocked with sediment so that, although the Trochacea are universally distributed on hard substrata between tide marks and in shallow water, they do not invade muddy areas.

In the Neritacea, the aspidobranch ctenidium is unsupported, has very short filaments, and bends to the right. Resemblance to the Trochacea is superficial. Reno-reproductive arrangements are different in the two groups, and although the Neritacea and Trochacea have the same environmental limitations in the sea (confined to hard substrata), the Neritacea have spread into fresh waters and onto land.

The Valvatacea, which are asymmetrically shelled mesogastropods lack-

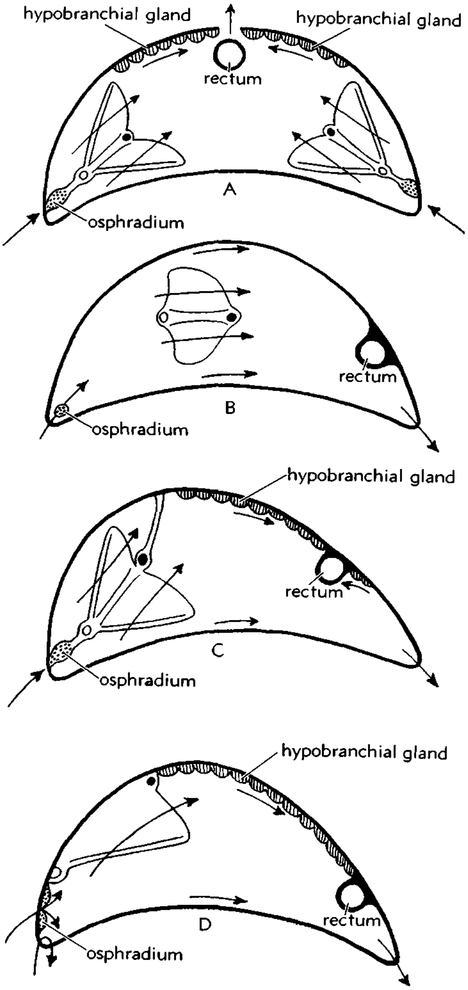

FIG. 11. Diagrams illustrating relations between ctenidia, osphradia, and hypobranchial glands in gastropods (29).——*A*. Zygobranchous archaeogastropod.——*B*. *Patelloida* (Acmaeidae), i.e., Patellacea with single aspidobranch ctenidium. Inhalant and exhalant currents indicated, also respiratory currents on ctenidia and direction of cleansing currents in mantle cavity (anteriorly directed current conveying material out through *inhalant* opening in *D*).

ing the right ctenidium, are referred to in describing the Mesogastropoda.

(iv) Secondarily symmetrical shell with loss of one or both ctenidia. This condition occurs in the Patellacea, also in the Cocculinaea and in *Septaria* amongst the Neritacea. All are limpets and the Patellacea are the most successful of the many groups that have independently assumed this form. In contrast with the Fissurellidae, which they resemble in form and in possessing a horseshoe-shaped shell muscle, they have one ctenidium, arising presumably from ancestors in which, as in the Trochacea, the right ctenidium was lost. In Acmaeidae, such as *Patelloida* (Fig. 11*B*), the left ctenidium is well developed and horizontally disposed, producing a respiratory current entering on the left and leaving the pallial grooves in the mid-line posteriorly; in others, such as *Lottia*, secondary pallial gills are also present in the pallial grooves. In the Patellidae these gills alone occur, although conditions in *Patina* appear intermediate between those in *Lottia* and in the supremely successful *Patella*, where the pallial gills provide an ideal mode of respiration under shore conditions and in which sediment is extruded by muscular instead of ciliary agencies (29).

Order MESOGASTROPODA

[=Caenogastropoda *(partim)*]

Except for the Valvatacea all members of the order Mesogastropoda and of the Neogastropoda possess a pectinibranch ctenidium, unless this has been lost (e.g., *Caecum* and some Heteropoda). This permits uninterrupted left-right flow through the mantle cavity and free disposal of sediment by tracts of cleansing cilia on the pallial floor, the ctenidial filaments, and the hypobranchial gland. A major difficulty presented by torsion is thus removed; in contrast to the Archaeogastropoda, the Mesogastropoda can occupy soft substrata. The left kidney is retained, so permitting free elaboration of the gonoducts on the right. Internal fertilization with direct development and in some groups viviparity now occurs. The Mesogastropoda have thus spread into fresh waters and, with loss of the ctenidium, onto land.

The Valvatacea resemble the pectinibranchs (i.e., Mesogastropoda, Neogastropoda) in all but the possession of an hermaphroditic reproductive system and the retention of an aspidobranch ctenidium.

The Mesogastropoda display a striking degree of adaptive radiation. Apart from the fresh-water and terrestrial Architaenioglossa and Valvatacea, they burrow in mud (e.g., *Turritella, Aporrhais, Struthiolaria*), move actively through sand (e.g., Naticacea), and swim or float in surface waters (Heteropoda and *Janthina,* respectively). Others (e.g., *Littorina*) retain a more primitive habit, but some have become cemented to the substratum (e.g., Vermetidae, which derive from animals with much-coiled shells, and *Hipponyx,* which, like all Calyptraeacea, is a limpet). Although the parasitic Aglossa should probably now be transferred to the Tectibranchia, *Thyca* (Calyptraeacea) remains an undoubted mesogastropod parasite.

Extremes of form are revealed by a comparison between the sessile Vermetidae and the more modified representatives of the highly active pelagic Heteropoda. In the former, the body, with its anteroposterior axis of growth, is completely subordinated to the mantle-and-shell, the rounded foot (with or without an operculum) having no function except as a plug to close the opening of the shell, the mucus from the pedal gland being used in some for food collection. Opposite conditions prevail in heteropods such as *Carinaria,* where the body is elongated with an enlarged head and a laterally compressed foot, the anterior portion of which is used as a fin. The visceral mass and the enclosing mantle-and-shell are greatly reduced, the ctenidium projecting from the small mantle cavity. Greater reduction of the mantle-and-shell occurs in *Pterotrachea* and *Firoloida,* all pallial organs being lost in the latter. The whole process of reduction of the mantle-and-shell and enlargement of the head and foot with elongation of the body is admirably shown in the series *Oxygyrus-Carinaria-Pterotrachea-Firoloida,* just as the reverse process of increasing domination by the mantle-and-shell can be traced from a *Turritella*-like stock feeding with ciliary currents to sessile operculate vermetids feeding in the same way, and so to those without an operculum and feeding by mucous strings (14).

The usually taenioglossid radula would appear more adaptable for a variety of feeding habits than is the scraping rhipidoglossid or docoglossid radula of the Archaeogastropoda. Apart from relatively unspecialized herbivores and omnivores, feeding habits in the Mesogastropoda are diverse, including groups of differently specialized carnivores such as the Naticacea, Cypraeacea, Tonnacea, and Heteropoda, no less specialized herbivores like *Lambis* and *Strombus* (feeding largely on epiphytic red seaweeds), detritus-feeders such as *Aporrhais* and *Hipponyx,* and ciliary feeders of diverse origin, including some Vermetidae, many Calyptraeidae and some Capulidae, and such forms as *Turritella* and *Viviparus.* In these the filaments of the pectinibranch ctenidium are lengthened and their cleansing frontal and adfrontal cilia together with tracts on the mantle surface are modified for food collection. Within the gut, esophageal glands persist except where, as in the ciliary feeders and some herbivores (e.g., Strombidae) there is a crystalline style (10). In the carnivores, the stomach becomes simpler, with greater development of extracellular digestion.

While many Mesogastropoda are of separate sexes, increasing numbers of hermaphrodites, usually protandric, are reported. The reproductive system (7) is divisible into (1) gonad, (2) gonadial region of duct forming a seminal vesicle in the male, (3) short renal region of duct (formerly right ureter) extending to the posterior end of the mantle cavity, (4) pallial region of duct reaching to the opening of the mantle cavity. In the male this may be a ciliated groove or be closed and has usually an associated prostate gland, the combined secretions passing to a nonretractile penis on the right side of the head. This organ is absent in some (e.g., *Turritella,* Vermetidae) where sperm is received in the inhalant current. The female pallial duct consists of an albumen gland, a capsule or jelly gland, and a bursa copulatrix, where the sperm is initially received and from which it passes by a nonglandular ciliated groove to the receptaculum seminis (Fig. 12). A remarkable diversity of protective capsules are here formed (23). Ovoviviparity occurs (e.g., in *Littorina rudis, Hydrobia jenkinsi, Viviparus viviparus*).

Order NEOGASTROPODA
[=Caenogastropoda (*partim*)]

In these gastropods, as in some of the Mesogastropoda, the mantle margin on the left side of the mantle cavity is extended to

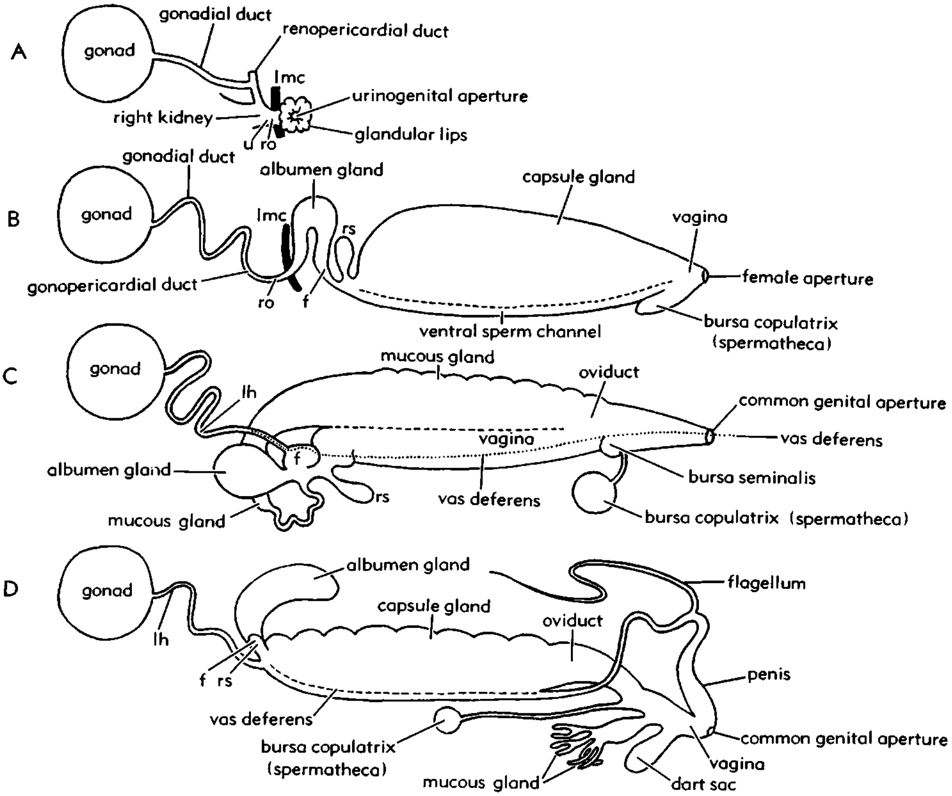

Fig. 12. Comparative diagrams of genital ducts in gastropods (7).——*A*. Archaeogastropod, Trochidae (female).——*B*. Stenoglossid, *Nucella* (female).——*C*. Opisthobranch *Aplysia* (hermaphrodite).——*D*. Pulmonate *Helix* (hermaphrodite). (Explanation: *f*, site of fertilization; *lh*, little hermaphrodite duct (gonadial and renal); *lmc*, limit of mantle cavity; *ro*, renal oviduct; *rs*, receptaculum seminis; *u*, ureter).

form an inhalant siphon, with a corresponding groove in the opening of the shell, which may be greatly prolonged, as in the Muricidae. There is a well-developed proboscis and a narrow radula, rarely lost, with not more than three teeth in a row. There is an unpaired esophageal gland (gland of Leiblein or else poison gland). The nervous system is more concentrated than in the other Prosobranchia. The osphradium is large and bipectinate and with little doubt serves here as a chemoreceptor. The animals are of separate sexes, with a large penis in the male.

These represent the leading characteristics of an order less diverse in form and habit than the Mesogastropoda. Almost all are marine, while most of the characteristic features can be related to a carnivorous or omnivorous scavenging habit. The proboscis, commonly of great length, with the narrow rachiglossid radula, fits them for eating out the bodies of carrion (e.g., *Buccinum, Nassarius,* and other whelks) or for boring through the shells of living prey such as barnacles or bivalves (e.g., *Nucella, Urosalpinx*). The more specialized Toxoglossa (e.g., *Conus*) kill their prey by means of the long proboscis armed with modified toxiglossid radula and associated poison gland. Possession of a siphon enables Stenoglossa to exploit soft substrata but they are not so restricted to this habitat as are, for instance, the mesogastropod Naticacea. They are well equipped with receptors, nervous system, and large foot, for locating and pursuing or reaching, their prey. Details for the reproductive system (Fig. 12*C*) are the same as in the Mesogastropoda.

Subclass OPISTHOBRANCHIA

The characteristic features of this subclass are the reduction and eventual loss of the shell, with accompanying detorsion. Only the primitive genus *Acteon* possesses an operculum and can withdraw completely within the shell. The mantle cavity migrates to the right and then posteriorly before opening out. Although in the Notaspida (e.g., *Pleurobranchus*) what has been described as a ctenidium persists, loss of all pallial organs usually accompanies loss of the cavity. Respiratory functions are assumed by undoubted secondary gills in the Nudibranchia, while protection, formerly afforded by the shell, is provided by repugnatorial glands or, in some Nudibranchia, by nematocysts obtained from coelenterate prey. With detorsion, the streptoneurous condition, retained in *Acteon,* gives place to a secondary euthyneury, while nerve ganglia tend to be concentrated around the esophagus; but both conditions occur in some Prosobranchia. The gut straightens (Fig. 2*E*), and external bilateral symmetry is regained. But the effects of asymmetrical coiling of the shell persist (i.e., the single auricle and asymmetry of renal and reproductive systems). Opening out of the mantle cavity may have to do with the inefficiency of the gills, the resemblance of which to ctenidia is probably only superficial. The radula is multiseriate, teeth being reduced in carnivores as in the Prosobranchia. Neither esophageal glands nor style-sac occurs (except possibly the latter in the thecasomatous Pteropoda). The reduced stomach (Fig. 2*E*) is associated with the development, probably from the esophagus, of a gizzard (e.g., *Scaphander, Philine*) or of a crop (e.g., *Aplysia*).

The reproductive system (Fig. 12*C*) is invariably hermaphroditic. Apart from *Acteon,* there is a retractile penis. This must have evolved independently of the pedal outgrowth present in this genus and in higher Prosobranchia (where it is sheltered in the mantle cavity). The pallial region of the hermaphrodite duct is fundamentally similar to that of a female prosobranch but typically divided longitudinally into male and female passages. *Actaeon* is not primitive in this respect but is so in that the pallial ducts do not sink into the haemocoel as they do in the higher Opisthobranchia. The albumen gland is an appendage to the female tract; eggs do not pass through it as they do in the Prosobranchia. Egg capsules are never formed, but the fertilized eggs are laid in jelly-like masses.

The Opisthobranchia are exclusively marine, their representatives displaying in this environment almost as great a range of adaptive radiation as do the Mesogastropoda. Reduction or loss of the shell proves no disadvantage except for invasion of fresh waters and the land, although the intertidal Onchidiidae have a lung. In habit they range from sand-burrowers, like *Acteon* and *Scaphander,* to herbivorous and carnivorous browsers, like *Aplysia* and many Nudibranchia, to parasitic Pyramidellidae and pelagic Pteropoda. Probably in no comparable group is there such a range of feeding habits, many genera living exclusively on a particular animal or plant (e.g., *Calma* on fish eggs, *Tritonia* on octocorals, and *Pleurobranchus* on simple ascidians). The radula can be highly specialized, notably in the Sacoglossa which suck plant tissues, while ciliary feeding mechanisms—on the epipodia, *not* in the mantle cavity—occur in the thecasomatous Pteropoda. The carnivorous Gymnosomata are the only Gastropoda to possess suckers.

Subclass PULMONATA

The pulmonate gastropods are widespread on land and have invaded fresh waters. Without a ctenidium they retain, with few exceptions, the mantle cavity which acts as a lung. Its reduced and contractile posterior opening forms the pneumostome; a secondary gill occurs in some fresh-water Planorbidae. Usually there is a well-developed shell but only in *Amphibola* an operculum. The radula is primitively multiseriate, but teeth are reduced, as usual, in correlation with the carnivorous habit. Unlike the Prosobranchia with their paired lateral jaws, the Pulmonata possess a single median jaw, which is dorsal. The esophagus lacks secreting pouches. The stomach (Fig. 2*E*) has lost its primitive ciliary sorting function and, apart from some ellobiids, all trace of the style region. There is typically a gizzard of gastric origin, not of esophageal origin, as in the Opisthobranchia. Extracellular digestion is highly developed, the digestive diverticula being the site both of secretion and of absorption.

The Pulmonata are euthyneurous owing to concentration of all nine nerve ganglia around the esophagus. The auricle is usually anterior, for only in a few detorted genera, such as the carnivorous slug *Testacella,* does it lie behind the ventricle.

Correlated with use of the mantle cavity as a lung, the ureter elongates and typically opens, together with the anus, outside the cavity. All Pulmonata are hermaphroditic, the primitive Ellobiidae being protandrous. In the great majority (*not* in *Helix,* Fig. 12*D*) there are separate male and female openings, the latter representing the original hermaphrodite opening. With the formation of a closed mantle cavity, the female opening comes to lie just in front of the pneumostome. The male opening is on the right side of the head, the penis being retracted into a preputium or penial sac. As in the Opisthobranchia, although for somewhat different reasons, the primitive penis is lost.

Order BASOMMATOPHORA

These pulmonates possess a single pair of noninvaginable tentacles with eyes at the base; all have a shell; the penis is usually removed from the female aperture; there is a veliger stage with reduced velum. The Basommatophora are a somewhat miscellaneous collection of possibly not closely related animals. The Ellobiidae and Otinidae range in habitat from estuarine and intertidal to coastal and inland terrestrial conditions and are certainly primitive. The remainder are divisible into the intertidal marine Amphibolacea and Patelliformia (Siphonariidae and Gadiniidae) and the fresh-water Hygrophila.

Order STYLOMMATOPHORA

There are here two pairs of invaginable tentacles with the eyes borne on the tips of the posterior pair; the male and female apertures usually open into a common vestibule (Fig. 12*D*). There is never a veliger in development. The shell may be reduced to calcareous granules (e.g., *Arion*). This purely terrestrial order (the Onchidiacea are primitive Opisthobranchia) contains very many species displaying great adaptive radiation and exploiting a great range of habitats on land.

The origin of the Pulmonata may be traced with greatest probability through the Ellobiidae (14, 15). But, like the higher Prosobranchia, if not the Opisthobranchia, they must initially have sprung from monotocardiate Archaeogastropoda with, of course, the functional kidney on the left side (i.e., as in Fig. 8*D*). Paleontological evidence indicates that all of these major groups appeared in the Paleozoic,[1] each of them displaying great subsequent adaptive radiation. At the same time the primitive Archaeogastropoda—notably the Patellacea (Docoglossa) and the Trochacea—continued to exploit the possibilities of life on hard substrata in the sea.

Class PELECYPODA

In the evolution of the Pelecypoda the mantle-and-shell presumably first extended and then became laterally compressed, eventually enclosing the body, thus becoming solely responsible for the outward form of the animal. In addition to the symmetrically disposed shell or pedal muscles, there was further attachment by a line of pallial muscles close to the margin of the shell. This may or may not have preceded lateral compression, but the former condition is indicated in Figure 13. Compression was accompanied by subdivision of the mantle into two lateral lobes and a mantle isthmus along the mid-line dorsally. At the same time, anterior and posterior embayments attributable to the mechanical effects of compression shortened the line of the mantle isthmus and so of the ligament which it secreted. Hence the shell consisted of two calcareous valves and a relatively uncalcified uniting ligament. Meanwhile, the valves became united by anterior and posterior adductors representing the local enlargement and cross fusion of the pallial muscles where these came in contact as a result of the bending of the mantle into two lobes along the line of the mantle isthmus (Fig. 13*C*). The contraction of these muscles caused approximation of the two valves, at the same time distorting the ligament by compressing it below the hinge or pivotal axis and subjecting it to tensile stress above this (TRUEMAN, 1951).

Enclosure of the head was accompanied by its reduction, eventually to no more than the site of the mouth opening, devoid of radula and other buccal organs. Food was conveyed from outside the shell, initially

---

[1] Contributors on Paleozoic gastropods to this *Treatise* doubt the recognition of pulmonates in pre-Mesozoic deposits. —ED.

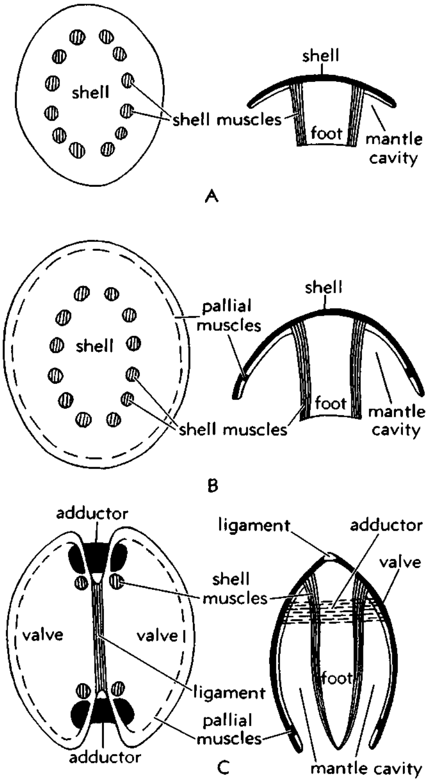

FIG. 13. Diagrams indicating possible stages in the evolution of the Lamellibranchia [Pelecypoda], dorsal view of shell with muscle attachments on left, transverse sections through mantle-and-shell and foot on right (32).——*A*. Primitive mollusk with flattened shell and paired shell muscles.——*B*. Later, with more concave shell overlapping laterally and with additional pallial muscles.——*C*. Compression of shell with two centers of calcification forming valves with ligament between, pallial muscle uniting to form adductors.

probably by palp prosboscides and only later by means of the water currents created by the enlarged ctenidia. The sensory functions of the head were taken over by the mantle margin, now in closest contact with the environment.

The shell (i.e., valves *and* ligament) in the Pelecypoda consists of (1) an external periostracum, (2) an outer, and (3) an inner, calcareous or ligament layer. Of these, the inner calcareous or ligament layer is secreted by the general surface of the lobes and the mantle isthmus, whereas the periostracum and outer calcareous or ligament layer are formed by the mantle edge, which is thrown into three folds (Fig. 14), outer, middle, and inner, of which the first is solely concerned with formation of the shell. Its outer surface secretes the outer calcareous layer of the valves and, at the depth of the dorsal embayments, the outer ligament layer. Its inner surface, including the depth of the groove between it and the middle lobe, secretes the noncalcareous periostracum, which covers *all* regions of the shell unless worn away.

The middle fold is largely sensory, being typically extended into tentacles and in some forms (e.g., *Pecten, Spondylus, Cardium*) carrying eyes. It is invariably most developed in the inhalant region, whether this be extensive (as in *Pecten* and *Ostrea*) or restricted to the margin of an inhalant siphon. The inner fold is muscular, controlling entrance into the mantle cavity of the powerful inhalant current created by the enlarged ctenidia in which much sediment may be carried. Where the entrance is widest, as in anisomyarian forms generally, this region is most developed, as in the "velum" or pallial curtains of *Pecten* or *Ostrea;* in siphonate genera it is correpondingly reduced, although here commonly taking the form of interdigitating rows of straining tentacles, as in the Myacea. In this group (as in others) this fold is also well developed around the exhalant opening, forming a membrane that directs the outflow clear of the inhalant stream.

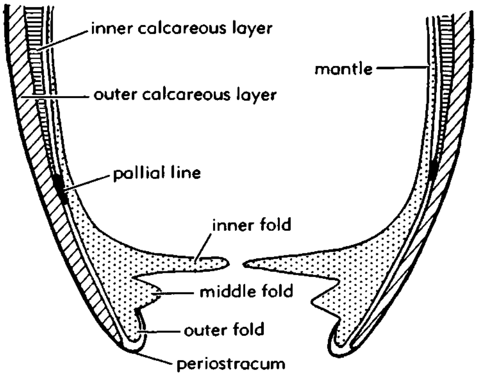

FIG. 14. Pelecypod, margin of mantle-and-shell showing three marginal mantle folds and three shell layers, periostracum being secreted by inner surface of outer mantle fold, outer calcareous layer by outer surface of outer mantle fold, and inner calcareous layer by general surface of mantle.

Complete enclosure of the body within the mantle folds permits the fusion of their margins. As noted above, this occurs initially in the formation of adductors by union of the inner mantle lobes and their contained pallial muscles. Localized fusions around the mantle margins later produce structural divisions between the exhalant and inhalant apertures, and between the latter and the pedal aperture, while in some pelecypods (e.g., Solenacea, Mactracea, Pandoracea) there is a fourth pallial aperture. Fusion is always preceded by local application of the mantle margins; it may take the form of ciliary junctions, cuticular fusion, or complete fusion of tissues. It may involve the inner mantle lobe only, or that together with the middle lobe, or also with the inner surface of the outer lobe, in which case the fused surface is covered with periostracum. Fusion of pallial muscles may lead to the formation of ventral adductors, as in the Tellinacea (30) and Adesmacea (21).

Siphons are formed by local hypertrophy of the mantle margins, being extended by intrinsic or extrinsic means and withdrawn by contraction of siphonal muscles representing local enlargements of the pallial musculature attached correspondingly farther from the edge of the shell. As in other regions of mantle fusion, siphons may be formed from (1) inner, (2) inner with middle, or (3) inner with middle together with inner surface of outer, folds of the mantle margin (Yonge, 1957*a*). Inhalant and exhalant tubes may be separate, as in the deposit-feeding Tellinacea (30) or, more commonly, be fused (as in the Myacea and Mactracea) where, the inner surface of the outer lobes being involved, the surface is covered with periostracum.

The ligament consists of periostracum (often worn away) with outer and inner ligament layers (Fig. 15). It may be increased in length by secondary extensions due to fusions, at one or both ends, of the inner or periostracum-secreting surface of the outer lobes or of their outer surfaces when a much thicker "fusion layer" is formed, either on the posterior side only, as in *Pinna* (Yonge, 1953*b*), or on both sides, as in the Pectinidae. The form of the ligament varies greatly, largely owing to bending of the mantle isthmus. The embayments may, however, extend until they meet, so dividing the shell into two valves, the ligament being lost. This occurs in the Adesmacea, being a prerequisite of the method of boring in these Pelecypoda (not necessarily true of other borers) where the two adductors contract alternately, the valves rocking on rounded dorsal, and in some cases also ventral, articulating surfaces.

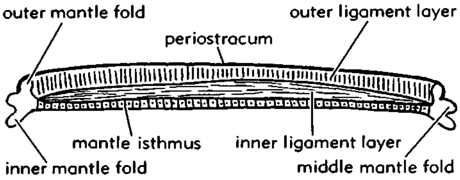

Fig. 15. Pelecypod, semidiagrammatic longitudinal section through ligament region of shell showing how three layers are secreted in the same manner as the three layers forming the rest of the shell.

Leaving external form until later, the enclosed body is little modified other than by compression. Bilateral symmetry is usually retained, the most notable exceptions being the monomyarians, which come to assume a horizontal posture either attached by byssus or cementation or else becoming secondarily free (32). But the primitive symmetry of the nervous, circulatory, and renal and reproductive systems is little affected, and there is still less effect on the organs in the mantle cavity. The extension both anteriorly and ventrally of the cavity permitted first lengthening and then deepening of the ctenidia. Despite their great modern success, conditions in the protobranchiate Nuculidae are in certain respects primitive and give important aid in following the course of evolution in the Pelecypoda.

As shown in Figure 16, the ctenidia are here restricted to the posterior half of the mantle cavity. They are attached by an elongate afferent membrane. Although increased in numbers, the filaments retain the primitive form; those of each ctenidium are attached by ciliary discs and also by terminal cilia to the filaments of the other ctenidium in the mid-line. Thus they constitute an effective partition between the inhalant and exhalant chambers, the more so because laterofrontal cilia (not present in the primitive filament) assist in preventing the passage of particles upward between the filaments. Nevertheless, sufficient particles

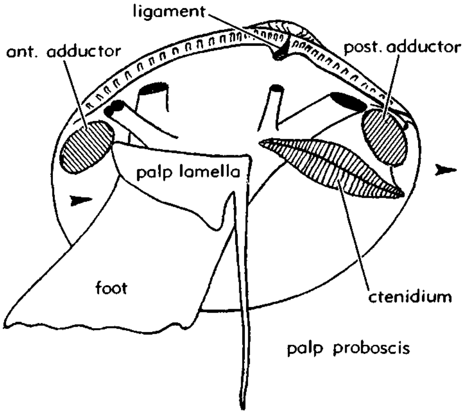

FIG. 16. *Nucula,* mantle cavity viewed from left side; arrows indicate positions of inhalant and exhalant currents.

penetrate for hypobranchial glands to be retained. The inhalant current enters *anteriorly;* this is primitive for the pelecypods, a direct consequence of the forward extension of the mantle cavity (as in the Polyplacophora). In the great majority of the Pelecypoda it has become posterior, ventral to the necessarily posterior exhalant current. This permits burrowing or boring with the anterior end downward or inward, the posterior end maintaining contact with the environment for oxygen and food. Among Eulamellibranchia, only the surface-dwelling or commensal Erycinacea (e.g., *Kellia, Lepton*) and the Lucinacea have an anterior inhalant current.

In *Nucula* the frontal cilia on the ctenidia retain their primitive function of cleansing; particles brought in with the inhalant current are conveyed to the mid-line and then passed forward but then are largely passed to the mantle surface, little being carried to the mouth. This mucus-laden waste material, or pseudofeces, is carried to the mantle margins opposite the base of the foot. There it accumulates for later ejection ventrally following sudden contraction of the adductors. Such accumulation of material, normally posteroventrally, and its periodic ejection from the inhalant chamber occur in all pelecypods. Where the mantle cavity is widely open (e.g., Pectinidae), there is great development of "quick" striated muscle for this purpose. From such cleansing reactions certain Pectinidae and Limidae have obtained the muscular activity demanded in their swimming movements.

Feeding is by way of the palp proboscides, which extend into the substratum, collecting organic deposits and passing them along a ciliated groove to the area between the palp lamellae. The inner faces of these palp lamellae are grooved and are supplied with diversely beating rows of cilia, which on a quantitative basis select what passes to the mouth. Presumably the labial palps were extended as the head lost contact with the environment while it was gradually enclosed by the mantle-and-shell. At the same time jaws, radula, buccal mass, and salivary and esophageal glands were lost.

Other primitive features of the Nuculidae include the taxodont dentition (but not the condensed ligament), presence of four pairs of pedal (shell) muscles, opening of the gonads into the ureters, and probably mode of life, i.e., burrowing—horizontally when once below the surface—into soft substrata. It is difficult to see how the gradual elongation of the palps could have come about except under such conditions; byssal attachment demands prior establishment of feeding on suspended matter by means of enlarged ctenidia.

Broadly speaking (disregarding the remaining protobranchs and the septibranchs), the pelecypods are ciliary feeders (the wood-boring Teredinidae with an accessory source of carbohydrate). The ctenidium is further elongated until it reaches almost to the mouth, the filaments being extended and bent back on themselves so that the four demibranchs occupy much of the mantle cavity. The palps are reduced to the sorting lamellae. The two arms of each filament are united by interlamellar junctions; in the filibranch condition successive filaments are attached by ciliary junctions but in the eulamellibranch condition by interfilamentary tissue connections. In the former, both blood vessels run along the axis, but in the latter only the afferent vessel; the efferent vessel divides into branches running along the dorsal margins of the demibranchs. In this manner a highly complex lattice-work with great surface area separates the inhalant and exhalant chambers (Fig. 17); the powerful current of water created by

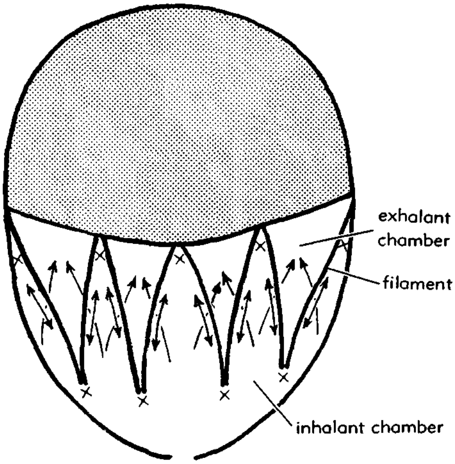

FIG. 17. Diagram indicating possible course of currents on the filibranch and eulamellibranch ctenidium; the arms of each of the filaments composing the four demibranchs have been drawn apart the better to indicate flow of water into the exhalant chamber. In different groups, and filaments, frontal cilia may beat dorsalward, ventralward, or both, the site of possible oralward currents being indicated by crosses.

the lateral cilia is effectively sieved, and the originally cleansing frontal cilia convey particles ventrally to the free margins and dorsally (or both ventrally and dorsally) to the axes or dorsal extremities of the demibranchs. There is great diversity in the arrangement of the ciliary patterns (ATKINS, 1936-43), but the end result is the same, passage of smaller mucus-entangled particles to the mouth and rejection of larger masses from ctenidia or palps or both. Mucous glands are abundant. Muscular activity plays an important part in the efficient functioning of the ctenidia.

The typically pelecypod gut (Fig. 2*F*) is highly adapted for dealing with continuous supplies of finely divided material, primarily of plant orign. Food enters the stomach as it leaves the palps. A crystalline style occurs in all but the protobranchs, where conditions in the gut are probably significantly different from those in the other pelecypods. The mucoid style is fashioned and driven stomachward by cilia; it contains carbohydrate-splitting enzymes continuously released as the head dissolves in the less acid medium of the stomach (25). The ciliary sorting area in the stomach sends fine particles into the ducts of the diverticula, while large particles, with waste from the diverticula, are carried into the mid-gut. A cuticular region forms a localized gastric shield, against which the head of the style impinges. In the protobranch Nuculidae and Nuculanidae and in the septibranchs it lines much or all of the stomach, which functions as a gizzard. With the possible exception of some protobranchs, absorption and intracellular digestion occur in the tubules of the diverticula, wandering amoebocytes assisting in digestion. The mid-gut and rectum are primarily concerned with consolidation of feces.

Typically, the pelecypod foot is laterally compressed and its frequent and probably primitive use is in plowing slowly through soft substrata, being pushed forward and dilated terminally, contraction of the pedal retractors then pulling the animal forward (Fig. 18). But it is capable of wide modification, in connection with rapid vertical burrowing (as in the Solenidae), with planting byssus threads (as in the Mytilidae), with sucker-like attachment while boring (as in the Adesmacea), or solely with cleansing the mantle cavity (as in certain Pectinidae—e.g., *Spondylus*). Cementation may be accompanied by loss of the foot (e.g., Ostreidae).

The nervous system calls for little comment; there is a single pair of so-called cerebropleural ganglia, in effect largely pleural and reflecting the increased importance of the mantle and effective loss of the head. Where there is concentration of ganglia, as in the Limidae, this takes place posteriorly instead of anteriorly as it does in the Gastropoda and Cephalopoda.

Enclosure of the body within the mantle-and-shell has imposed restrictions on reproduction. With no possibility of internal fertilization, there is no penis and no elaboration of female genital ducts. In either sex the gonad opens by way of a short duct into the exhalant chamber, by way of the ureter in the protobranchs, by way of a common opening with the kidney in filibranchs such as *Pecten,* and separately in the eulamellibranchs. Hermaphroditism of various types is not uncommon, while a probably basic protandry may take the form of alternating hermaphroditism, as in the Ostreidae. In

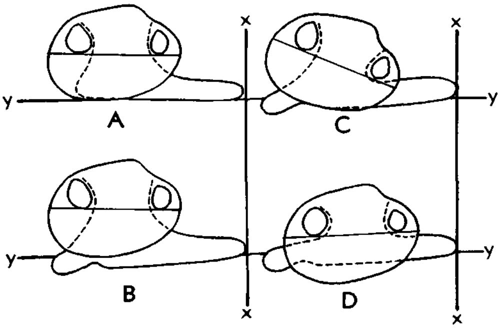

FIG. 18. Diagrammatic representation of shallow digging movements in *Venerupis (Paphia)*; progressive stages indicated in *A-D* (xx and yy being vertical and horizontal lines of reference). (After QUAYLE.)

Xylophaga there is sexual dimorphism, when in the male phase the animal stores sperm for use in the later female phase.

A few pelecypods incubate the eggs in the mantle cavity, usually suprabranchially, except in certain Ostreidae where they are retained in the *inhalant* chamber, having initially to pass through the ctenidium against the water flow, the larvae being eventually expelled ventrally by sudden contraction of the adductor. A parasitic stage in the life history follows incubation in the freshwater Unionacea.

The form of the Pelecypoda is the result of growth of the mantle-and-shell (Fig. 19). Direction of growth at any marginal region of the valve may be resolved (19) into different components: (1) radial, radiating from the umbo and acting in the plane of the generating curve—invariably present and affecting the form of both valves; (2) transverse, acting at right angles to the plane of the generating curve, possibly reduced or absent on one valve, e.g., *Corbula* [*Aloidis*], *Pecten* (but not *Chlamys*), *Pandora;* (3) tangential, acting tangentially to and in the plane of the generating curve, well displayed in *Isocardia* [*Glossus*] and *Chama* but less obviously in *Cardium* and the Mytilidae, although with important consequences in these (34). An invariable effect is anterior splitting and posterior extension of the ligament. The final result of such splitting was seen in the extinct rudistids where the two valves separated, while, owing to absence of a transverse component in the growth of one valve and presence of a most unusually large one in the other, the former valve became essentially an "operculum" closing the deep cavity produced by the latter.

The most convenient way to consider problems of form in the Pelecypoda is by reference to axes or projections from the curved surface of the mantle-and-shell in the sagittal plane, namely, the anteroposterior and median axes of the body with the hinge and demarcation lines of the mantle-and-shell (35). Attempts to compare the form in different pelecypods by means of co-ordinates (THOMPSON, 1942) are possible only if the mantle-and-shell and the body are considered separately; the former may be related by the use of *radial* co-ordinates but the latter only by that of *rectangular* ones. The form finally assumed by any pelecypod is the result of interaction in growth of the mantle-and-shell on the one hand and of the body on the other. For instance, changes in form of the mantle-and-shell (due to changes in growth gradients marginally) affect the disposition but not the proportions of the body (e.g., Solenidae) (Fig. 20*B*). Changes in proportions of the body do occur but only when this is byssally attached, the region of such attachment being a fixed point. The anterior regions of the body may then be reduced (Fig. 20*C*), a condition which, as shown in anisomyarian forms, leads by way of heteromyarianism to monomyarianism (32). This provides another notable instance of the plasticity of the molluscan body. In the Tridacnidae the monomyarian condition has been produced by the mantle-and-shell rotating through an angle of 180 degrees in the sagittal plane in relation to the byssally attached body (32).

Enclosure of the body within the mantle-and-shell has restricted evolutionary potentiality within the Pelecypoda as compared with the Gastropoda, yet this is a supremely successful class. The protective shell is doubtless a factor; only in the commensal, and in one case parasitic, Erycinacea is it enclosed and reduced. But the use of the primitively respiratory ctenidia as organs of feeding, with correlated modification of the gut, is the most important factor. Both soft and hard substrata have been exploited, the latter by byssus attachment and by cementation, the former by burrowing.

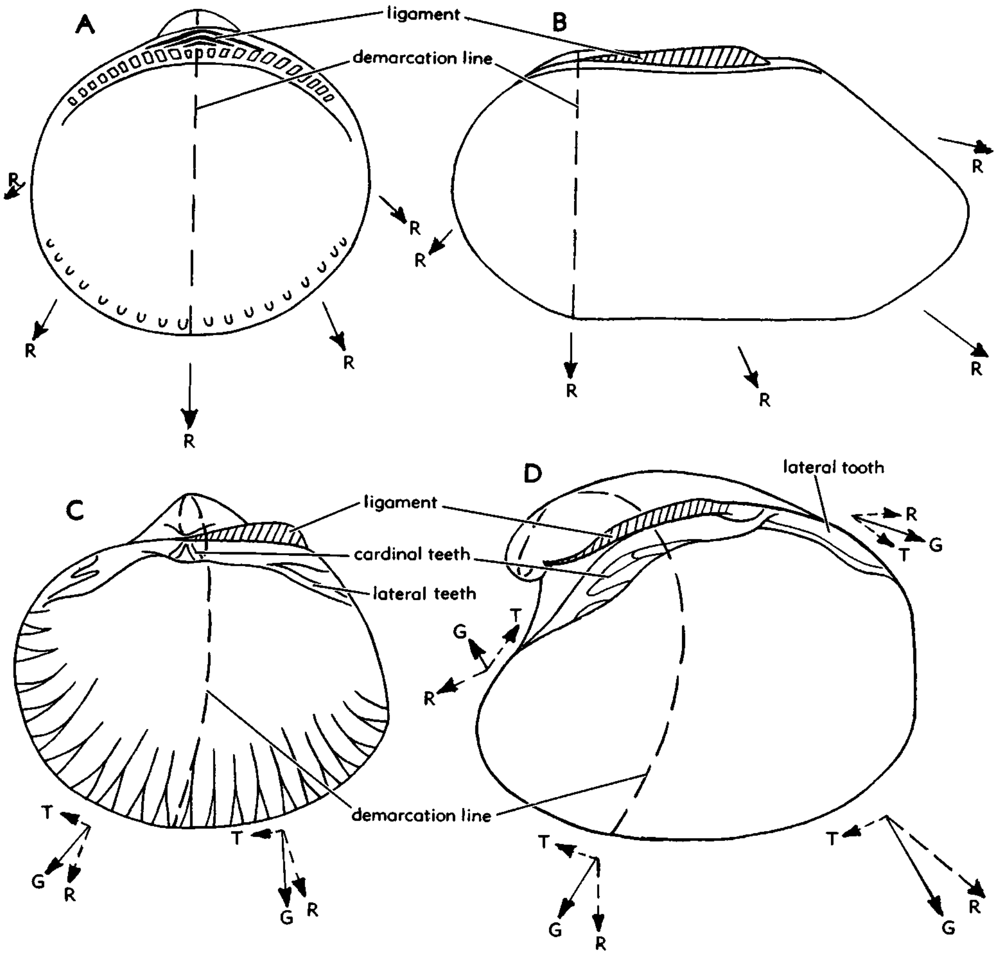

FIG. 19. Diagrams of left valves of pelecypods showing efferent or radial component *(R)* in growth and influence on this of tangential component *(T)* where this occurs, as in *Cardium* and *Isocardia;* the resultant direction of growth at different points around the margin indicated by *G;* demarcation line (i.e., projection on sagittal plane of the line of maximum inflation on each valve) being curved (19).——*A. Glycymeris. B. Anodonta.*——*C. Cardium.*——*D. Isocardia.*

Swimming is possible in the Pectinidae and in *Lima,* but as a result of freedom following byssal attachment and by means of mechanisms primarily concerned with cleansing of the mantle cavity. Boring has been achieved in various groups independently and from modification of different initial habits; following byssal attachment, as in the Mytilidae (e.g., *Botula* and *Lithophaga,* boring mechanically and by acid, respectively); following byssal attachment and "nestling," as in *Hiatella* [*Saxicava*]; following deep burrowing, as in *Platyodon* (Myacea); following burrowing into stiff substrata such as clay, as in the Adesmacea where, especially in the Teredinidae, there is also the capacity for boring in wood, which involves further specialization.

Classification of the Pelecypoda is difficult. To associate the four protobranchiate families comprising the Nuculacea with the Arcacea on the basis largely of the taxodont dentition is certainly unsound. Although in major respects the Nuculidae are primitive (but also very successful), the Malletiidae and Nuculanidae (more suitably

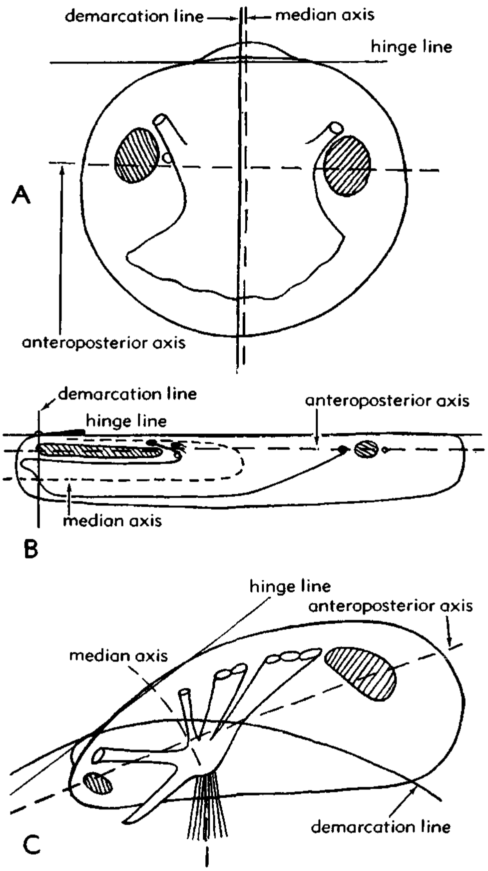

Fig. 20. Symmetry of body and of mantle-and-shell in pelecypods.——*A. Glycymeris,* body and mantle-and-shell both symmetrical in respect of median axis and demarcation line, respectively.——*B.* Solenidae, mantle-and-shell elongated posteriorly, secondary effects on disposition but not on proportions of body.——*C. Mytilus,* proportions of body affected owing to byssal attachment leading to heteromyarianism, secondary effect on mantle-and-shell.

considered together as one family) have highly specialized pumping ctenidia that in many ways are more elaborate than those of the eulamellibranchs. The protobranchiate ctenidia in the Solemyidae are enlarged for ciliary feeding, this family not possessing palp proboscides (28). It may well prove necessary to divide the Pelecypoda into two subclasses, of which the Protobranchia would be one. The final position of the septibranch families (Poromyidae and Cuspidariidae) also remains to be determined. Their septa certainly "pump," as do the ctenidia of the Nuculanidae; but they are carnivorous, the palps being reduced (26).

Class SCAPHOPODA

In this small but distinctive class, the body is completely wrapped around by the mantle-and-shell, which, beginning as a cuplike structure, fuses ventrally during early development. There is no compression but the animal is elongated, the head appendages and the foot projecting from the wider anterior opening of the shell, the other end extending above the surface of the soft substratum in which these animals invariably, somewhat obliquely, burrow. There is no ctenidium, a current of water being drawn in posteriorly, partly due to extension of the foot and partly (at least in *Dentalium*) to action of cilia on a series of ridges on the ventral side in front of the anus (Fig. 21). Periodically, water is expelled backward, probably as the foot is being withdrawn, when defecation may also occur. There are no separate inhalant and exhalant apertures as in other Mollusca. The head bears numerous ciliated and prehensile captacula, which collect food particles both from the substratum and from material carried in with the inhalant current which accumulates on the ciliated ridges. These animals are thus deposit feeders. The gut is less reduced than in the Pelecypoda, possessing a dorsal mandible, a short radula with five teeth in each row, and a pair of esophageal pouches. The small size and inactivity of the Scaphopoda are reflected in the great reduction of the circulatory system which contains no heart. The paired kidneys communicate only with the exterior. There are the usual four pairs of nerve ganglia. As in the Polyplacophora there is a subradular organ with an associated ganglion. The animals are of separate sexes and have a single posteriorly extended gonad which opens by way of the right kidney (i.e., corresponding to the left —post-torsional—kidney in the Gastropoda).

Class CEPHALOPODA

In this class of exclusively marine and bilaterally symmetrical animals, the Mollusca attain a degree of structural com-

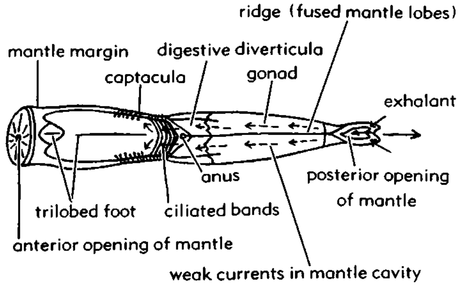

FIG. 21. *Dentalium entalis,* ventral aspect, animal removed from shell and foot withdrawn, showing currents in mantle cavity.

plexity and of metabolic efficiency which represent the summit of evolution in the absence of segmentation. Their living representatives are divisible into the two orders (1) Tetrabranchia, with two pairs of ctenidia and numerous arms and comprising the genus *Nautilus,* and (2) Dibranchia, with one pair of ctenidia and ten or eight arms. The latter consist of three suborders: (a) Decapoda, having four pairs of normal arms and one pair of longer, more or less retractile, "tentacular" arms—the cuttlefishes and squids belong to this suborder; (b) Vampyromorpha (20), comprising the archaic bathypelagic genus *Vampyroteuthis,* in which one of the five pairs of arms consists of long mobile filaments which are retractile into special pockets; and (c) Octopoda, which possess four pairs of arms all similar, apart from some modifications in respect of reproduction.

While all are predacious carnivores, the modern Cephalopoda have exploited the major marine habitats. Squids inhabit surface waters and cuttlefishes and octopods respectively sandy and rocky bottoms in shallow water. Other squids, including *Architeuthis,* the largest of invertebrates, and also certain octopods, are bathypelagic or live on or near the sea floor in abyssal depths. Many of them are strikingly modified, some being so gelatinous as to resemble coelenterates.

Comments on these most elaborately constructed animals can only cover a few aspects of structure chosen to emphasize both their fundamental molluscan nature and at the same time the extent to which the potentialities latent in the molluscan ground plan have been realized in the Cephalopoda.

The manner in which the characteristic form of the modern Cephalopoda has been attained may be briefly outlined. The first stage was probably the cutting off within the domelike shell of the primitive mollusk of first one and then a succession of chambers (Fig. 22). These must have been traversed with a siphuncle through which tissue extended, i.e., unlike the superficially somewhat similar chambering which occurs in some elongated gastropod shells (e.g., the vermetids). At the same time the terminal chamber deepened and was necessarily accompanied by a pronounced ventral flexure of the animal within. The head and the opening into the mantle cavity came to face ventrally, being separated only by the much-reduced foot. Initially in the form of overlapping flaps, eventually as a closed tube or

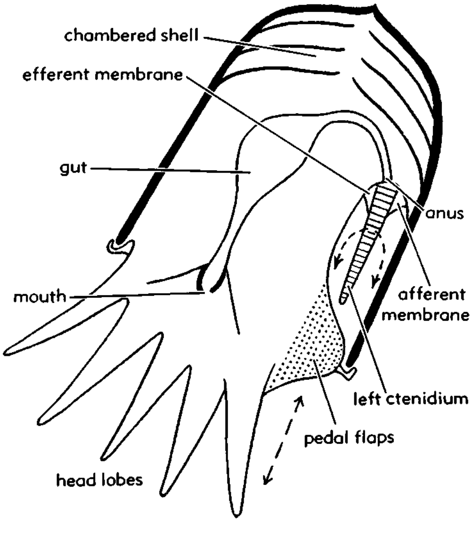

FIG. 22. Possible early stage in evolution of a cephalopod showing chambering of shell with development of head lobes and modification of the foot to form flaps at the entrance to the mantle cavity. With the dorsal elongation of this, the anus has begun to migrate from the primitively dorsal to the primitively ventral (topographically upper) position that it occupies in the Cephalopoda. At the same time, the efferent membrane has been reduced to the size of the afferent membrane, which itself becomes extended in the Dibranchia (Fig. 24). Direction of water flow in the mantle cavity is uncertain depending on the part played by the pedal flaps (cf. *Nautilus*).

funnel, the foot came into functional association with the mantle cavity. Conversion of the shell into a hydrostatic organ enabled the Cephalopoda at some early stage to change from the primitive bottom-living habit to a pelagic or bathypelagic habit, as in the ammonites, while by the same means the modern *Nautilus* may float with the shell breaking the surface. The fact that it was lighter than water permitted elongation without necessary coiling of the shell—not feasible in the benthonic Gastropoda. Such straight-shelled Cephalopoda (e.g., *"Orthoceras"*) indicate how the later belemnites and the modern Dibranchia have evolved. Exogastric coiling also occurred and in a planispiral form (e.g., ammonites and modern *Nautilus*).

In the Cephalopoda, to a much greater extent than in the other molluscan classes, the shell became overgrown by the mantle, so that of modern forms only *Nautilus* has an external shell, although the purely internal shell of the bathypelagic *Spirula* retains the primitive chambered shell with a siphuncle. But in all the Dibranchia, like the extinct belemnites, the shell is enclosed, forming the internal skeleton of the elongated, streamlined decapod squids and cuttlefishes and being reduced almost to a vestige in the paired or unpaired stylets of the more baglike Octopoda with their more varied and often bottom-living habit. Throughout these changes, the fundamental molluscan features remain unchanged, the major elaboration being the appearance of the characteristic prehensile arms surrounding the head. These are organs of feeding, which also assist in locomotion in *Nautilus* and again, secondarily, in Octopoda. They are not here considered to be of pedal origin.

In their most highly evolved form, as exhibited by the modern Dibranchia, the Cephalopoda may be said to have reconciled the conflict between the growth axes of the body and those of the mantle-and-shell. The anterior head and the ventral foot, which forms the funnel, have come to lie side by side. They occupy one end of the elongate animal, with the tip of the visceral mass and of the contained shell at the other. The mantle cavity remains posterior. With the adoption of a horizontal posture, shown most clearly in a cuttlefish or a squid (Fig. 23), the head and the funnel lie in front, with the dorsal extremity behind and the mantle cavity beneath. The major axis of the animal is thus really ventrodorsal, but since anterior head and ventral foot are now associated, this means that in effect the two axes coincide.

This change indicates, at any rate, the structural background which has made possible the speed and power displayed by the Cephalopoda in such marked contrast to other Mollusca. Speed is due above all else to modification of the foot, the agent of jet propulsion. In *Nautilus,* where the mantle wall is not muscular, a water current is created by pulsations of the funnel in which there are both proximal "circular" muscles for expulsion of water and distal longitudinal muscles used for steering by directing the flow of water; these muscles are attached to the shell. In the Dibranchia the outer wall of the mantle cavity, no longer confined within a shell, contains a thick layer of circular muscle, the contraction of which provides a much greater expulsive force than is possible with the gentle funnel movements in *Nautilus*. Longitudinal muscles predominate in the funnel; both sets of muscles are attached to the internal skeleton (i.e., guard, phragmacone, and pro-

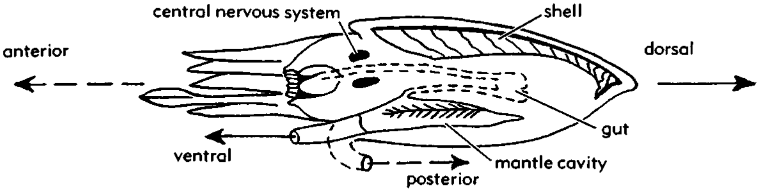

FIG. 23. Dibranchiate cephalopod, diagram showing disposition in life with reconciliation of growth axes of body (anteroposterior) with those of mantle (dorsoventral), also how direction of movement (arrows at extreme left and right) is controlled by direction of jet flow through the funnel.

ostracum) or to its derivatives. With its highly mobile tip, the funnel directs a powerful stream of water to produce so efficient a means of jet propulsion that, over short distances, squids are probably the fastest moving creatures in the sea.

The evolutionary changes within the mantle cavity are of major significance (29). In the primitive condition (Fig. 4), with ctenidium attached by a long efferent and a very short afferent membrane and with anus and urinogenital openings dorsal to it, the respiratory current, created by lateral cilia on the filaments, entered ventrally and left dorsally. In the Dibranchia (Fig. 24) the same organs (apart from osphradia and hypobranchial glands) are present but the ctenidia are attached exclusively by the afferent membrane, and the respiratory current, created by contraction of the pallial musculature, is in the *opposite* direction. But with the anal and other openings now on the efferent side of the ctenidia, their products continue to leave with the exhalant current through the funnel. A hypothetical intermediate stage (Fig. 22) indicates that the mantle cavity has elongated dorsally, the ctenidia at the same time migrating in this direction so that they come to lie on either side of the anus (as do the two pairs of ctenidia in *Nautilus*). The efferent attachment was reduced to the length of the afferent one, so that the ctenidia (again as in *Nautilus*) were only attached proximally. The foot then formed the bilobed flap which must have preceded the formation of the unfused funnel still retained in *Nautilus*. What cannot be determined is whether the respiratory current was produced by lateral cilia, and so followed the primitive course, or whether it was the result of muscular contraction (initially no doubt by movements of the funnel, as in *Nautilus*), in which case it would change direction.

The effects on the organs of the pallial complex have been considerable. At an early stage the hypobranchial glands probably disappeared, the greater respiratory flow rendering them unnecessary. The osphradia may well have been retained wherever blocking of the cavity with sediment represented a danger. In *Nautilus* they are so retained, in association with all four ctenidia, and presumably for this reason, since the respiratory current is relatively gentle, but they are absent in the Dibranchia. The effect on the filaments of change in direction of the respiratory current, now from afferent to efferent side, has been countered by the appearance of secondary skeletal rods on the *afferent* side of the filaments where they arise within a membrane that extends from the afferent surface of the filaments to the afferent membrane by which the ctenidia are now attached. This important distinction between the primitive aspidobranch filament and that of the Cephalopoda is indicated in Figure 25. In addition, the respiratory surface of the filaments is greatly increased by lateral, followed by secondary, foldings. The increasing complexity of this folding can be traced in development; in adults there is increasing complexity in the series *Nautilus*-Decapoda-Octopoda (e.g., *Eledone*). With the adoption of a more passive benthonic life in the Octopoda and eventual change in some deep-sea species to

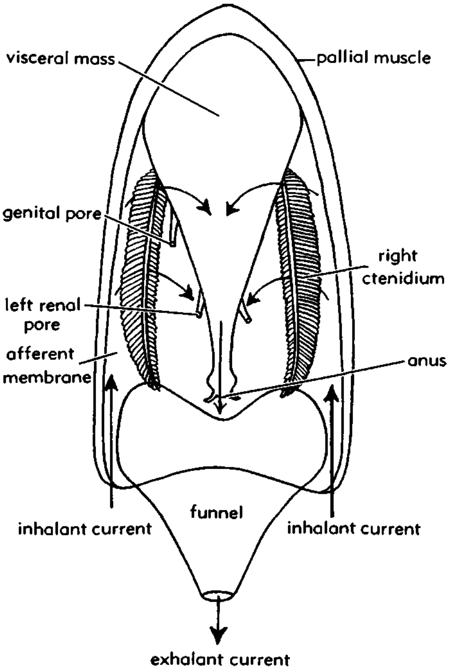

FIG. 24. *Sepia,* disposition of organs in the mantle cavity, viewed from posterior ("under") side (29).

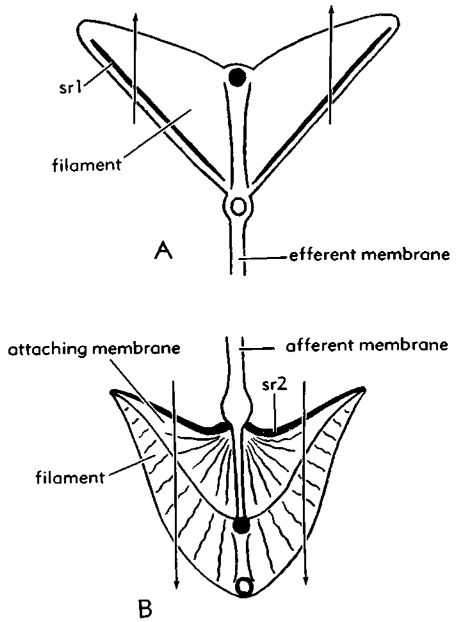

FIG. 25. Comparison between axis seen in section and filaments of *(A)* aspidobranch ctenidium of Gastropoda and *(B)* ctenidium of decapod (e.g. *Sepia*) (29). (Explanation: *sr1,* primitive skeletal rod, efferent side within filament; *sr2,* secondary rod, along free border of membrane which attached filament to afferent membrane. Arrow shows direction of respiration current.)

a medusa-like form of swimming by means of the webbed arms (e.g., Cirromorpha), the opening into the mantle cavity is reduced and so are the ctenidia, which finally become vestigial in the abyssal Vitrelodonellidae, where respiration must be carried on through the general body surface.

Although the elaborate circulatory system is typically molluscan, with a heart consisting of a ventricle and a pair of auricles (two pairs in *Nautilus*) enclosed in a pericardium, there is a notable advance in the substitution, apart from *Nautilus,* of capillaries for sinuses. This applies both to the systemmatic and the branchial circulation, additional branchial hearts providing the force needed to drive the blood through the ctenidial capillaries.

It is here convenient to refer to the relationship between the Tetrabranchia and the Dibranchia. NAEF (1913, 1926) and others who believe that primitively the Mollusca had two pairs of ctenidia, maintain that the tetrabranchiate condition is primitive. This is *not* here maintained. Although the "Tetrabranchia" are the oldest of existing Mollusca, there is no evidence that the primitive nautiloids had two pairs of ctenidia; that is assumed from conditions in *Nautilus.* The early Cephalopoda were probably sluggish animals like other Mollusca and eventual duplication of the ctenidia in the capacious mantle cavity may have been associated with increased activity and heightened metabolism. But this tetrabranchiate condition was only one of two solutions; the other, as shown below, being that achieved in the Dibranchia, which retained the primitive single pair of ctenidia.

Owing to the comparatively low oxygen-carrying powers of their haemocyanin and its slow rate of oxygenation, the increasing respiratory needs of the evolving Cephalopoda could have been met by morphological changes which increased *either* the surface *or* the efficiency of the respiratory system in the following ways: (1) by the maintenance of the primitive circulatory system but increase of the respiratory surface by duplication of the ctenidia, an increased respiratory current being produced by the pulsations of the overlapping pedal folds forming the funnel (i.e., as in *Nautilus*); and (2) by the retention of the single pair of ctenidia but their increased efficiency by acquisition of capillary circulation with accessory branchial hearts; at the same time a much more powerful respiratory current was produced by the pallial musculature under precise nervous control, which developed following the reduction and overgrowth of the shell (i.e., as in Dibranchia).

So far as the mantle cavity was concerned, these two possible lines of cephalopod evolution could have diverged during the Triassic when the belemnites appeared,[1] the Tetrabranchia appearing about the same time. If so, then the ammonites, arising from a more primitive nautiloid stock in the Devonian, need not have possessed two pairs of ctenidia unless, in association with the same metabolic reason, they were independently duplicated. However, it was the second alternative, first exploited possibly by the belemnites, which proved the more

---

[1] Actually, numerous undoubted belemnites now are known from Mississippian rocks in North America.—ED.

successful. It permitted the evolution of rapid locomotion by mechanisms concerned initially with increasing the force of the respiratory current. The acquisition of a mantle cavity of this type, combined with development from the foot of the highly mobile funnel, was clearly a prime factor in the survival of the modern Dibranchia and in their successful colonization of all zones in the sea.

The nervous system which controls the all-important contractions of the pallial musculature and mediates between the elaborate receptors, notably the eye, and these and other effectors, is of great complexity. It is concentrated around the esophagus in a massive "brain," which is protected in a cranium. It is difficult to homologize the various regions with the ganglia of other Mollusca owing to the great length of time since the Cephalopoda diverged and the exceptional evolutionary progress that has since occurred within this class. The central nervous system is divisible into three divisions comprising 14 lobes—namely, the subesophageal ganglia with four lobes, the supraesophageal ganglia with eight and the large optic division with two. The subesophageal lobes consist of the brachial, pedal, palliovisceral, and *lobus magnocellularis,* this so named because in it reside the large cells of the giant nerve fiber system (Fig. 26), which, as shown by YOUNG (37), control the movements of the mantle and the funnel, i.e., the organs largely concerned with the precise capture of active prey. This system is present in all Decapoda but not in the demersal Octopoda, although the *lobus magnocellularis* is retained.

Impulses are set up, often presumably as a result of stimulation from the eye by way of the optic ganglia, in either of these giant cells and so carried to seven pairs of second-order giant neurons in the pallioviscera lobe, the axons of which control the muscles concerned with expulsion of water from the mantle cavity. They run direct to the retractor muscles of the funnel and head and, by way of the stellate ganglia where they make contact with third-order giant fibers, to the pallial muscles. Hence, a single impulse set up in the giant cells brings about a sudden contraction, producing sudden expulsion of water through the funnel and so a darting movement of the animal in the opposite direction to that in which the funnel is pointed. Speed of conduction, made possible by the large axons, is all-important. Other large motor cells in the *lobus magnocellularis* may constitute the center for controlling the composite set of movements—by arms, mantle and funnel—by which prey is seized.

Just as with the respiratory, circulatory, muscular, and nervous systems, that of digestion represents a strikingly efficient development of primitive molluscan features. It has been most thoroughly studied in the squids (2), where the process is so efficient that a complete meal can be digested in four to six hours, *Sepia* taking about twice and *Octopus* about three times as long. Prey seized by the two long arms is carried to the mouth, where it is killed by poison from

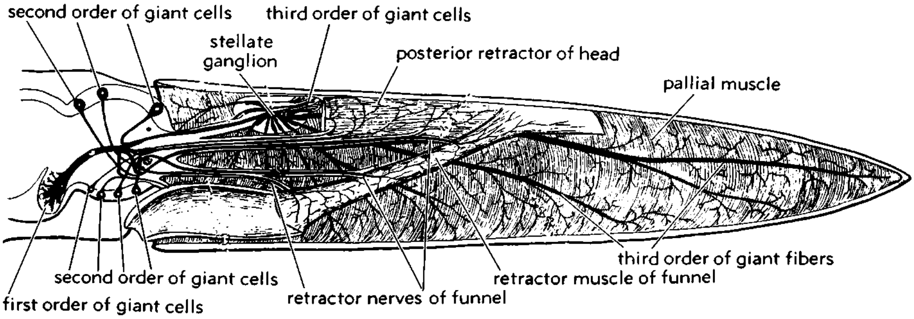

FIG. 26. Diagram of squid, *Loligo pealii,* showing arrangement of giant nerve fibers controlling movements of pallial muscles and retractors of head and funnel (28).

buccal glands; it is then bitten by the jaws and swallowed by aid of the radula. In the Octopoda digestive enzymes may be regurgitated and ejected into the body of the prey (e.g., a crab), and the products of this "extra-intestinal" digestion later are sucked in. The digestive diverticula consist of two distinct glands, the so-called "liver" and "pancreas." Digestion is exclusively and most effectively extracellular, enzymes com-

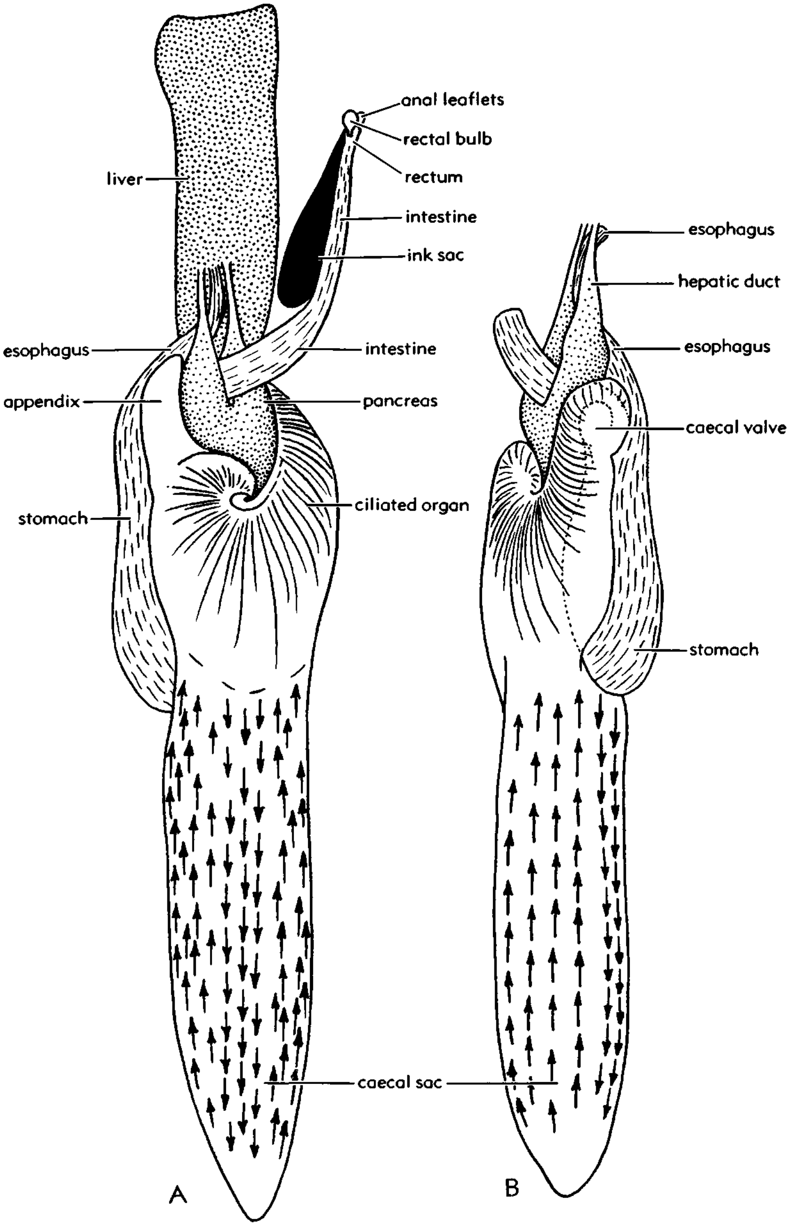

FIG. 27. *Loligo* spp., mid-gut and mid-gut glands, *(A)* ventral view, *(B)* left side (2). Arrows indicate alternative systems of ciliary currents in the caecal sac.

ing from both of these sources although by a common "pancreatic" duct. By a striking parallel with conditions in the vertebrates, digestion occurs in two stages, the first in the actively churning and chitin-lined stomach by the agency of "pancreatic" secretion, and the second by enzymes from the "liver" in the long caecum which extends dorsal to (or "behind") this. As the partly digested food enters the caecum (Fig. 27) from the stomach, it first encounters a ciliated organ—most probably related to the ciliary region in the stomachs of other Mollusca—where solid particles are collected and passed by a groove into the intestine. Absorption of the final products of digestion in the remaining fluid takes place through the walls of the caecum, but also—especially during the breeding season when the caecum may be restricted by the enlarged gonad—in the intestine. The whole process is one of striking efficiency, involving "delicate interplay of the muscular action of the stomach, caecal sac, esophageal, intestinal, and hepatic sphincters, and hepatopancreatic fold and caecal valve" (2).

The Cephalopoda are invariably of separate sexes, some (e.g., *Argonauta*), displaying marked sexual dimorphism. The gonad, within the large genital coelom, is single, with ducts opening directly into the mantle cavity. These are primitively paired, but in many cases (including *Nautilus*), are reduced to one. Development is direct and fertilization internal. This involves the presence of glands in association with both oviduct and *vas deferens* for the production, respectively, of protective capsules for the eggs and of spermatophores. The latter are conveyed into the mantle cavity of the female at copulation by the agency of a seasonally modified arm (hectocotylus) in the Dibranchia and of the spadix (permanent modification of four arms) in *Nautilus*. In this remarkable way internal fertilization has been retained despite increased enclosure of the female reproductive opening within the mantle cavity.

REFERENCES

Atkins, D.

(1) 1936-43, *On the ciliary mechanisms and interrelationships of lamellibranchs, Parts I-VIII:* Quart. Jour. Micr. Sci. (London), v. 79, p. 339-373, p. 375-421, p. 423-445; v. 80, p. 321-329, p. 331-344, p. 345-436; v. 84, p. 187-256.

Bidder, A. M.

(2) 1950, *The digestive mechanism of the European squids Loligo vulgaris, Loligo forbesii, Alloteuthis media, and Alloteuthis subulata:* Same, v. 91, p. 1-43.

Boettger, C. R.

(3) 1954, *Die Systematik der euthyneuren Schnecken:* Deutsch. zool. Gesell., Verhandl. (Leipzig), p. 253-280.

Crofts, D. R.

(4) 1937, *The development of Haliotis tuberculata, with special reference to the organogensis during torsion:* Roy. Soc. (London), Philos. Trans., ser. B, v. 228, p. 219-268.

(5) 1955, *Muscle morphogenesis in primitive gastropods and its relation to torsion:* Zool. Soc. London, Proc., v. 125, p. 711-750.

Fretter, V.

(6) 1937, *The structure and function of the alimentary canal of some species of Polyplacophora (Mollusca):* Roy. Soc. Edinburgh, Trans., v. 59, p. 119-164.

(7) 1946, *The genital ducts of Theodoxus, Lamellaria and Trivia, and a discussion on their evolution in the Prosobranchs:* Marine Biol. Assoc. United Kingdom (Plymouth), Jour., v. 26, p. 312-351.

Garstang, W.

(8) 1928, *The origin and evolution of larval forms:* Rept. Brit. Assoc. Glasgow, 1928, sec. D, p. 77-98.

Goodrich, E.

(9) 1945, *The study of nephridia and genital ducts since 1895:* Quart. Jour. Micr. Sci. (London), v. 86, p. 113-392.

Graham, A.

(10) 1939, *On the structure of the alimentary canal of style-bearing prosobranchs:* Zool. Soc. London, Proc., ser. B, v. 109, p. 75-112.

(11) 1949, *The molluscan stomach:* Roy. Soc. Edinburgh, Trans., v. 61, p. 737-778.

Knight, J. B.

(12) 1952, *Primitive fossil gastropods and their bearing on gastropod classification:* Smithson. Misc. Coll. (Washington), v. 117, no. 13, p. 1-56.

Lemche, H.

(13) 1957, *A new living deep-sea mollusc of the Cambro-Devonian Class Monoplacophora:* Nature (London), v. 179, p. 413-416.

Morton, J. E.

(14) 1955a, *The evolution of vermetid gastro-*

pods: Pacific Science (Honolulu), v. 9, p. 3-15.

(15) 1955b, *The evolution of the Ellobiidae with a discussion on the origin of the Pulmonata:* Zool. Soc. London, Proc., v. 125, p. 127-168.

(16) 1955c, *The functional morphology of the British Ellobiidae (Gastropoda Pulmonata) with special reference to the digestive and reproductive systems:* Roy. Soc. (London), Philos. Trans., ser. B, v. 239, p. 89-160.

Naef, A.

(17) 1913, *Studien zur generellen Morphologie der Mollusken, 1:* Ergebn. Zool. (Jena), Band 3, p. 73-164.

(18) 1926, *Studien zur generellen Morphologie der Mollusken, 3:* Same, Band 6, p. 27-124.

Owen, G.

(19) 1953, *The shell in the Lamellibranchia:* Quart. Jour. Micr. Sci. (London), v. 94, p. 57-70.

Pickford, G. E.

(20) 1946-49, *Vampyroteuthis infernalis Chun, an archaic dibranchiate cephalopod. I. Natural history and distribution. II. External anatomy:* Dana Reports (Carlsberg Foundation, Copenhagen), nos. 29, 32.

Purchon, R. D.

(21) 1955, *The structure and function of the British Pholadidae (rock-boring Lamellibranchia):* Zool. Soc. London, Proc., v. 124, p. 859-911.

Thiele, J.

(22) 1931-35, *Handbuch der systematischen Weichtierkunde:* Fischer (Jena), v. 1, 2.

Thorson, G.

(23) 1946, *Reproduction and larval development of Danish marine bottom invertebrates:* Meddelelser Kommissionen Danmarks Havundersøgelser, ser. Plankton (København), v. 4, no. 1.

Trueman, E. R.

(24) 1951, *The structure, development and operation of the hinge ligament of Ostrea edulis:* Quart. Jour. Micr. Sci. (London), v. 92, p. 129-140.

Yonge, C. M.

(25) 1926, *Structure and physiology of the organs of feeding and digestion in Ostrea edulis:* Marine Biol. Assoc. United Kingdom (Plymouth), Jour., v. 14, p. 295-386.

(26) 1928, *Structure and function of the organs of feeding and digestion in the septibranchs, Cuspidaria and Poromya:* Roy. Soc. (London), Philos. Trans., ser. B, v. 216, p. 221-263.

(27) 1939a, *On the mantle cavity and its contained organs in the Loricata (Placophora):* Quart. Jour. Micr. Sci. (London), v. 81, p. 367-390.

(28) 1939b, *The protobranchiate Mollusca: a functional interpretation of their structure and evolution:* Roy. Soc. (London), Philos. Trans., ser. B, v. 230, p. 79-147.

(29) 1947, *The pallial organs in the aspidobranch Gastropoda and their evolution throughout the Mollusca:* Same, v. 232, p. 443-518.

(30) 1949, *On the structure and adaptations of the Tellinacea, deposit-feeding Eulamellibranchia:* Same, v. 234, p. 29-76.

(31) 1952, *Studies on Pacific coast mollusks. IV. Observations on Siliqua patula Dixon and on evolution within the Solenidae:* Univ. California Publ. Zool. (Berkeley), v. 55, p. 421-438.

(32) 1953a, *The monomyarian condition in the Lamellibranchia:* Roy. Soc. Edinburgh, Trans., v. 62, p. 443-478.

(33) 1953b, *Form and habit in Pinna carnea:* Roy. Soc. (London), Philos. Trans., ser. B, v. 237, p. 335-374.

(34) 1955, *Adaptation to rock boring in Botula and Lithophaga (Lamellibranchia, Mytilidae) with a discussion on the evolution of this habit:* Quart. Jour. Micr. Sci. (London), v. 96, p. 383-410.

(35) 1957a, *Mantle fusion in the Lamellibranchia:* Pubbl. Staz. zool. Napoli, v. 29, p. 151-171.

(36) 1957b, *Reflexions on the Monoplacophoran, Neopilina galatheae Lemche:* Nature (London), v. 179, p. 672-673.

Young, J. Z.

(37) 1939, *Fused neurons and synaptic contacts in the giant nerve fibres of cephalopods:* Roy. Soc. (London), Philos. Trans., ser. B, v. 229, p. 465-503.

SCAPHOPODA

By N. H. Ludbrook[1]

Class SCAPHOPODA Bronn, 1862

[=Cirrhobranchiata de Blainville, 1825; Lateribranchiata Clark, 1851; Solenoconchia Lacaze-Duthiers, 1857; Prosopocephala Bronn, 1862]

Marine, bilaterally symmetrical mollusks protected by an external elongate, tubular, tapering, calcareous shell, open at both ends and generally somewhat curved. Concave side of shell dorsal, convex side ventral; aperture or anterior opening larger, apex or posterior opening simple or variously slit or notched, some forms with terminal pipe. Shell substance of 3 distinct layers (Fig. 28). Shell secreted by a mantle of same shape, larger (anterior) opening of which is contracted by a muscular thickening of the mantle and gives egress to the long conical foot; smaller (posterior) opening serves as outlet for organic waste and genital products. Mouth furnished with a radula, borne on a cylindrical snout and surrounded by a rosette of lobes; a cluster of threadlike, distally enlarged appendages known as "captacula" springs from its base. No eyes or tentacles; otocysts present. Liver 2-lobed, symmetrical; gut strongly convoluted, anus ventral and somewhat anterior, kidney openings near it. Heart rudimentary; no gills, respiration performed by the general integument. Nervous system with well-developed ganglia united by commissures. Gonad simple, sexes separate, reproduction without copulation. *?Ord., Dev.-Rec.*

Scaphopoda are without exception benthonic marine animals, the described Recent species being approximately equally distributed between the neritic and bathyal realms. Littoral species are few. They live partly embedded in mud or sand on the sea bottom, with only the smaller posterior end protruding into the water. Food consists of Foraminifera or similar organisms captured by the captacula (4, 5, 8).

Earliest geologic record of the Scaphopoda is from the Ordovician of Russia; it is, however, doubtful whether most of the species described therefrom have been correctly placed systematically. None have been recorded from the Silurian, but the class is well represented in the Devonian where three genera are recognized. Generic divergence was gradual during late Paleozoic and early Mesozoic, and modern forms did not appear until early Cretaceous. Maximum development of the class is attained in Recent times, the number of living species being in excess of the total number recorded from the Tertiary (Fig. 29).

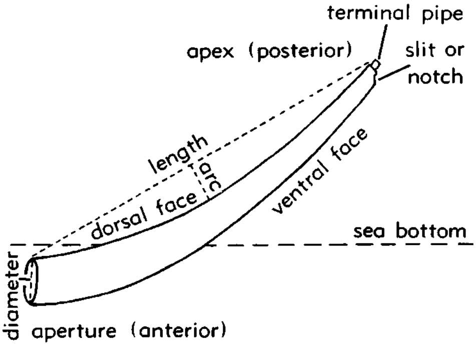

Fig. 28. Morphological features of Scaphopoda.

Family DENTALIIDAE Gray, 1834

[Antalinae Stoliczka, 1868; Scaphopoda G. O. Sars, 1878]

Shell generally tapering regularly throughout, sculptured or smooth, diameter greatest at aperture. Animal has conical foot with an encircling sheath expanded laterally and interrupted dorsally. *?Ord., Dev.-Rec.*

Dentalium Linné, 1758 [**D. elephantinum;* SD Montfort, 1810]. Shell curved and tapering, longitudinally sculptured, smooth or annulated. Embryonic whorls minute, fragile, and lost at an early growth stage. Apex commonly modified by a slit or notch due to absorption. Anterior aperture circular, or oblique, in many forms modified by longitudinal ribbing (4). *M.Trias.-Rec.,* cosmop.

D. (Dentalium) [=*Paradentalium* Cotton & Godfrey, 1933]. Prismatic or decidedly ribbed, especially toward apex where transverse section is polygonal; apex without notch or slit or with a short one (3). *U.Cret.-Rec.,* cosmop.——Fig. 30,*4. D. (D.) elephantinum* Linné, Rec., Asia-E.Indies; ×0.5 (Pilsbry & Sharp, 1897).

D. (Antalis) H.Adams & A.Adams, 1854 [*non Dentale* DaCosta, 1778; *nec Antalis* Hermannsen, 1846 (ICZN op. 361)] [**D. entalis* Linné, 1758; SD Pilsbry & Sharp, 1897] [=*Entalis* Gray, 1847 (*non* Sowerby, 1839); *Entaliopsis*

---

[1] Paleontologist, Department of Mines, Adelaide, South Australia.

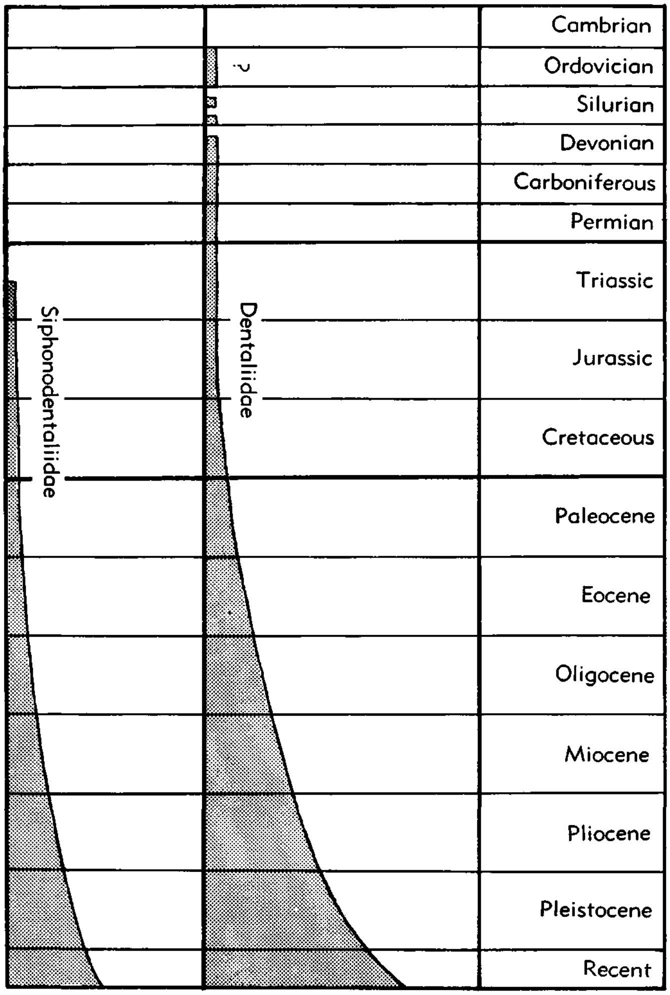

FIG. 29. Stratigraphic distribution of Scaphopoda. Increasing width of the shaded areas diagrammatically indicates expansion in numbers of known genera and subgenera (Ludbrook, n).

NEWTON & HARRIS, 1894]. Less strongly ribbed than *D. (Dentalium)*, apical section not polygonal, apex generally with a V-shaped notch on or near convex side and a solid plug with central pipe or orifice (5). *M.Trias.-Rec.*, cosmop.——FIG. 30,*5*. **D. (A.) entalis* LINNÉ, Plio.-Rec., Eu.-N.Am.; *5a*, side; *5b,c*, posterior extremity; ×1 (5).

D. (Bathoxiphus) PILSBRY & SHARP, 1897 [**D. ensiculus* JEFFREYS, 1877]. Thin, conspicuously compressed laterally, nearly or quite smooth, with broad apical slit on convex side (5). *Rec.*, Eu.-N.Am.-Afr.-E.Indies.

D. (Coccodentalium) SACCO, 1896 [**D. radula* SCHRÖTER, 1784]. Shell with longitudinal, strongly granose ribs. Apex commonly truncate with a small central pipe. *M.Eoc.*, Eu.-E.Indies; *Rec.*, E.Indies.

D. (Compressidens) PILSBRY & SHARP, 1897 [**D. pressum* PILSBRY & SHARP, 1897]. Small, decidedly tapering, conspicuously compressed between convex and concave sides, weakly sculptured, nearly smooth; apex simple (5). *L.Oligo.*, Eu.-C.Am.-E.Indies; *Rec.*, N.Am.-C.Am.-Austral.-E. Indies.

D. (Episiphon) PILSBRY & SHARP, 1897 [**D. sowerbyi* GUILDING, 1834; SD SUTER, 1913]. Small, very slender, rather straight, needle-shaped or truncated, thin and fragile, glossy and smooth; apex with projecting pipe, or simple (5). *L.Jur.-Rec.*, cosmop.

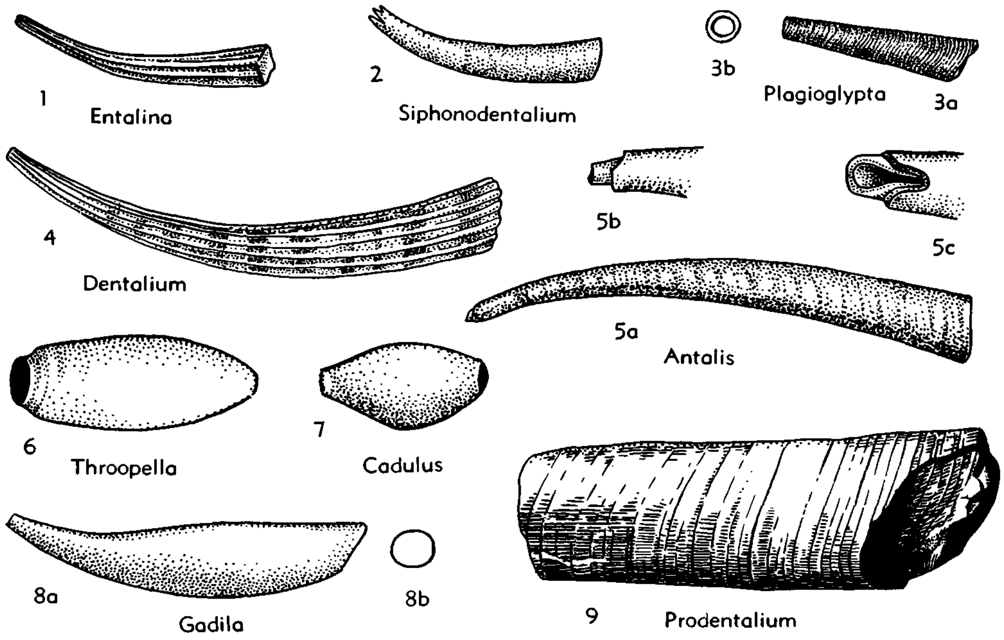

Fig. 30. Genera of the scaphopod families Dentaliidae and Siphonodentaliidae.

D. (Fissidentalium) Fischer, 1885 [**D. ergasticum*] [=*Schizodentalium* Sowerby, 1894]. Large and solid, with many longitudinal riblets, apex typically with a long slit, commonly simple (5). *L.Cret.-Rec.*, cosmop.

D. (Fustiaria) Stoliczka, 1868 [**D. circinatum* Sowerby, 1823; SD Pilsbry & Sharp, 1897]. Arcuate, polished, sculptured with regular encircling grooves that divide surface of the tube into short, oblique segments. Aperture circular, apex round or ovate, with very long straight linear slit on convex side. *L.Cret.-Tert.*, Eu.-Asia-E.Indies-Afr.-S.Am.; *Rec.*, E.Indies.

D. (Gadilina) Foresti, 1895 [**D. triquetrum* Brocchi, 1814]. Smooth and slender, imperfectly triangular in section, concave side flattened, convex side rounded (5). *L.Mio.*, Eu.-E.Indies-Austral.; *Rec.*, E.Indies.

D. (Graptacme) Pilsbry & Sharp, 1897 [**D. eboreum* Conrad, 1846; SD Woodring, 1925]. Shell with close, fine, deeply engraved longitudinal striae near apex, remainder smooth (5). *L.Eoc.*, Eu.-N.Am.; *Rec.*, cosmop.

D. (Heteroschismoides) Ludbrook, *nom. subst.*, herein [*pro Heteroschisma* Simroth, 1895 (*non* Wachsmuth, 1893)] [**D. subterfissum* Jeffreys, 1877; SD Pilsbry & Sharp, 1897 (*pro Heteroschisma* Simroth) herein affirmed *pro Heteroschismoides*]. Coarsely striate or ribbed longitudinally with apical slit on concave side (5). *Rec.*, Atl.

D. (Laevidentalium) Cossmann, 1888 [**D. incertum* Deshayes, 1825]. Moderate or large in size, smooth, with growth lines only; circular or slightly oval in section; apex simple or with slight notch on the convex side (5). *M.Trias.-Rec.*, cosmop.

D. (Lobantale) Cossmann, 1888 [**D. duplex* Defrance, 1819]. Slender, compressed, smooth; interior with 2 longitudinal ribs placed laterally one on each side, giving transverse section a bilobed shape (5). *M.Eoc.*, Eu.

D. (Pseudantalis) Monterosato, 1884 [**D. rubescens* Deshayes, 1825; SD Sacco, 1897]. Thin, shining, smooth; apex with long, straight, linear slit on the convex side. *L.Cret.-Rec.*, N.Hemi.

D. (Rhabdus) Pilsbry & Sharp, 1897 [**D. rectius* Carpenter, 1865]. Nearly straight or slightly curved, shell very thin throughout and glossy, some with annular swellings; surface brilliant, polished, without longitudinal sculpture; aperture and apex simple (5). *L.Plio.*, E.Indies; *Rec.*, N.Am.-C.Am.-S.Am.-Asia-E.Indies.

D. (Tesseracme) Pilsbry & Sharp, 1898 [**D. quadrapicale* Sowerby, 1860; SD Woodring, 1925]. Square at or near apex, with angles on convex, concave, and lateral sides, becoming suborbicular at aperture. Apex with or without a short pipe (5). *M.Eoc.*, N.Am.-C.Am.; *Rec.*, N.Am.-C.Am.-E.Indies-Afr.

Plagioglypta Pilsbry & Sharp, 1897 [**Dentalium undulatum* Münster, 1844]. Shell tapering, circular or elliptical in section, without longitudinal sculpture, with close and fine obliquely encircling wrinkles throughout or on anterior portion. Aperture with a fairly long and broad slit. *?L.Ord.*, Russia; *U.Dev.-U.Cret.*, N.Am.-S.Am.-Eu.-Asia. ——Fig. 30,*3*. **P. undulata* (Münster), Trias., Aus.(Tyrol); *3a,b*, side view and transv. sec., ×1 (Kittl, 1891).

Prodentalium Young, 1942 [**P. raymondi*]. Shell with oblique growth lines and fine longitudinal ribs generally with a slightly zigzag alignment. *Dev. - Penn.(U.Carb.)*, N.Am.-Eu.-Asia. —— Fig. 30,*9*. **P. raymondi*, Penn., USA(N.Mex.); ×0.5 (Young, 1942).

Family SIPHONODENTALIIDAE Simroth, 1894

[Gadilinae Stoliczka, 1868; Siphonopoda G. O. Sars, 1878; Siphonopodidae Simroth, 1894]

Scaphopoda having the foot either expanded distally in a symmetrical disc with crenate continuous edge and with or without a median, finger-like projection, or simple and vermiform, without developed lateral processes. Shell small and generally smooth, commonly contracted toward mouth (8). *?M.Trias., L.Cret.-Rec.*

Cadulus Philippi, 1844 [**Dentalium ovulum*]. Tubular, circular or oval in section; somewhat arcuate, varying from cask-shaped to acicular, more or less bulging or swollen near middle or anteriorly, contracting toward aperture. Surface smooth or delicately striated (5). *L.Cret.*, Eu.-N. Am.-Greenl.; *Tert.-Rec.*, cosmop.

C. (Cadulus). Cask-shaped, short and obese, conspicuously swollen in middle, tapering rapidly toward both ends. Aperture simple. Apex simple, with wide circular callus or ledge within (5). *U.Cret.*, N.Am.; *Tert.*, N. Am.-W. Indies-Eu.; *Rec.*, Eu.-N. Am.-S. Am.-W. Indies-Afr.-E.Indies. ——Fig. 30,*7*. **C. (C.) ovulum* (Philippi), Mio.-Rec., Italy; ×4 (Pilsbry & Sharp, 1897).

C. (Dischides) Jeffreys, 1867 [**Ditrupa polita* S.V.Wood, 1842] [=*Discides* Sacco, 1897]. Rather slender, only slightly bulging, apex cut into ventral and dorsal lobes by 2 deep lateral slits, one on each side (5). *M.Eoc.*, Eu.; *Rec.*, Eu.-E.Indies-Austral.-Oceanica.

C. (Gadila) Gray, 1847 [**Dentalium gadus* Montagu, 1803] [=*Helonyx* Stimpson, 1865; *Loxoporus* Jeffreys, 1883]. Rather slender and decidedly curved, convex ventrally, concave dorsally; more or less swollen near middle or toward aperture, more tapering toward apex, which lacks callus or has weak callous ring far within. Edges not slit (5). *L.Cret.-Rec., cosmop.*——Fig. 30,*8*. **C. (G.) gadus* (Montagu), Rec., Jamaica; *8a,b*, side and transv. sec., ×2 (Pilsbry & Sharp, 1897).

C. (Gadilopsis) Woodring, 1925 [**Ditrupa dentalina* Guppy, 1874]. Moderately small, very slender, needle-shaped, slightly swollen very near aperture; sculptured with oblique growth lines on posterior; apical opening small, unslit. *L.Mio.-L.Plio.*, W.Indies-C.Am.-N.Z.

C. (Platyschides) Henderson, 1920 [**C. grandis* Verrill, 1884]. Shell with 2 or 4 broad apical slits, lobes between low and wide (3). *M.Oligo.-Rec.*, N.Am.-C.Am.-S.Am.-W.Indies.

C. (Polyschides) Pilsbry & Sharp, 1897 [**Siphodentalium tetraschistum* Watson, 1897]. Only slightly inflated above middle, apex with 4 or more slits (3). *M.Eoc.*, Eu.-N.Am.-W.Indies-C. Am.; *Rec.*, N. Am.-W. Indies - S. Am. - E. Indies-Austral.-Antarctica.

Entalina Monterosato, 1872 [**Dentalium tetragonum* Brocchi, 1814; SD Sacco, 1897] [=*Eudentalium* Cotton & Godfrey, 1933]. Shell *Dentalium*-like, small, largest at aperture, thence tapering to apex; strongly ribbed, angular in section near apex. Foot expanding distally into disc with digitate periphery, and having a median process or filament (5). *?M.Trias.*, Eu.; *Tert.*, Eu.-E.Indies; *Rec.*, Eu.-Afr.-N. Am.-E. Indies-Austral. —— Fig. 30,*1*. *E. quinquangularis* (Forbes), Rec., Eu.; ×1 (Pilsbry & Sharp, 1897).

Siphonodentalium M.Sars, 1859 [**Dentalium vitreum* M.Sars, 1851 (*non* Gmelin, 1791 =*Dentalium lobatum* Sowerby, 1860)] [=*Siphodentalium* Monterosato, 1874; *Siphonodontum, Tubidentalium* Locard, 1886]. Shell a smooth, arcuate, slightly tapering tube, largest at aperture, section circular or nearly so. Apex rather large, either slit into lobes or simple. Foot capable of expanding into terminal disc (5). *Paleoc.*, Eu.-Asia-Austral.; *Rec.*, Eu.-N.Am.-Arctic-W.Indies-E.Indies-Austral.-Antarctica.

S. (Siphonodentalium). Apex slit into lobes. *M. Eoc.*, Eu.Asia; *Rec.*, Eu.-N.Am.-Arctic-W.Indies-Antarctica.——Fig. 30,*2*. **S. lobatum* (Sowerby), Rec., Atl.; ×1 (Pilsbry & Sharp, 1897).

S. (Pulsellum) Stoliczka, 1868 [**S. lofotense* M. Sars, 1864; SD Cossmann, 1888] [=*Siphonentalis* G.O.Sars, 1878]. Like *Siphonodentalium* but without apical slits. Foot-disc has filiform tentacle in middle. *Paleoc.*, Eu.-Asia; *Rec.*, Eu.-N.Am.-E. Indies-Austral.

INCERTAE SEDIS

?Throopella Greger, 1933 [**T. typa*]. Shell tapering at each end, posterior more attenuate, anterior end crateriform with oblique, circular opening; collar or peristome in opening folding back on outside. *U.Dev.*, N.Am.——Fig. 30,*6*. **T. typa*, USA(Mo.); ×1 (Greger, 1933). Possibly not a scaphopod.

GENERIC NAMES FOR SUPPOSED SCAPHOPODA BUT BELONGING TO OTHER ORGANISMS

Ditrupa auctt. [*non* Berkeley, 1835]. Vermes.

Gadus auctt. [*non* Linné, 1758]. Pisces.

REFERENCES

Deshayes, M. G. P.

(1) 1825, *Anatomie et monographie du genre Dentale:* Soc. Histoire nat., v. 2, p. 322-378, pl. 15-18 (Paris).

Gardner, J. S.

(2) 1878, *On the Cretaceous Dentaliidae:* Geol. Soc. London, Quart. Jour., v. 34, p. 56-65.

Henderson, J. B.

(3) 1920, *A monograph of the East American scaphopod mollusks:* Smithson. Inst. U. S. Natl. Mus., Bull. 111, 177 p., 20 pl.

Lacaze-Duthiers, Henri

(4) 1856, *Histoire de l'organization et du dévelopement du Dentale:* Ann. Sci. nat., ser. 4, Zoologie, v. 6, p. 225-281; v. 7, p. 5-51; 171-225; v. 8, p. 18-44.

Pilsbry, H. A. & Sharp, B.

(5) 1897-98, *Scaphopoda: in* TRYON, G. W., Manual of Conchology, v. 17, 280 p., 39 pl.

Plate, L. H.

(6) 1892, *Über den Bau und die Verwandschaftsbeziehungen der Solenoconchen:* Zool. Jahrb., Abt. für Anatomie und Ontogenie der Thiere, v. 5, p. 301-386.

Richardson, L.

(7) 1906, *Liassic Dentaliidae:* Geol. Soc. London, Quart. Jour., v. 62, p. 573-596.

Simroth, H.

(8) 1894-95, [*Scaphopoda*]*:* in BRONN, H. G., Klassen und Ordnungen des Thier-Reichs, v. 3, p. 354-467.

AMPHINEURA

By ALLYN G. SMITH[1]

CONTENTS

INTRODUCTION

The Amphineura are strictly marine mollusks. A living amphineuran has a typical bilaterally symmetrical body with an anterior mouth and a posterior anus. The foot is ventral and adapted for creeping. The animal has a partly or completely enclosed mantle. Internally the alimentary tract is nearly straight, generally with a radula present in a poorly defined head. Gills project into a shallow mantle cavity situated on either side of the foot between it and the mantle edge; they may be paired or many, posterior or lateral. The nervous system consists of an esophageal ring with ganglia and four longitudinal cords, two of which are ventral and two lateral. There are no cephalic eyes, tentacles, or otocysts.

The name Amphineura was proposed first in 1876 by HERMAN VON IHERING as a phylum separate from the Mollusca, to include the classes Placophora (chitons) and Aplacophora (Solenogastres). Until recent years most students of the classification of these marine invertebrates have considered the Amphineura as a class consisting of two orders, Polyplacophora (or Loricata), including the chitons, and Aplacophora, comprising forms without shell covering, known also as Solenogastres. The Amphineura are here considered as a class separate from the Gastropoda and are treated as composed of the subclasses Polyplacophora and Aplacophora.

---

[1] Research Malacologist, California Academy of Sciences, San Francisco, Calif.

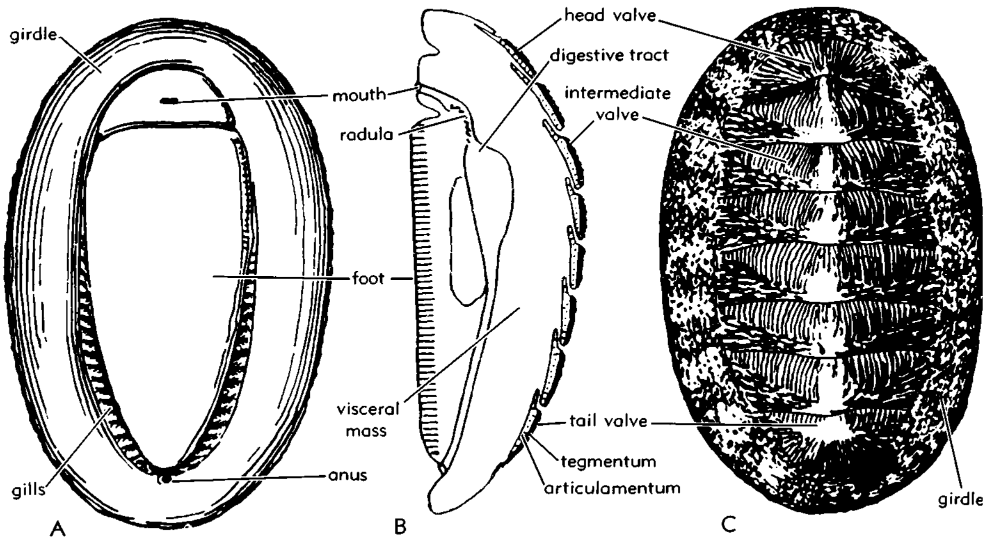

FIG. 31. General features of a modern amphineuran—a moderately large chiton (Polyplacophora), ×1, showing ventral and dorsal aspects *(A,C)* with median longitudinal section *(B)*. (Modified from Moore in Moore, Lalicker & Fischer, "Invertebrate Fossils," copyright 1952, courtesy of McGraw-Hill Book Company, New York.)

The Polyplacophora, or chitons, generally have a series of eight overlapping shells or valves, situated dorsally, and held in place by a tough muscular girdle, which may be either nude or variously ornamented with spicules, scales, bristles, or hairy protuberances. Earliest fossil polyplacophoran remains (generally separate valves) occur in the Upper Cambrian and have been found sparingly in rocks of all geological ages, but they seem to be rarest of all in Mesozoic deposits. The chitons are most prolific at the present day and comprise an extensive world-wide group.

The Aplacophora, or Solenogastres, are wormlike invertebrates representing a specialized and probably degenerate group with definite amphineuran characters. Adults have no shells. No fossil remains have been reported; hence the group is at present of no particular significance to paleontologists.

POLYPLACOPHORA
GENERAL FEATURES

The Polyplacophora, commonly known as chitons, are sluggish crawlers on the sea bottom. They live on or under rocks, in the interstices of coral, in coral holes, and in seaweed holdfasts; a few specialized types occur between the sheaths of certain species of eel-grass. They are found mostly in the littoral zone but may be present at all depths down to 2,300 fathoms. Species have been described from nearly all seas.

They have an evenly elliptical or elongate outline and their thickness along the median dorsal line is roughly one-fourth of their greatest width (Fig. 31). The body is bilaterally symmetrical. No head is visible from the dorsal side and there are no tentacles or other projections reaching beyond the periphery of the animal. A marginal band of muscular tissue, generally of uniform width, is commonly differentiated from the central portion of the back. This band, called the **girdle,** belongs with the soft parts. Its covering may be nude and leathery, or it may consist of various types of decorative processes, including fine to coarse calcareous spicules or spines, small, rounded imbricate scales, or chitinous hairy projections of simple or dendritic form. The girdles of some species may have these decorations in various combinations, whereas others display conspicuous bunches of spicules, called sutural tufts, that occur at regular intervals (Fig. 32).

The central part of the back consists of a calcareous shell in the form of a series of articulating pieces (normally eight) with

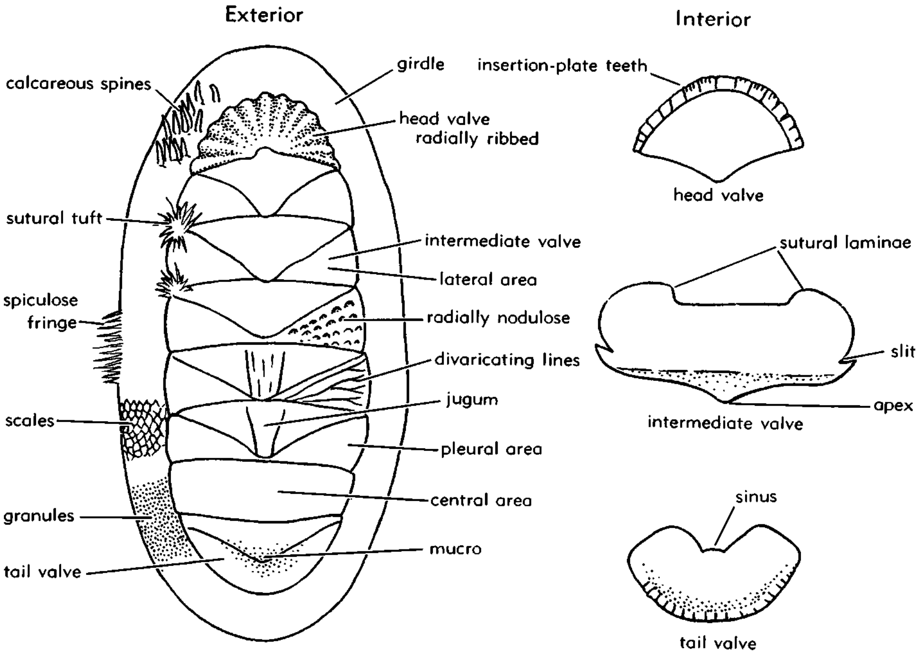

FIG. 32. Morphological features of Polyplacophora. (Modified from F. M. Bayer in R. Tucker Abbott, "American Seashells," copyright 1954, courtesy of D. Van Nostrand Company, Inc., Princeton, N.J.)

joints between them running transverse to the axis of the body. This allows a chiton, when disturbed, to roll up like a pill bug (wood louse), bending at each joint between the shell pieces. The surface of the separate shells may be smooth or variously sculptured with ribs, pustules, or microscopic granules, occurring alone or in combination. This sculpture is invariably in low relief, when present, without the prominent protuberances or projections that are found on some gastropods. In a few species the dorsal shells may be almost or completely buried in an extension of the girdle over them.

The underside of a chiton consists mostly of a broad, flat muscular **foot,** like that of a marine snail. A well-marked groove is visible along the border, for the mantle cavity opens in this position. At one end is the **head,** which is identified merely by a constriction separating it from the foot and by the presence of the mouth opening. The anus is at the opposite extremity.

A chiton of average size is 1 to 3 inches long and its width amounts to about a fourth to a third of its length. Some minute species measure only 0.25 inch long in the adult stage, but the largest known species, the giant chiton of the West Coast of North America, reaches a length of 13 to 14 inches.

Coloration of the upper part of the shells is quite variable, even between individuals of the same species, although in most species the color pattern is fairly constant. Black, brown, white, and various tints of red and green form the usual color range, some species being quite strikingly maculated or banded.

The food habits of chitons are not well known. Some are wholly herbivorous, feeding on various kinds of marine algae; others feed on bryozoans, hydroids, and even on very young barnacles; still others appear to be more or less omnivorous. Seemingly, a close relationship is discernible between food habits and the ecological niches where chitons normally live. Also, there is evidence that polyplacophorans have homing habits similar to those of limpets, coming out from their hiding places at night in order to feed and then returning to the same spot where they stay during the day.

Breeding seasons vary with species. Eggs are laid in jelly-like strings or masses, similar to those of many gastropods. Most chitons pass through a free-swimming larval stage of short duration before settling to the bottom to begin development of the parental form. Several species in the Callistoplacidae, however, are reported to be viviparous, brooding their young between the underside of the mantle and the foot until they are fully formed with complete shells.

MORPHOLOGY OF SOFT PARTS

Strange to say, main features of the soft anatomy of chitons are more important in paleontological study than the characters of the hard parts, for a comparison of the internal organization of chitons with the structure of gastropods and other mollusks throws considerable light on the evolutionary significance of the symmetrical or asymmetrical arrangements of the body parts. The shell of chitons furnishes little help in this direction, and accordingly, analysis of its special features merits effort only in proportion to the importance of the group as fossils, which is not great, although it can throw some light on interesting evolutionary development.

The soft parts of a chiton are essentially those of a simplified, perfectly symmetrical prototype mollusk, which has posterior placement of the respiratory apparatus and anus. The chiton does not quite meet these specifications because the gills, though symmetrically paired, are multiplied in number, especially in the more highly developed groups, evidently by proliferation from an original single pair. Some chitons have two gills on each side of the anus but in others the number ranges to 40 on each side, filling most of the anteriorly extended mantle cavities that stretch like grooves along the sides of the body to the head. Whether few or many gills are present, one pair dominates in size; and because this pair is located at or near the rear end of the mantle cavity, it may be interpreted as the primitive initial pair, corresponding to the single pair in primitive marine snails. The gill structure is also the same, having double rows of leaflets.

The alimentary tract is a tube extending from the mouth, on the underside of the head, to the anus located on the mid-line of the body at the rear. Chitons have a hard rasplike mouth structure composed of horny recurved denticles borne on a tough, flexible ribbon. This is the **radula,** which is bilaterally symmetrical and has eight denticles of varying strength and configuration on each side of a central one, or a total of 17 in each transverse row. The strongest of these denticles is the so-called major lateral, which occupies a position second to the right and left of the central row.

The polyplacophoran heart contains two auricles. There are two kidneys. All chitons are unisexual. In most species the gonad is single and median, lying on the dorsal side of the body between the aorta and the intestine. The genital aperture is situated in front of the renal aperture between two of the posterior gills.

The anatomy of the chitons undoubtedly closely approaches the internal organization of the ancient primitive snails, which are characterized by bilateral symmetry of form. Chitons are specialized in the adaptation of their body for longitudinal bending. They have persisted throughout geologic time with extremely little change. The archaic symmetrical gastropods, however, vanished early in Mesozoic time. Moreover, in the modern chitons there is no present indication of continuing degradation of essential parts.

MORPHOLOGY OF HARD PARTS

The discrete calcareous shell elements of chitons ordinarily comprise eight main pieces that somewhat inaptly are called **valves.** Although living specimens have been found occasionally with seven or nine normally formed valves, these are rare deviations. However, what appears to be a perfectly normal seven-valved species has been discovered in the late Ordovician of Scotland, enough examples having been collected to verify its validity. The matrix in which it occurs indicates a sand-dwelling type, which, if true, makes it the only one known with this habitat.

The chiton valves cover the central part of the back. They are formed as transverse thickenings of the dorsal cuticle behind the velum, the upper shell layer being the first to be laid down. All eight valves generally make their appearance simultaneously but in some species the eighth valve is formed later than the others. Until recently, chiton valves were considered to consist of two layers. The upper or dorsal layer, termed

tegmentum (*tegmen*, roof), is relatively soft, being perforated by a labyrinth of fine and coarse pores. The lower or ventral layer, called **articulamentum,** is quite different in structure and appearance, for it is dense, porcelaneous, and laminated. This lower layer projects into the girdle and underlies the valves next in series, like tiles on a roof. Head and tail valves are usually different in shape from the six intermediate valves, the latter commonly being similar in contour. Based on the investigations of KNORRE (1925) and BERGENHAYN (1931), chiton valves have been shown to contain four layers, which are (1) the **periostracum,** an extremely thin outer dorsal layer equivalent to that of other mollusk types; (2) the tegmentum, immediately underlying the periostracum; (3) the **articulamentum** *(sensu stricto),* or layer composing the insertion plates and the sutural laminae of a valve; and (4) the **hypostracum,** or lowest ventral layer underlying the articulamentum and having a somewhat different crystalline structure. In some of the more highly developed chitons another layer, the **mesostracum,** occurs between the articulamentum and the tegmentum. The existence of all or only some of these shell layers in the valves of both Recent and fossil chitons serves as a further indication of evolutionary development and thus is being found helpful in classification of these animals.

MORPHOLOGICAL TERMS APPLICABLE TO POLYPLACOPHORA

The following alphabetically arranged glossary applying to the Polyplacophora defines the terms most commonly used by specialists in descriptions and in systematic keys developed for identification purposes.

aesthete. Sensory organ terminating in the tegmentum of certain chiton species. Larger ones, called *megalaesthetes,* take the form of eyes, with cornea, lens, pigment layer, iris, and retina, and may or may not be accompanied by one or more smaller ones, called *micraesthetes.* The eyes in a living chiton shell, when present, appear as tiny black spots, scattered or in regular lines radiating from the apex of a valve on the dorsal side.

apex. Central point of the posterior edge of an intermediate valve; sometimes termed the beak or umbo of the valve.

apical area. Short part of the periostracum and tegmentum on the head and intermediate valves of all chitons that is adjacent to the posterior dorsal edge of a valve and which extends over the edge and onto the ventral side.

apophyses (or apophysis plates). *See* sutural laminae.

articulamentum. Formerly used to indicate the inner, usually hard, semiporcelaneous shell layer, generally projecting past the tegmentum on the sides and front of the valves to form the insertion plates and the sutural laminae; recently restricted to indicate the shell layer between tegmentum and hypostracum, called the articulamentum *(sensu stricto)* and composed of several separate components of crystalline shell structure.

beak. Angular projection of the apex of an intermediate valve. A similar projection of the upper surface of the valve anteriorly and between the sutural laminae is termed a *false beak.* Beaked valves are termed *mucronate.*

body valve. See intermediate valve.

central area. Upper surface of an intermediate valve lying centrally, usually differing in sculpture from the lateral areas.

dorsal area. See jugal area.

eaves. Portions of the tegmentum just over the line where the insertion plates and the sutural laminae project from under it.

eave tissue. Composition of the shell material that forms the eaves; this may be porcelaneous or "spongy," i.e., riddled with microscopic tubules.

false beak. See beak.

gills (or ctenidia). Triangular branchial plumes underneath the girdle and protected by the foot, extending from near the tail forward from a fourth to the entire length of the foot; gills are *posterior* (short) in the lower chiton groups, and long *(ambient)* in the more highly developed groups.

girdle. Flexible muscular integument, plain or "leathery," or variously ornamented, in which the valves are imbedded and which holds them in place.

head valve. Anterior valve, numbered *i* in the series.

hypostracum. Lowest ventral calcareous layer of a valve.

insertion plate. Narrow marginal extension of the articulamentum layer in the head and tail valves and at the sides of the intermediate valves, which project into the girdle; sometimes termed the *lamina of insertion.* This structure is absent or nearly obsolete in lower groups of chitons.

intermediate valve. Any one of the valves between head and tail valves; sometimes called *median* or *body valve.* Numbered, in order, *ii* to *vii,* respectively, from the head end of the animal.

jugal angle. Angle formed by the two halves of an intermediate valve.

jugal area (or tract). Upper surface of a valve immediately adjacent to the jugum, sculptured differently from the rest of the surface in some forms; also called *dorsal area.*

jugal sinus. Depression or "bay" between sutural laminae; sometimes called *sutural sinus*.

jugum. Longitudinal ridge of an intermediate valve, when present; may be sharp or rounded.

lamina of insertion. See insertion plate.

lateral area. Portion of upper surface of an intermediate valve, commonly triangular in shape, lying at the side and toward its posterior, usually sculptured diagonally and set off from remainder of upper surface by a diagonal ridge of varying prominence.

lateropleural area. Entire upper portion of the side slopes of an intermediate valve in some species; a term used to denote sculpture of a valve that is much the same, with no particular line of demarcation between the lateral and pleural areas.

median valve. See intermediate valve.

mesostracum. Calcareous shell layer in certain more highly developed living chiton species, lying between the tegmentum and the articulamentum *(s. s.)*.

mucro. Point or projection on the tail valve, usually marking a separation between the configuration of the central and posterior areas. The mucro may be prominent or obsolete; anterior, median or posterior in position; elevated or depressed in shape; or rarely may be curved upward.

mucronate valve. *See* beak.

periostracum. Uppermost, extremely thin layer of a valve on top of the tegmentum, composed of organic material.

pleural area. Side slopes of the upper part of a valve, not including the jugal area or lateral areas where the latter are well differentiated.

posterior sinus. Embayment in posterior median line of a tail valve, formed by the tegmentum and in some forms by the articulamentum also.

radula. Bilaterally symmetrical lingual ribbon set with chitinous denticles. There is a simple-cusped central rachidian tooth, on each side of which, in order, are a translucent minor lateral or varying form, a major lateral with a conspicuous black cusp having 1 to 4 denticles (larger than on any other teeth), two bosslike or thickened uncinal plates of irregular shape, a twisted spatulate uncinal, and three scalelike or slightly thickened external uncini—a total of 17 in each transverse row.

scales. Term usually used to denote small calcareous bodies decorating the dorsal side of the girdle in many species; normally, they are closely set or overlapping and of various shapes, smooth or with minute striations.

slit. Abrupt transverse indentation in the insertion plate.

slit ray. Shallow groove or row of pores or pits extending from a slit to the apex of the valve on the ventral side.

spicules (or spines). Dorsal girdle decorations varying widely with species in size, shape, and frequency. They may be closely set, sparse, gathered into scattered conspicuous bunches, or a combination of these. Both scales and spicules may occur together.

sutural laminae. Sharp, platelike anterior projections of the articulamentum varying in prominence, extending from either side of an intermediate or tail valve. When present, they are lobe-shaped, project into the girdle, and are overlapped by the posterior portion of the preceding valve when in normal position. These two laminae may be separated by a sinus or partially joined by a laminar extension of the articulamentum. (Also called apophysis plates.)

sutural plate. Lamina of articulamentum across the jugal sinus of intermediate and tail valves, extending between the sutural laminae. This is usually thin, when present, and may be finely denticulated and notched at the sides.

sutural sinus. See jugal sinus.

tail valve. Posterior valve.

teeth. Portions of articulamentum between slits, usually most prominent in the tail valve. Teeth may be *pectinated* (crenulated or finely cut like a comb) or *propped* (with edges thickened on the outside); they are sharp and smooth in many species. This term applies to the valves of a chiton and should not be confused with the denticles of the radula, also called teeth.

tegmentum. Outer, usually softer and somewhat porous calcareous layer of a valve just below the periostracum; this shell layer, together with the mesostracum (when present) and articulamentum layers, corresponds to the *ostracum* of gastropods and pelecypods.

terminal area. Upper surface of head or tail valve. Tail valves in some species are separated into a central area and a posterior area by two dividing lines on either side of the valve radiating from the mucro.

uncinal plate. *See* radula.

valve. One of the discrete shells or "plates" of chiton skeleton; commonly numbered *i* to *viii* beginning with the head valve to indicate the exact position.

valve coverage (or overlap). When two contiguous valves lie in such a relation to each other that the rear edge of one covers the whole front edge of the one posterior to it, this is termed *complete coverage*. If only a small part of the front edge of the next valve is overlapped, coverage is termed *partial*. If only the apical part of a valve overlaps the next one, this is called *jugal coverage*. The extent of valve coverage in some primitive chiton species is indicated by the degree to which the tegmentum of the apical area extends over the edge of a valve on to the ventral side.

OCCURRENCE AS FOSSILS

Undoubted chiton species have been reported and described from rocks of practically all ages from Upper Cambrian to Tertiary. In the search for a true ancestral form from which the chitons stemmed, one must look far back in the Precambrian, for such a form must have been extremely ancient.

Most Paleozoic chitons are distinguished from later ones by weak development of imbrication of the valves. These fitted against each other with only a very slight overlap and are characterized by the complete absence of projecting structures such as the insertion plates and sutural laminae of modern forms. In some species the valves are massive and thick with little or no indication of an articulamentum layer. Mesozoic and Cenozoic chitons are much like modern forms and are about the same in size, although an undescribed species from the Permian of Texas has large valves, indicating that the animal was at least 5 inches long. In general, most Paleozoic types of polyplacophorans died out before the Mesozoic. However, one of the more primitive living genera *(Lepidopleurus)* has had an extraordinarily long existence, being reported as far back as the Carboniferous.

The number of described species of fossil chitons has not been exactly determined but must be at least 350. This does not include a number of species, mistaken for chitons and described as such, but which actually belong elsewhere. Some are based on barnacle plates, partial casts of trilobites or other crustaceans, inside casts of portions of the septa of ammonites, and aptychi of ammonites. Certain older patellid gastropods also were originally thought to be chitonoid. A census of the distribution of fossil species of chitons by geological age made by C. T. BERRY (1939) showed totals of 90 Paleozoic species, 21 Mesozoic species, and 145 Cenozoic species, 256 in all. Since 1939, numerous additional species have been described but hardly any from the Mesozoic, which emphasizes an apparent scarcity of chitons in this part of the column that is noteworthy. Chitons exhibit an almost explosive development in Recent time, as evidenced by the fact that no less than 500 species and subspecies have been described. A compilation of data made by me, in which *nomina nuda* and synonymized species are excluded but which takes account of unnamed species reported in the literature shows distribution of presently known fossil polyplacophorans as follows: Ordovician, 9; Silurian, 8; Devonian, 16; Carboniferous and Permian, 40 (Paleozoic, 73, amounting to 22 per cent of total); Triassic, 6; Jurassic, 18; Cretaceous, 7 (Mesozoic, 31, amounting to 9 per cent of total); Eocene, 20; Oligocene, 8; Miocene, 93; Pliocene, 67; Pleistocene, 50; Tertiary undifferentiated, 10 (Cenozoic, 248, amounting to 69 per cent of total). In this tabulation species known also from the Recent include: Miocene, 2; Pliocene, 14; Pleistocene, 40; Tertiary undifferentiated, 3.

Normally, only the disarticulated valves of fossil chitons are found, but there are instances in which all eight valves have been discovered together. Only two instances are known of the fossil occurrence of other chiton parts. One from the Ordovician clearly shows a mass of spicules in what once was the girdle of a complete individual (Fig. 33,*2*). The other from Middle Pennsylvanian rocks carries the impression of at least eight rows of denticles in the radula (Fig. 33,*1*). Theoretically, in any adequate sample of disarticulated valves, the end valves should be found in the ratio of one to three intermediate valves. This may not hold true for certain species having massive tail valves that are less liable to destruction or disintegration. The spongy tegmentum layer also often is lost in fossilization, leaving little on which to base a firm identification. While girdle scales, spicules or other girdle processes have not been reported except in one instance, this does not mean that they should not be diligently looked for when microscopic work is done on the washings of marine sediments. A single girdle scale or spicule of characteristic form could easily be sufficient for generic identification.

CLASSIFICATION

Classification of chitons is in a "fluid" state and probably will continue for some time. Most present-day systems stem largely from PILSBRY's magnificent work published in the *Manual of Conchology,* volumes 14 and 15 (1892-94), and are based on valve and girdle configuration and characters. The radula, though used by THIELE and others for systematic arrangement, has not proved adequate by itself. The chiton classification most useful to paleontologists must

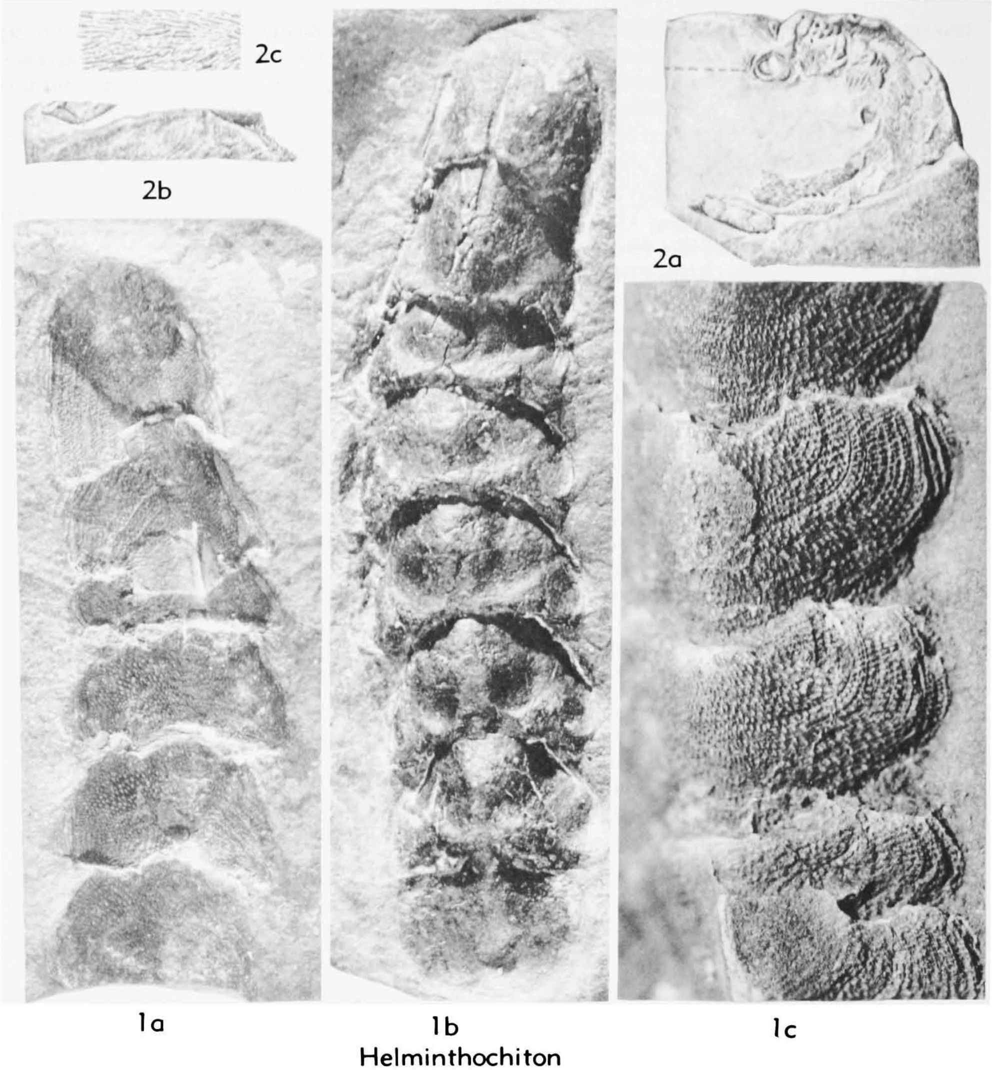

FIG. 33. Paleozoic chitons *(Helminthochiton)*. *1. H. concinnus* RICHARDSON, holotype, M.Penn.(Desmoines.), Francis Creek Sh., near Coal City, Ill.; *1a,* anterior part of specimen, mold of dorsal side, showing head valve and next-following intermediate valves, ×2.4; *1b,* mold of underside of shell showing all eight valves with impression of radula on head valve (at top) and intermediate valve *ii* behind it, ×2.4; *1c,* intermediate valves showing ornament, ×5 (50). *2. H. thraivensis* COWPER REED, Ord., Scot.; *2a,* long. sec. of complete individual showing preserved mass of spicules, ×1; *2b,* internal mold of 3 successive valves, side view, ×3; *2c,* enlarged portion of spicular mass, ca. ×5 (COWPER REED).

of necessity omit girdle characters, important though these may be. For the present, at least, it would seem logical to use PILSBRY's system, based largely on valve configuration, modified where appropriate by a consideration of the valve structure as developed by KNORRE and BERGENHAYN. The systematic classification of the Polyplacophora used in the following pages has been developed with this in mind, with the view, also, to avoid over-complication. Admittedly it may be far from an adequate and workable system but should serve the needs of workers on this interesting not-well-known group.

APLACOPHORA

GENERAL FEATURES

The Aplacophora have a subcylindrical or vermiform body without shelly plates or valves, at least in the adult stage. The body is completely invested by a mantle consisting of a spiculose integument, which may be continuous or interrupted by a longitudinal central furrow. The calcareous spicules are of various shapes and in some genera have an internal cavity. The foot is rudimentary or aborted. The mantle cavity terminates in a posterior cloaca containing rudimentary gills in addition to outlets of the anus and nephridia. In one order (Neomeniida) the animals are hermaphrodite, but in the other (Chaetodermatida) the sexes are separate.

Habitats of the Aplacophora range from shallow marine water down to at least 8,000 feet. Some burrow in mud; others are associated with colonial coelenterates. They are found in nearly all seas.

No fossil remains of aplacophorans have been reported so far, although future careful micropaleontological investigations may result in identifying spicules belonging to this group.

CLASSIFICATION

The Aplacophora are divided into 2 orders defined mainly by the presence of a distinct longitudinal ventral groove (Neomeniida) or its absence (Chaetodermatida), but also by the bisexual nature and lack of a differentiated liver in the first and by the unisexual nature and presence of a liver in the second. The Neomeniida generally are grouped in 4 famiiles (67 genera, 160 species), whereas the Chaetodermatida contain a single family (4 genera, 27 species). These are indicated with brief diagnoses in the latter part of the following section devoted to systematic descriptions.

SYSTEMATIC DESCRIPTIONS

Class AMPHINEURA von Ihering, 1876

[=Isopleura Lankester, 1883; Aculifera Hatschek, 1888]

Aquatic, marine, bilaterally symmetrical mollusks having an external mantle that bears a series of exposed dorsal or, less commonly, internal calcareous plates, or is stiffened by disseminated calcareous spicules. Head partially or not differentiated in form; body oval, elongate, or flattened; foot expanded and developed for creeping or wormlike, with a ventral groove or none. Nervous system consisting of an esophageal ring with ganglia and 4 longitudinal cords, 2 ventral and 2 lateral; no cephalic eyes, tentacles or otocysts. Gills paired or many, posterior or lateral; mouth anterior, usually with a radula; anus posterior and median. *U.Cam.-Rec.*

Subclass POLYPLACOPHORA de Blainville, 1816

[*nom. correct.* Gray, 1821 (*ex* Polyplacophores de Blainville, 1816), validation proposed L. R. Cox, ICZN pend.] [=Loricata Schumacher, 1817; Crepipoda Goldfuss, 1820; Polyplaxiphora Férussac, 1821; Polyplaxiphora de Blainville, 1824 (*non* Férussac, 1821); Lamellata Latreille, 1825; Polyplaxiphorae Menke, 1828; Polyplakiphora de Blainville, 1829; Cyclobranchia Swainson, 1840 (*non* Cuvier, 1817); Placophora von Ihering, 1876; Polyplaciphora Dall, 1879; Polybranchiata Spengel, 1881; Lepidoglossa Thiele, 1893]

Amphineurans of type commonly called chitons, protected by an encircling girdle in which a dorsal series of calcareous plates or valves, generally 8, is partially or wholly imbedded, valves overlapping in greater or lesser degree; head differentiated; with ventral sole adapted for creeping; gills numerous, occupying a ventral groove between foot and girdle; radula present, heterodont. Sexes separate. *U.Cam.-Rec.*

Order PALEOLORICATA Bergenhayn, 1955

[=Eoplacophora Pilsbry, 1893 (*partim*)]

Primitive chitons with valve structure consisting of periostracum, tegmentum, and hypostracum, lacking articulamentum, and therefore without insertion plates and sutural laminae; valves generally thick and massive. *U.Cam.-U.Cret.*

Suborder CHELODINA Bergenhayn, 1943

Shell composed of 8 valves with tegmentum which may or may not be divided into fairly well-marked areas; sculpture, when present, consisting of fine to coarse transverse growth lines or ridges, generally following configuration of anterior edge of valves. *L.Ord.-U.Cret.*

Family CHELODIDAE Bergenhayn, 1943

Intermediate valves longer than wide; tegmentum not divided into areas, or if present, developed very weakly. *L.Ord.-U.Cret.*

Chelodes Davidson & King, 1874 [**C. bergmani*] [?=*Sagmaplaxus* Oehlert, 1881]. Body fairly large and much elongated; intermediate valves heart- or wedge-shaped, thick and massive, with length of each 1.5 times width, and in longitudinal cross section sloping away from well-developed semicircular or angular transverse ventral ridge located subcentrally; apical areas long, extending on ventral side of valve to internal ridge; anterior sides of valves may be rolled over edges so as to form narrow channels and a small pocket at apex; valve coverage partial. *L.Ord.-Sil., ?L. Dev.,* Eu.(Swed.-Scot.-?Fr.-Czech.) - N. Am.(Ala-Minn.).——FIG. 34,*5*. **C. bergmani* M.Sil.(Gotl.), Swed.; *5a,* reconstr., ×0.75; *5b,c,* valve (type), ×2.25 (8*).

Family GOTLANDOCHITONIDAE Bergenhayn, 1955

Relatively small, with intermediate valves wider than long, approximating those of living chitons in general configuration; tegmentum with weak or clearly developed areas. *Sil.*

Gotlandochiton BERGENHAYN, 1955 [**G. interplicatus*]. Tegmentum areas clearly defined; valve coverage jugal or complete. *Sil.,* Swed.——FIG. 34,*4*. **G. interplicatus,* Gotl.; reconstr., ×1 (8*).——FIG. 34,*7*. *G. troedssoni* BERGENHAYN, Gotl.; intermed. valve (type), ×3.4 (8*).——FIG. 34,*8*. *G. laterodepressus* BERGENHAYN, Gotl.; intermed. valve (type), ×3.5 (8*).

Family SCANOCHITONIDAE Bergenhayn, 1943

Intermediate valves wider than long, nearly semicircular or triangular in shape, with tegmentum divided into distinct areas. *U.Cret.*

Scanochiton BERGENHAYN, 1943 [**S. jugatus*]. Outline of intermediate valves nearly semicircular; tegmentum divided into lateral and pleural areas, and broad, triangular, elevated jugal area; head valve semicircular, lacking well-marked division into tegmentum areas; valve coverage partial. *U. Cret.,* Eu.(Swed.).——FIG. 34,*6*. **S. jugatus,* Senon.(Mammillatus Z.); *6a,* reconstr., ×1 (8*); *6b,* intermed. valve (type), ×4; *6c,* head valve, ×4 (*6b,c,* 42*).

Olingechiton BERGENHAYN, 1943 [**O. triangulatus*]. Intermediate valves triangular; tegmentum divided into a raised rectangular jugal area flanked by 2 rather narrow, unwaved lateral areas, sculptured throughout by minute tubercles and distinct lines of growth; valve coverage jugal; end valves unknown. *U.Cret.,* Eu.(Swed.).——FIG. 34,*3*. **O. triangulatus,* Senon. (Mammillatus Z.); *3a,* reconstr., ×1 (8*);*3b,* 2 associated intermed. valves (type), ×2.5 (42*).

Haeggochiton BERGENHAYN, 1955 [**H. haeggi*]. Intermediate valves trapezoidal; tegmentum surface divided into 2 distinct lateral areas raised above a depressed and somewhat concave median area; valve coverage jugal; end valves unknown. *U.Cret.,* Eu.(Swed.).——FIG. 34,*1*. **H. haeggi,* Senon. (Mammillatus Z.); *1a,* reconstr., ×1 (8*); *1b,* half of intermed. valve (type), ×6.25 (8*).

Ivoechiton BERGENHAYN, 1955 [**I. levis*]. Intermediate valves rectangular in shape, high-arched and rounded, with jugal angle of about 90°; surface of tegmentum not divided into distinct areas, completely smooth; valve coverage complete; end valves unknown. *U.Cret.,* Eu.(Swed.).——FIG. 34, *2*. **I. levis,* Senon. (Mammillatus Z.); *2a,* reconstr., ×1 (8*); *2b,* intermed. valve (type), ×2 (8*).

Suborder SEPTEMCHITONINA Bergenhayn, 1955

Body narrow, wormlike, about 17 times longer than wide, with 7 exposed, long and narrow, overlapping dorsal valves. *U.Ord.*

Family SEPTEMCHITONIDAE Bergenhayn, 1955

Surface of tegmentum of all valves divided into distinct areas; valve coverage complete. *U.Ord.*

Septemchiton BERGENHAYN, 1955 [**S. vermiformis*]. Head and intermediate valves with triangular anterior area bounded by 2 lateral areas; tail valve with very long triangular central area terminating in a posterior mucro near end of valve, and bounded by very narrow, short posterior area which is perpendicular to valve axis; sides of valves slope rather steeply from a sharp jugal ridge; areas of tegmentum are set off by well-developed ridges decorated with small, closely set tubercles. [Fossils occur in a fine-grained sandstone matrix, leading to supposition that the animal was a sand dweller.] *U.Ord.* Eu.(S.Scot.).——FIG. 35,*1*. **S. vermiformis; 1a,b,* head and intermed. valves showing sculpture, ×8; *1c-e,* schematic diagrams of valve areas; *1f,* reconstr., ×1.6 (8*).

Order NEOLORICATA Bergenhayn, 1955

Valve structure consisting of periostracum, tegmentum, articulamentum *(s.s.)*, and hypostracum layers, some more highly developed groups with mesostracum layer also; except in more primitive families, articulamentum extending out from under tegmentum in form of insertion plates and sutural laminae. *Carb.-Rec.*

Suborder LEPIDOPLEURINA Thiele, 1910

[Eochitonia DALL, 1889 *(partim)*; =Eoplacophora PILSBRY, 1893 *(partim)*; Protochitonina ASHBY, 1929 *(partim)*; Lepidopleurida THIELE, 1931; Gryphochitonida QUENSTEDT, 1932 *(partim)*; Isoplacophora COTTON & WEEDING, 1939 *(partim)*]

Tegmentum surface of head valve with a single shell area only, located anteriorly, on intermediate valves divided into a central and 2 lateral areas but on tail valve into central and posterior areas with a mucro (Fig. 36,*1a-c*). *Carb.-Rec.*

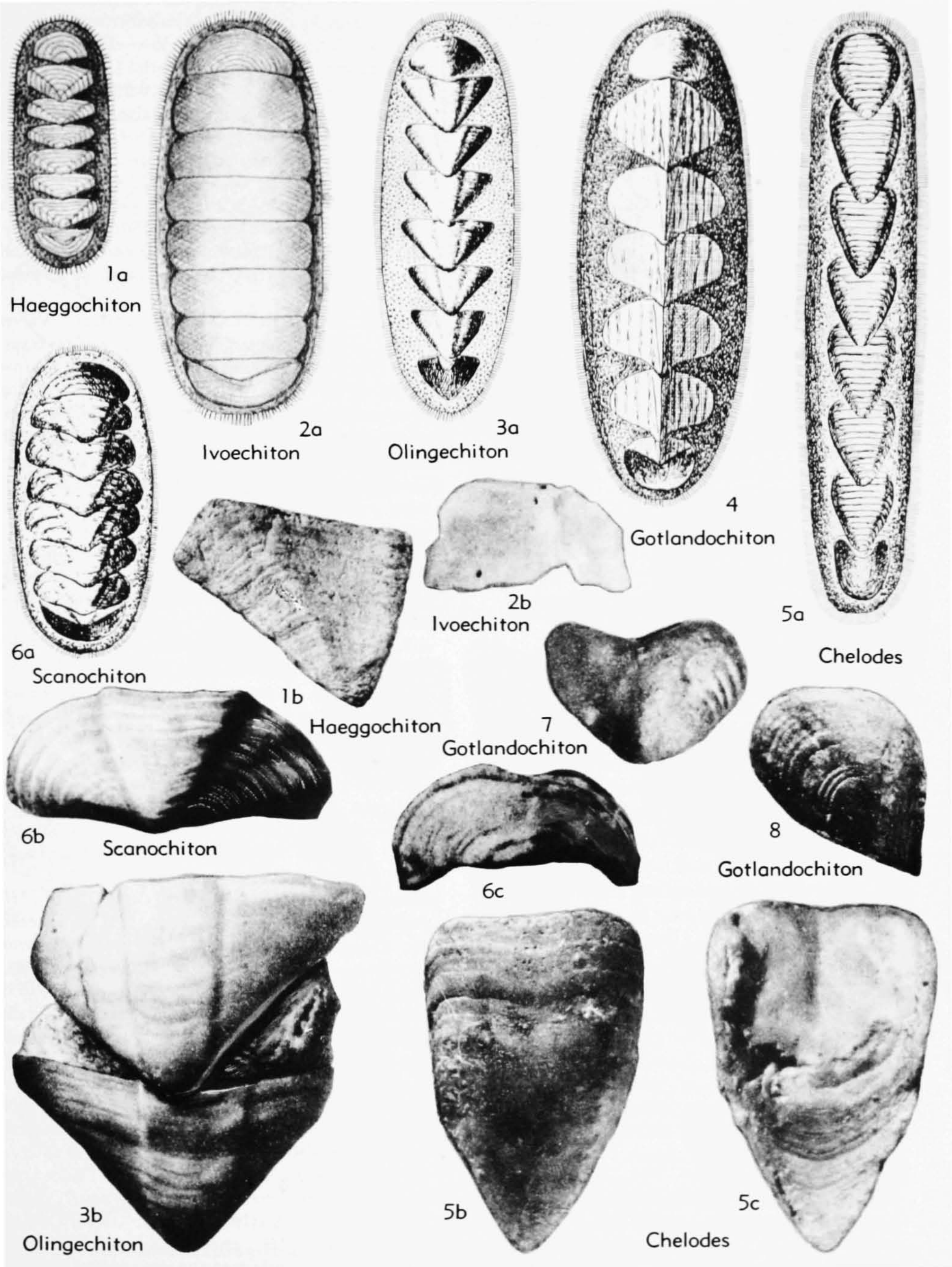

FIG. 34. Paleoloricata; Chelodina (Chelodidae, Gotlandochitonidae, Scanochitonidae) (p. I49-I50).

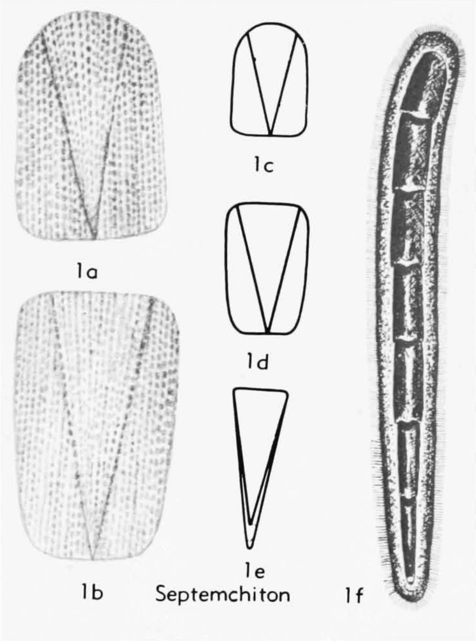

FIG. 35. Paleoloricata; Septemchitonina (Septemchitonidae) (p. 150).

Family LEPIDOPLEURIDAE Pilsbry, 1892

[=Holochiton FISCHER, 1885 (classed as genus); Eochiton FISCHER, 1885 (classed as subgenus); Leptochitonidae DALL, 1889 *(partim)*; Gryphochitonidae PILSBRY, 1900 *(partim)*; Protochitonidae ASHBY, 1925 *(partim)*]

Relatively small (less than 2 inches long); valves generally sculptured with granules closely set in lines or quincunx; valve coverage complete; girdle narrow, minutely spiculose or scaly; insertion plates lacking, or if present, weak and unslit; articulamentum layer usually consisting only of weakly developed sutural laminae in valves *ii* to *viii*. Gills short, posterior. [Recent species range from shore to 2,300 fathoms.] *Carb.-Rec.*

Lepidopleurus LEACH in RISSO, 1826 (*non* CARPENTER in DALL, 1879) [**Chiton cajetanus* POLI, 1791; SD GRAY, 1847] [=*Leptochiton* GRAY, 1847; *Deshayesiella* CARPENTER in DALL, 1879; *Rhombichiton* DEKONINCK, 1883; *Beanella* THIELE, 1893 (*non* DALL, 1882); *Pilsbryella* NIERSTRASZ, 1905; *Parachiton* THIELE, 1909; *Terenochiton* IREDALE, 1914; *Xiphiozona* BERRY, 1919; *Belchiton* ASHBY & COTTON, 1939]. Elongate-ovate chitons with relatively thin valves, round-backed or with moderately distinct jugal angle; lateral areas of intermediate valves indefinitely marked but in a few species standing out sharply; sculptural features of all valves not at all prominent, generally consisting of an over-all granular background; jugal area usually obscure, not distinct from pleural areas. *Carb.-Rec.;* cosmop. [*Carb.,* Eu.(Belg.-Eng.-Scot.-USSR); *Eoc.,* Eu.(Fr.); *Mio.,* Eu.(Fr.-Ger.-?Italy-Vienna Basin) - Austral.-N. Z.; *Plio.,* Eu. (Italy)-Austral.-N.Z.; *Pleist.,* Eu.(Italy-Norway)-N.Am. (Calif.); *Rec.,* nearly all seas].——FIG. 36,*5*. *L. laterodepressus* BERGENHAYN, Carb. (300 ft. below Hosir Ls.), Scot.; *5a,* reconstr., ×0.5; *5b,* intermed. valve dorsal view, ×1.5; *5c,d,* valve *ii*, dorsal and side view, ×1.5 (42*).——FIG. 36,*4*. **L. cajetanus* (POLI), Tert.-Rec., living spec., Medit.; *4a,b,* head and intermed. valves dorsal, ×3.2; *4c,d,* intermed. and tail valves, side, ×1 (25*). [In classification adopted by many authors, *Leptochiton, Deshayesiella, Pilsbryella, Parachiton, Terenochiton,* and *Xiphiozona* are accepted as subgenera of *Lepidopleurus.*]

Oldroydia DALL, 1894 [**O. percrassa*]. Valves heavy, strongly sculptured, with irregular transverse ribs that in life are well separated by narrow extensions of girdle reaching to jugum, resulting in coverage that is partial to apical only; articulamentum well developed, unslit; tegmentum with posterior extension between rather large sutural laminae; jugal area prominent, sculptured differently from pleural areas; lateral areas not differentiated. *Rec.,* USA(Calif.).

Protochiton ASHBY, 1925 [**Acanthochites (Notoplax) granulosus* ASHBY & TORR, 1901]. No insertion plates in head and tail valves, intermediate valves having incomplete unslit insertion plates; articulation well developed; all valves except head valve about as broad as long, strongly sculptured, with rows of elongate granules; articulamentum of tail valve ending in callus, beyond which tegmentum is produced posteriorly almost 0.25 of its total length. *M.Mio.,* Austral.(Victoria).——FIG. 36,*7*. **P. granulosus* (ASHBY & TORR) Balcombian, Balcombe Bay, Victoria; *7a,b,* head valve, dorsal and ventral (×2); *7c,* intermed. valve (holotype, ×2); *7d,e,* tail valve, dorsal and ventral (×2) (1*).

Helminthochiton SALTER in M'COY, 1846 [**H. griffithi*] [=*Gryphochiton* GRAY, 1847; *Chonechiton* CARPENTER in DALL, 1882; *Glaphurochiton* RAYMOND, 1910; *Gryptochiton* ZITTEL (BROILI edit.), 1924, and DECHASEAUX in PIVETEAU, 1952 *(errore)*]. Similar to *Lepidopleurus* but generally much larger, with shell areas of articulamentum less developed; head valve with no articulamentum *(s. s.)*; intermediate and tail valves with narrow, widely separated sutural laminae and no insertion plates; all valves usually as long as wide, subquadrate; tail valve with subcentral mucro. *L.Ord.-Carb.,* Eu.-N.Am. [*L.Ord.(Arenig.),* Czech.; *M. Ord.,* Scot.; *Sil.,* Ire.; *L.Carb.(Tournais.),* Belg.-?USSR; *Miss.,* USA(Ind.); *Penn.,* USA(Pa.-Ill.)].——FIG. 36,*3*. **H. griffithi,* Sil., Ire.(Galway); *3a,b,* dorsal and side views, posterior part of shell, ×2, ×1 (51*).——FIG. 36,*2*. *H. priseus* MÜNSTER, L.Carb.(Tournais.), Tournai, Belg.; *2a,* complete specimen, ×1 (49*); *2b-d,* side, dorsal, and ventral views of intermed. valve, ×1 (23*). Also, Fig. 33.]

Pterochiton CARPENTER in DALL, 1882 [**Chiton eburonicus* RYCKHOLT, 1845] [=*Loricites* CARPENTER in DALL, 1882; *Anthracochiton* ROCHEBRUNE, 1883]. Shell elongated, leptoidal; valves

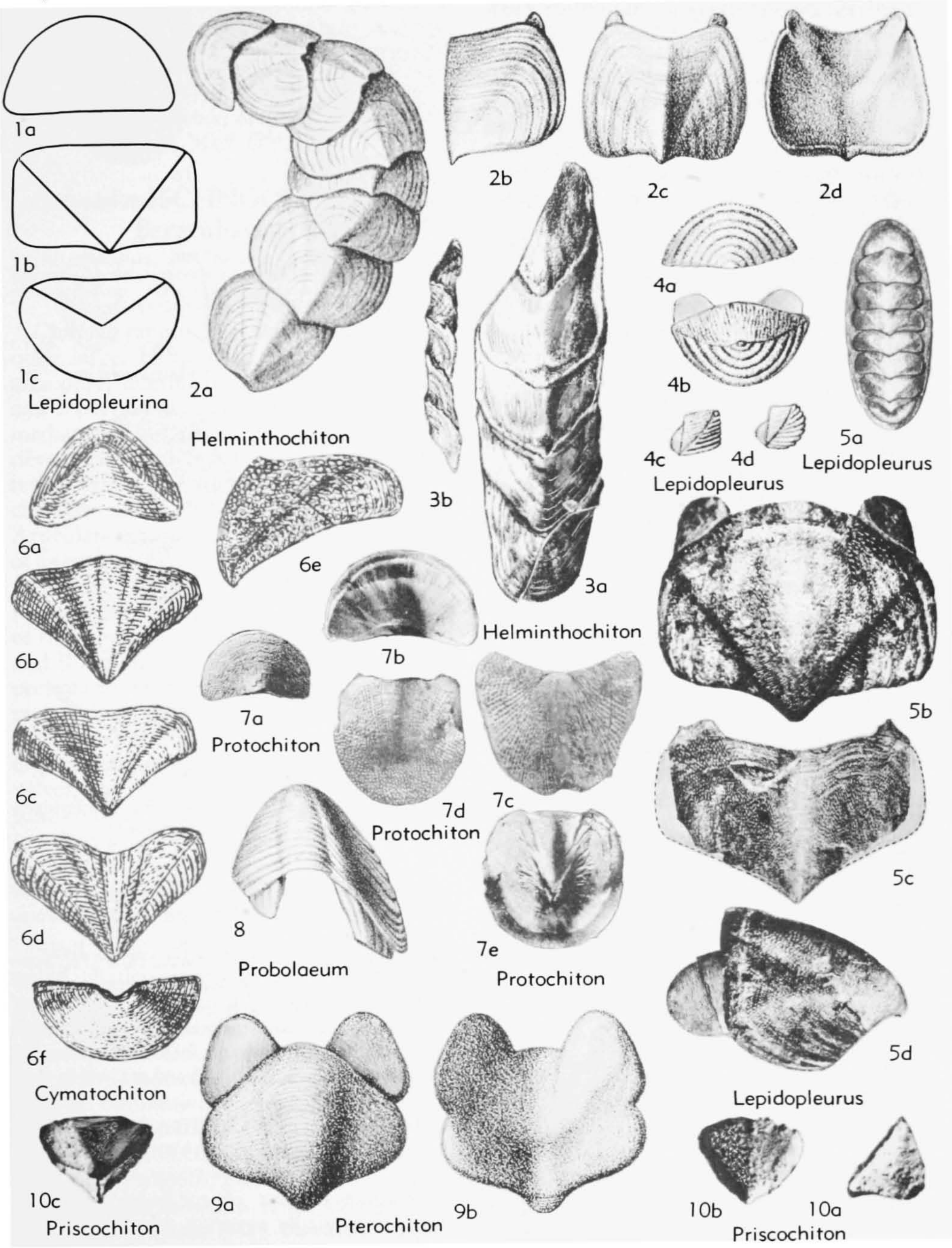

FIG. 36. Neoloricata; Lepidopleurina (Lepidopleuridae) (p. 150-154). [*1a-c.* Divisions of shell areas of Lepidopleurina, schematic; *1a,* head valve; *1b,* intermediate valve; *1c,* tail valve (*Aa*—anterior area, *Ac*—central area, *Al*—lateral area, *Ap*—posterior area).]

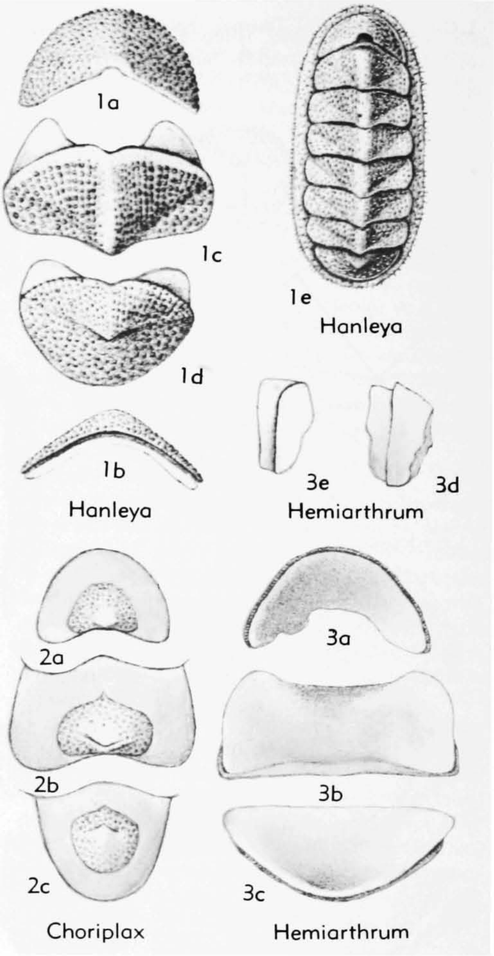

FIG. 37. Neoloricata; Lepidopleurina (Hanleyidae, Choriplacidae) (p. 154-155).

laterally excavated, posteriorly acuminate; last valve regular, mucro ischnoidal; anterior valve (?usually) sinuate; apophyses large, sinus wide. *L.Carb.*, Eu.(Belg.-Ire.).——FIG. 36,9. **P. eburonicus* (RYCKHOLT), Tournais., Belg.(Visé); *9a,b*, dorsal and ventral views of intermed. valve, ×1 (30*).

Probolaeum CARPENTER in DALL, 1882 [**Chiton corrugatus* SANDBERGER, 1853 (=*C. subgranosus* SANDBERGER, 1842)]. Shell leptoidal, elongate, largely projecting; central intermediate valve with central area extending in front of jugum; anterior valve sinuate; posterior valve doubtful. *Dev.*, Eu.(Ger.)-?N.Am.(Que.).——FIG. 36,8. **P. subgranosus* (SANDBERGER), Ger.(Villmar); ?head valve, ×? (52*).

Cymatochiton DALL, 1882 [**Chiton loftusianus* KING, 1848]. Intermediate valves longer than wide, with somewhat elevated, projecting apex, jugum acute; lateral areas flat, not waved; sutural laminae moderately developed, widely spaced, with very broad jugal sinus; valves thrown forward from apex, giving them a triangular aspect. Differs from *Probolaeum* in transverse instead of squared shape of intermediate valves, and in nonwaved end valves. *Perm.*, Eu.(Eng.-Ger.).——FIG. 36,6. **C. loftusianus* (KING), Magnesian Ls., Eng.(Durham); *6a*, head valve; *6b-e*, intermed. valves; *6f*, tail valve; all dorsal except *6e*, side view, ×1 (46*).

Priscochiton DALL, 1882 [**Chiton canadensis* BILLINGS, 1865]. Small, ?head valve rounded, triangular in dorsal aspect, with acute pointed apex; tegmentum of apical area recurved toward ventral side for short distance back of apex forming 2 minute convex plates visible only from ventral side of valve; side view cone-shaped in outline. Known only from 2 ?head valves. *M.Ord.*, N.Am.(Que.).——FIG. 36,10. **P. canadensis* (BILLINGS), Ottawa F.(Blackriv.) Ottawa River; *10a-c*, side, dorsal, and ventral views of ?head valve, *10c*, showing rolled over tegmentum at apex, ×2 (53*).

Family HANLEYIDAE Bergenhayn, 1955

Head valve with insertion plate lacking slits but roughened at edge; intermediate valves lacking insertion plates; tail valve with or without insertion plates; sutural laminae well developed in intermediate and tail valves, eaves small; girdle with fine spines but usually no pores. *Pleist.-Rec.*

Hanleya GRAY, 1857 [**H. debilis* (=**Chiton hanleyi* BEAN in THORPE, 1844)] [=*Hanleia* CARPENTER, 1873 *(nom. null.)*; *Hanleyia* DALL, 1879 *(nom. null.)*] [*non Hanleya* ADAMS & ANGAS, 1864]. Small granulose chitons with jugal angle and flat side slopes; tegmentum areas of lepidopleuroid type; valve structure normal for family but tail valve lacking insertion plate. *Pleist.*, Norway; *Rec.*, sub-Arctic seas.——FIG. 37,1. **H. hanleyi* (BEAN), *Rec.*, Norway; *1a,b*, head valve, dorsal and anterior edge; *1c,d*, intermed. and tail valves, dorsal; ×5.4 (25*); *1e*, entire specimen, ×2.7 (25*).

Hemiarthrum CARPENTER in DALL, 1876 [**H. setulosum*]. Differs from *Hanleya* in presence of insertion plate in tail valve; girdle poriferous, lateral pore tufts small. *Rec.*, Antarctic seas.——FIG. 37,3. **H. setulosum*, S.Atl.; *3a-c*, head, intermed., and tail valves, ventral; *3d,e*, head and tail valves, side; ×2.25 (25*).

Family CHORIPLACIDAE Cotton & Weeding, 1939

[=Choriplaxidae BERGENHAYN, 1955]

Elongate chitons of medium size with thin horny girdle covering whole shell like periostracum except for apices of valves, which constitute the tegmentum; articulamentum very large, sutural laminae and sinus obsolete; insertion plates large, unslit or with obsolete slits; whole shell transparent. *Rec.*

Choriplax Pilsbry, 1894 [**Microplax grayi* Adams & Angas, 1864] [=*Microplax* Adams & Angas, 1864 (*non* Fieber, 1861)]. Shell structure as in family, tegmentum heart-shaped, girdle nude. *Rec.*, Austral.——Fig. 37,*2*. **C. grayi* (Adams & Angas), Sydney Harbor; *2a-c*, head, intermed., and tail valves, dorsal, ×2.5 (25*).

Suborder ISCHNOCHITONINA Bergenhayn, 1930

[=Eochitonia Dall, 1889 *(partim)*; Opsichitonia Dall, 1889 *(partim)*; Mesoplacophora Pilsbry, 1893 *(partim)*; Teleoplacophora Pilsbry, 1893; Chitonina Thiele, 1931 *(partim)*; Isoplacophora Cotton & Weeding, 1939 *(partim)*]

Chitons ranging in size from small to quite large. Head valve with anterior shell area only; intermediate valves with median and 2 lateral areas; tail valve with separated median and posterior areas; apical areas well developed in valves *i* to *vii*. Lateral and posterior areas sculptured alike, differing in character from that of the median areas. Articulamentum well developed, consisting of insertion plates and sutural laminae, latter lacking only in valve *i*. Insertion plates in all valves divided by varying numbers of slits, forming teeth, which may be smooth and sharp on both sides, strongly or weakly pectinated or buttressed on outside. Slit rays generally present and well developed. Girdle exceedingly variable in width and ornamentation, not encroaching over tops of valves, leaving a large expanse of tegmentum compared with extent of articulamentum layers. *?Trias., Rec.*

Family SUBTERENOCHITONIDAE Bergenhayn, 1930

Shell small, elongate, elevated, and carinated. Articulamentum as in Hanleyidae except that insertion plate in head valve extends somewhat farther around, is multiple-slitted and furnished with slit rays on ventral side. Intermediate and tail valves unslit or with diminutive slit rays. Sculpture simple, generally consisting of quincuncially arranged pustules. Girdle narrow, decorated with small, smooth, imbricating scales. *Rec.*

Subterenochiton Iredale & Hull, 1924 [**Ischnochiton gabrieli* Hull, 1912]. Characters of family. *Rec.*, Austral.——Fig. 38,*1*. **S. gabrieli* (Hull), holotype; *1a*, entire animal, ×6; *1b-f*, valves, ×9; *1g*, section of girdle, ×12 (11*).

Family ISCHNOCHITONIDAE Dall, 1889

[=Chitonaceae Hinds, 1845 *(partim)*; Tonicelloidea Simroth, 1894 *(partim)*; Callochitonidae Thiele, 1910 *(partim)*; Trachydermoninae Thiele, 1910; Lepidochitonidae Iredale, 1914]

Ovate to elongate chitons of variable size. Tegmentum of intermediate valves divided into lateral and central areas by diagonal rib (commonly indistinct) extending from apex to anterior outer angle of valves on each side. Articulamentum of head and tail valves multiple-slitted, that of intermediate valves with single slit or in some groups with 2 or more slits on each side. Teeth sharp-edged, not pectinated, grooved, or buttressed on outside. Eaves not porous. Sutural laminae sharp and well developed. *Eoc.-Rec.*

Ischnochiton Gray, 1847 [**Chiton textilis* Gray, 1828; SD Gray, 1847]. [=*Lepidochiton* Carpenter, 1857; *Ischnoradsia* Carpenter in Dall, 1879; *Beanella* Thiele, 1893 (*non* Dall, 1882): *Lophyriscus, Leptopleura, Stereoplax, Rhodoplax* Thiele, 1893; *Levicoplax* Iredale & Hull, 1925; *Diktuonus* Ashby, 1931]. Shell oval or subovate, up to 2 inches in length but generally smaller. Tegmentum sculpture of lateral areas of intermediate valves usually raised, consisting of smooth or beaded radial ribs that vary in strength; on central areas sculpture may be finely granular throughout or consist of longitudinal ribs accompanied in some species by transverse riblets. Tail valve with well-developed mucro. Articulamentum of head and tail valves usually with more than 8 slits in insertion plates, that of intermediate valves typically single-slitted or with 2 or more slits in some groups. [A widespread and variable genus found from shore to depths of 100 fathoms or more.] *U.Eoc.*, Eng.(Isle of Wight); *Oligo.*, USA(Fla.)-N.Z.; *Mio.*, C.Eu.-E.Afr.-Austral.; *Plio.*, USA(N.Car.-Fla.)-Austral.(Victoria); *Pleist.*, USA (Calif.); *Rec.*, cosmop.

I. (Ischnochiton). *U.Eoc.-Rec.*, cosmop.——Fig. 38, *9*. **I. (I.) textilis* (Gray), Rec., W.Afr.; *9a-c*, head, intermed., and tail valves, dorsal, ×2.5 (41*).——Fig. 38,*10*. *I. (I.) numantius* Cotton & Godfrey, L.Plio., Victoria; tail valve, ×2 (11*).——Fig. 43,*4*. *I. (I.) spiculosus* (Reeve), Plio., USA(N.Car.); intermed. valve, dorsal, ×10 (9*). The following additional subgenera based on Recent species have been defined from various localities:

I. (Stenosemus) Middendorff, 1847 (**Chiton albus* Linné, 1767; SD Winckworth, 1926] [=*Lepidopleuroides* Thiele, 1893].

I. (Ischnoradsia) Shuttleworth, 1853 [**Chiton australis* Sowerby, 1840; SD Pilsbry, 1892] [=*Lepidoradsia* Carpenter in Dall, 1879].

I. (Heterozona) Carpenter in Dall, 1879 [_*Ischnochiton (H.) cariosus_ Carpenter in Pilsbry, 1892; SD Pilsbry, 1892].

I. (Ischnoplax) Carpenter in Dall, 1879 [_*Chiton pectinatus_ Sowerby, 1840].

I. (Radsiella) Pilsbry, 1892 [_*Ischnochiton tridentatus_ Pilsbry, 1893].

I. (Lophyropsis) Thiele, 1893 [_*Chiton (Ischnochiton) imitator_ E.A.Smith, 1881 (_nom. correct._ A.G.Smith, herein, _pro L. imitatrix_ Thiele, 1893)].

I. (Haploplax) Pilsbry, 1894 [_*Lophyrus smaragdinus_ Angas, 1867] [=_Chartoplax_ Iredale & Hull, 1924; _Radsiella_ Thiele, 1893 (_non_ Pilsbry, 1892)].

I. (Chondropleura) Thiele, 1906 [_*Lophyrus exaratus_ G.O.Sars, 1878; SD A.G.Smith, herein].

I. (Anisoradsia) Iredale & May, 1916 [_*Ischnochiton (A.) mawlei_].

I. (Rhombochiton) Berry, 1919 [_non_ Lindström, 1884, _nom. null. pro Rhombichiton_ DeKoninck, 1883)] [_*Chiton regularis_ Carpenter, 1855].

I. (Tripoplax) Berry, 1919 [_*Trachydermon trifidus_ Carpenter, 1864] [=_Ischnoradsia_ Carpenter in Dall, 1879 (_non_ Shuttleworth, 1853)].

I. (Strigichiton) Hull, 1923 [_*Ischnochiton verconis_ Torr, 1911].

I. (Autochiton) Iredale & Hull, 1924 [_*Ischnochiton torri_ Iredale & May, 1916].

I. (Euporoplax) Iredale & Hull, 1924 [_*Chiton virgatus_ Reeve, 1847].

I. (Euretoplax) Iredale & Hull, 1924 [_*Ischnochiton wilsoni_ Sykes, 1896].

I. (Isochiton) Ashby & Cotton, 1934 [_*Ischnochiton (I.) bardwelli_].

I. (Ovatoplax) Cotton & Weeding, 1939 [_*Ischnochiton (Haploplax) mayi_ Pilsbry, 1895].

Lepidozona Pilsbry, 1892 [_*Chiton mertensii_ Middendorff, 1846] [=_Lepidopleurus_ Carpenter in Dall, 1879 (_non_ Leach in Risso, 1826); _Solivaga_ Iredale & Hull, 1925; _Gurjanovillia_ Jakoleva, 1952]. Similar to _Ischnochiton_ except that valves _ii_ to _viii_ have a delicately denticulate lamina across sinus, separated from sutural laminae on each side by small notch; insertion teeth sharp, somewhat rugose, fairly thick. Tegmentum sculpture on lateral areas of intermediate and end valves comprising radial rows of pustules or graniferous ribs; central areas sculptured with longitudinal riblets and latticed interstices. Mucro low, inconspicuous, nearly flat, subcentral. Girdle scales strongly convex, smooth or striated. [Modern species found between tides to moderate depths.] _Neogene_ (Japan) - _Pleist._(Calif. - BajaCalif.) - _Rec._ (NW.Pac.-NE.Pac.) —— Fig. 38,_11_. _*L. mertensii_ (Middendorff), Pleist., Calif.(SanPedro); _11a,b_, intermed. and tail valve, dorsal, ×1.4 (10*).——Fig. 38,_8_. _L. californiensis_ (Berry), Pleist. (U.San Pedro), Calif.(San Diego); intermed. valve, dorsal, ×1.5 (10*).

Stenoplax Carpenter in Dall, 1879 [_*Chiton limaciformis_ Sowerby, 1832]. Small to large (4 in.), with elongate body, length as much as 7 times width. Intermediate valves generally low-arched, rounded, with lateral areas ranging from subobsolete to prominently raised above central areas; tail valve large, somewhat more than semicircular, depressed, with inconspicuous subcentral mucro. Insertion plates of end valves with 9 to 15 slits and of intermediate valves with 1 to 3 or more slits. Surface may show smooth polish, over-all minute granulations, or rather strong vermiculate ribs on lateral areas and in some also on central areas. Girdle narrow, decorated with small to extremely minute imbricating scales, smooth and polished or delicately striated. Sutural sinus wide and straight between rather narrow, elongate sutural laminae. [Species live typically under smooth stones buried in sand near low-tide mark but some are adapted to a special habitat in root sheaths of sea grasses, thus accounting for their elongated shape.] _U.Eoc. (Auversian)_, Eng.; _?Plio._, Calif.; _Pleist._, Calif.-BajaCalif.; _Rec._, NW.Pac.(Japan)-NE.Pac.(Calif.)-Carib.

S. (Stenoplax). _U.Eoc._, _?Plio._, _Pleist.-Rec._, Eu.-Carib.-W.N.Am.-Japan.——Fig. 38,_7_. _*S. (S.) limaciformis_ (Sowerby), Rec., Carib.; _7a_, entire animal, ×1.5; _7b_, valves _vii_, _viii_, ×2 (25*).——Fig. 38,_12_. _S. (S.) conspicua_ (Carpenter), Pleist., Calif.; _12a,b_, head valve; _12c,d_, intermed. valve; _12e,f_, tail valve; all ×1 (10*). Other subgenera based on Recent species include:

S. (Stenochiton) Adams & Angas, 1864 [_*Stenochiton juloides_] [=_Zostericola_ Ashby, 1919].

S. (Stenoradsia) Carpenter in Dall, 1879 [_*Chiton magdalenensis_ Hinds, 1844] [=_Maugerella_ Dall, 1879].

Lepidochitona Gray, 1821 [_*Chiton marginatus_ Pennant, 1777 (=_*Chiton cinereus_ Linné, 1767)] [=_Trachydermon_ Carpenter, 1864; _Craspedochilus_ G.O.Sars, 1878; _Leptochitona_ Pilsbry, 1893 (_nom. null._); _Adriella_ Thiele, 1893; _Spongioradsia_ Pilsbry, 1894; _Lepidochiton_ Thiele, 1928, and subseq. authors (_non_ Carpenter, 1857)]. Small to medium-sized, similar to _Ischnochiton_, rather elevated, with subangular jugal ridge. Tail valve usually smaller than head valve; end valves with 9 to 12 slits in insertion plates; intermediate valves single-slitted; eaves generally somewhat spongy. Surface of tegmentum smooth or finely granulose, with little change between central and lateral areas of intermediate valves, lateral areas not prominent. Girdle clothed with minute scale-like processes. _?U.Plio._, Italy; _Pleist._, USA(Calif.)-Norway; Rec., cosmop. (temperate and colder seas).——Fig. 38,_2_. _*L. cinerea_ (Linné), Rec., North Sea; _2a_, entire animal, ×1; _2b,c_, intermed. valve, ×2 (25*).——Fig. 38,_14_. _L. keepiana_ Berry, Pleist., Calif.; intermed. valve, ×2 (10*).

Oligochiton Berry, 1922 [_*O. lioplax_]. Medium in size. Surface of tegmentum smooth, lateral areas not

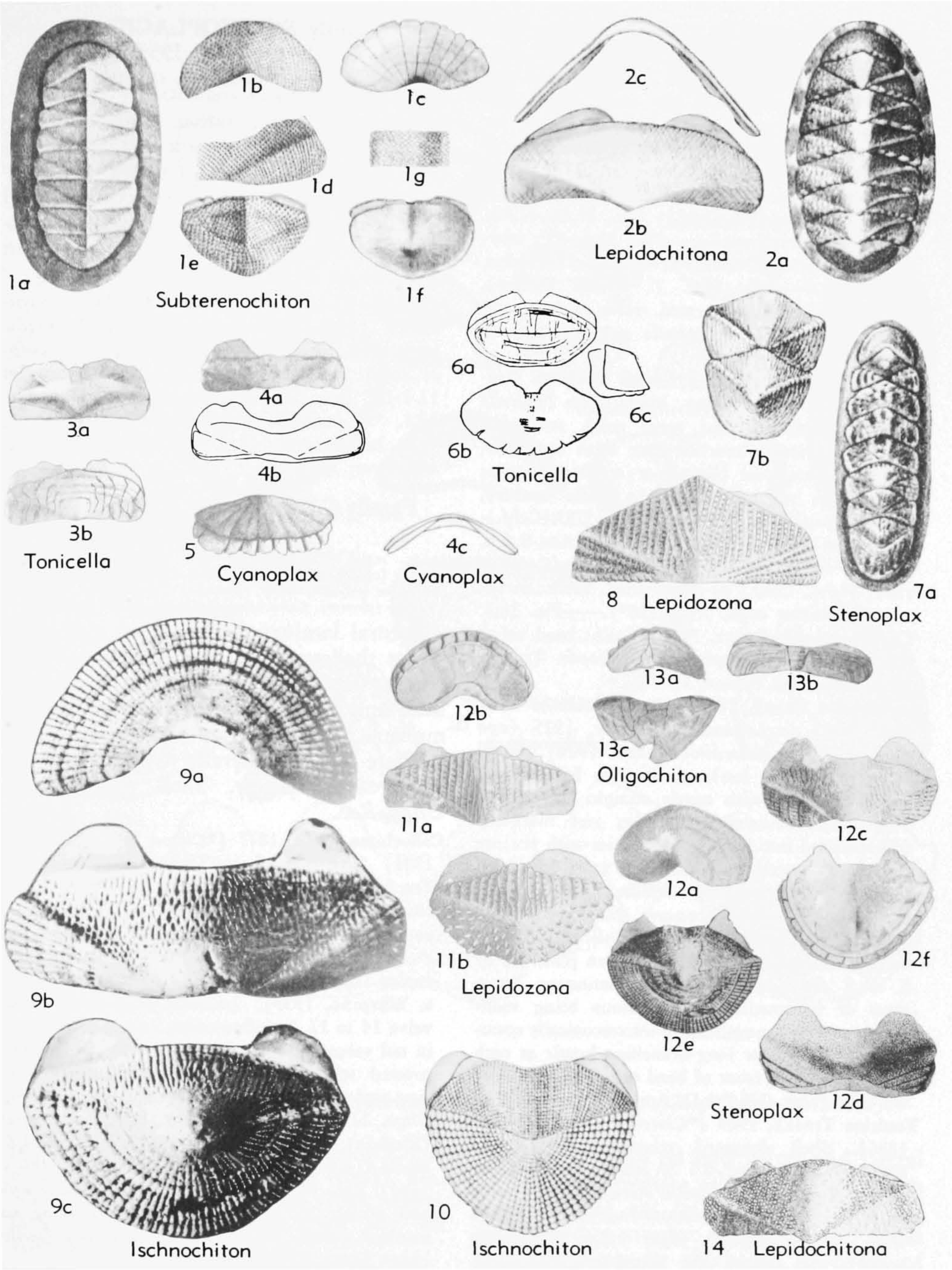

FIG. 38. Neoloricata; Ischnochitonina (Subterenochitonidae, Ischnochitonidae) (p. 155-158).

well defined; insertion plates and teeth present but very short; sutural laminae low and wide, separated by wide, shallow sinus; eaves spongy; slits numerous in end valves, probably 2 or 3 on a side in intermediate valves. *Oligo.*, Can. (B.C.).——FIG. 38,*13*. **O. lioplax; 13a-c,* head, intermed., and tail valves, ×1 (10*).

Tonicella CARPENTER, 1873 [**Chiton marmoreus* FABRICIUS, 1780] [=*Tonicia* GRAY, 1847; *Platysemus, Stenosemus* MIDDENDORFF, 1847; *Boreo-*

chiton G.O.Sars, 1878; *Toniciella* Thiele, 1893 *(nom. null.)*]. Small to medium-sized, low-arched, with rounded backs. Valve structure generally as in *Ischnochiton* but eaves spongy and intermediate valves single-slitted; lateral areas indistinctly developed. Surface of tegmentum smooth or microgranulose. Girdle appearing nude or with very small scales. *Pleist.,* Eu.(Denm.-Norway)-USA(Calif.)-Mex.(BajaCalif.); *Rec.,* N.Atl.-N.Pac. (shore to 35 fathoms).——Fig. 38,*6.* **T. marmorea* (Fabricius), Rec., Norway; *6a-c,* tail valve, ×1 (48*).——Fig. 38,*3. T. lineata* (Wood), Pleist., Calif.; *3a,b,* intermed. valve, ventral and dorsal, ×1 (10*). [*Tonicella* = *Clathropleura* Tiberi, 1877].

Cyanoplax Pilsbry, 1892 [**Chiton hartwegii* Carpenter, 1855; SD Pilsbry, 1893]. Like *Tonicella* but valves thicker and more solid, somewhat beaked anteriorly. Insertion-plate teeth stout, obtuse, crenulate, and bilobed or trilobed at tips; eaves wide, spongy or pitted. Girdle leathery, minutely papillose. *?Eoc.,* Fr.; *Pleist.,* USA(Calif.)-Mex.(BajaCalif.); *Rec.,* E.Pac. (N.Am.-S.Am. coasts).——Fig. 38,*4.* **C. hartwegii* (Carpenter); Pleist., Calif.; *4a-c,* intermed. valve, dorsal, ventral, anterior edge, ×1.5 (10*).——Fig. 38,*5. C. fackenthallae* Berry, Pleist., Calif.; head valve, ×1.5 (10*). [*Cyanoplax* = *Mopaliopsis* Thiele, 1893; *Mopaliella* Thiele, 1909].

Basiliochiton Berry, 1918 [**Mopalia heathii* Pilsbry, 1898] [=*Lophochiton* Berry, 1925 (*non* Ashby, 1923); *Ploiochiton* Berry, 1926]. Small (length 1 in. or less), medium to high-arched, widely carinate, with nearly straight side slopes. Tegmentum minutely granulose, not markedly differentiated into areas, some species with obscure ribbing on lateral areas and tail valve, which is semicircular in posterior outline, with anterior mucro, posterior slope concave. Head valve with 8 slits, intermediate valves single-slitted, and tail valve with regular crescentic insertion plate cut by 5 to 8 slits, insertion plates continuous across sinus of intermediate valves, sinus being moderately to very spongy. Girdle microscopically spiculose, bearing rather long branching bristle at each suture, 2 to 5 in front of head valve and 2 behind tail valve. *Rec.,* NE.Pac.(N.Am. W. coast).

Tonicina Thiele, 1906 [**Chiton zschaui* Pfeffer, 1886]. Shell elongated, relatively small, high-arched, width about 0.5 of length. Tegmentum shining, under magnification showing fine growth striae and minute granulation. Intermediate valves with bluntly angular jugal ridge, somewhat beaked, with central and lateral areas separated by low angle; insertion plates narrow; sutural laminae small; head valve long, tail valve small, distinctly narrower than head valve and notably shorter; slits of insertion plates unknown. Girdle narrow, granulose. *Rec.,* S.Georgia.

Family SCHIZOPLACIDAE Bergenhayn, 1955

[*nom. correct.* A. G. Smith, herein (*pro* Schizoplaxidae Bergenhayn, 1955)]

Relatively small, rather elevated, oval-shaped chitons with rounded jugum differing from all others in structure of intermediate valves, which have central jugal slit filled by narrow wedge of horny cartilage, narrowing to point in front, similar in composition to bivalve ligament. *Rec.*

Schizoplax Dall, 1878 [**Chiton brandtii* Middendorff, 1846]. Shell and girdle like *Tonicella,* tegmentum remarkably porous where exposed at small eaves and jugal sinus. Slit formula: 11-1-11. *Rec.,* Okhotsk Sea-Aleutian I.——Fig. 39,*1.* **S. brandtii* (Middendorff), Aleutian I.; *1a,b,* head valves; *1c,d,* intermed. valves; *1e,f,* tail valves; ×2 (25*).

Family CALLOCHITONIDAE Plate, 1899

[*nom. transl.* Thiele, 1910 (*ex* Callochitoninae Plate, 1899)] [=Ischnochitonidae Dall, 1889 *(partim)*; Ischnochitoninae Pilsbry, 1893 *(partim)*; Tonicelloidea Simroth, 1894 *(partim)*; Callochitonidae Thiele, 1910 *(partim)*]

Sutural laminae connected or continuous across shallow jugal sinus. Insertion plates tending to be propped on outside, those of head and tail valves cut into more teeth by multiple slitting than in other groups; intermediate valves generally with 3 or more slits; eaves spongy. Shell eyes present. *Oligo.-Rec.*

Callochiton Gray, 1847 [**Chiton laevis* Montagu, 1803] [=*Clathropleura* Tiberi, 1877 *(partim)*; *Trachyradsia* Carpenter in Dall, 1878; *Collochiton* Sars, 1878 *(nom. null.)*; *Stereochiton* Carpenter in Dall, 1882; *Icoplax* Thiele, 1893; *Eudoxoplax* Iredale & May, 1916; *Paricoplax, Quaestiplax* Iredale & Hull, 1929; *Acutoplax* Cotton & Weeding, 1939]. Insertion-plate slits in head valve 14 to 17, in intermediate valves normally 3, in tail valve 11 to 18. Girdle fairly wide, leathery, covered with longitudinally packed minute narrow scales or spicules with only tips showing. *Oligo.,* N.Z.; *L.Mio.,* Eu.(Austr.); *?L.Plio.* Austral. (Victoria); *Rec.,* Antarct.-S.Afr.-Austral.-N.Z.-Medit.-G.Brit.——Fig. 39,*7.* **C. laevis* (Montagu), Rec., North Sea; *7a,b,* intermed. valve, side and dorsal; *7c,* tail valve, ventral, showing slit insertion plates; ×2 (25*). [*Callochiton*=*Ocellochiton* Ashby, 1939].

Eudoxochiton Shuttleworth, 1853 [**Acanthopleura nobilis* Gray, 1843]. Similar to *Callochiton* but slits in insertion plates more numerous, up to 27 in end valves and 4 to 7 in intermediate valves. Girdle leathery, wide and thin, covered with short,

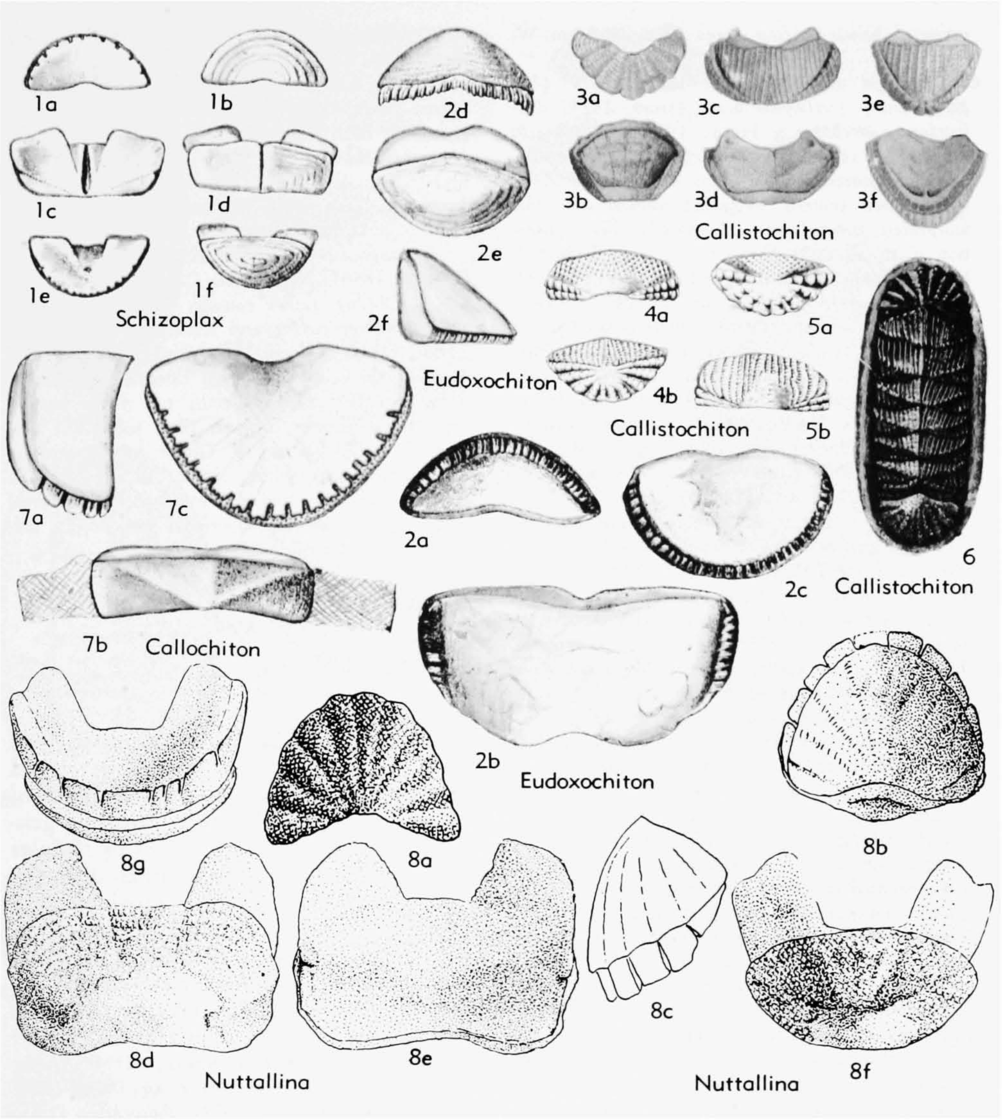

FIG. 39. Neoloricata; Ischnochitonina (Schizoplacidae, Callochitonidae, Callistoplacidae) (p. 158-160).

stiff bristles, sparsely set. *Rec.*, Austral.-N.Z.-Kermadec I.——FIG. 39,2. **E. nobilis* (GRAY), Rec., N.Z.; *2a-c,* head, intermed., tail valves, ventral, showing slit insertion plates, ×1.5; *2d-f,* tail valve, ×1 (25*).

Family CALLISTOPLACIDAE Pilsbry, 1893

[*nom. transl.* DAVIS, 1954 (*ex* Callistoplacinae PILSBRY, 1893)] [=Callistochitoninae BERRY, 1922; Callistochitonidae IREDALE & HULL, 1923]

Small to medium in size, with strongly sculptured tegmentum usually showing heavy radial ribs on end valves and lateral areas of intermediate valves; insertion plates in all valves cut by teeth that generally correspond in number and position to radial ribs, teeth usually thickened at edges of slits and in some groups peculiarly scalloped. No shell eyes present. Girdle narrow, variously ornamented. *L.Mio.-Rec.*

Callistoplax CARPENTER in DALL, 1882 [**Chiton retusus* SOWERBY, 1832]. Tegmentum sculpture as in family; differs from *Callistochiton* primarily in girdle ornamentation, which is nude except for series of bristle-bearing pores. *Rec.*, W.S.Am.-W. Mex.

Callistochiton Carpenter in Dall, 1879 [**C. palmulatus*] [=*Lophochiton* Ashby, 1923; *Callistelasma* Iredale & Hull, 1925; *Callistassecla* Iredale & Hull, 1925]. Tegmentum conspicuously sculptured, central areas smooth in middle, with netted pattern or pitted toward apex, or sculptured throughout with parallel lirae. Insertion plates short, smooth or nearly so, festooned, being curved outward at ribs and slit at rib terminations, thickened outside at edges of slits; end valves multiple-slitted, intermediate valves single-slitted; sinus squared; mucro median, usually depressed. Girdle narrow, poreless, densely set with minute striated or smooth imbricating scales. *L.Mio.*, E.Afr.(Mafia I.); *L.Plio.*, Austral.(Victoria); *Plio.*, USA(Calif.)-Mex.(BajaCalif.); *Rec.*, nearly all temperate seas.——Fig. 39,*6*. **C. palmulatus*, *Rec.*, USA(Calif.); entire specimen, ×2 (25*).——Fig. 39,*3*. *C. crassicostatus* Pilsbry, Pleist. USA(Calif.); *3a,b*, head valve; *3c,d*, intermed. valve; *3e,f*, tail valve; ×2.5 (10*).——Fig. 39,*4*. *C. inexpectus* Ashby & Cotton, L.Plio., Austral.(Victoria); *4a,b*, intermed. and tail valves, dorsal, ×2 (4*).——Fig. 39,*5*. *C. reticulatus* Ashby & Cotton, L.Plio., Austral.(Victoria); *5a,b*, intermed. and tail valves, dorsal, ×2 (4*).

Nuttallochiton Plate, 1899 [**Schizochiton hyadesi* Rochebrune, 1889] [=*Notochiton* Thiele, 1906]. Medium in size, carinated, tegmentum sculptured with ribs or rows of tubercles; sutural laminae short and wide, almost connected across small jugal sinus and extending around sides of intermediate valves. Girdle spiculose, having short thick spicules with single or groups of larger spicules between. *Rec.*, S.Am.-Antarct.

Nuttallina Dall, 1871 [**Chiton scaber* Reeve, 1847 (*non C. scaber* de Blainville, 1825) =**Acanthopleura fluxa* Carpenter, 1864] [=*Nuttalina* Fischer, 1885 *(nom. null.)*; *Nutallina* Pallary, 1900 *(nom. null.)*]. Elongate, narrow, medium-sized chitons with granulose tegmentum surface, head valve with numerous low radiating ribs, intermediate valves with 2 ribs on lateral areas; mucro somewhat posterior; insertion plates sharp, cut by slits corresponding to dorsal ribs; teeth of tail valve directed forward; sutural laminae well developed, elongate, with deep jugal sinus between. Girdle clothed with minute striated and flattened scales and with marginal row of striated bristles. *Pleist.*, USA(Calif.); *Rec.*, Eu.(Medit.)-Japan-NE.Pac.——Fig. 39,*8*. *N. californica* (Nuttall in Reeve), Pleist. USA (Calif.); *8a-c*, head valve; *8d,e*, intermed. valve; *8f,g*, tail valve; ×5 (10*).

Middendorffia Carpenter in Dall, 1882 [**Chiton polii* Philippi, 1836 (=*C. cinereus* Poli, 1791, *non* Linné, 1767)] [*nom. correct.* Fischer, 1885 (*pro Middendorfia* Carpenter in Dall, 1882)] [=*Beania* Carpenter in Dall, 1879 (*non* Johnston, 1840); *Beanella* Dall, 1882; *Dawsonia* Carpenter, 1873 (*non* Hartt, 1868; *nec* Nicholson, 1873; *nec* Fritsch, 1879)]. Like *Nuttallina* except intermediate valves with single slit, insertion-plate teeth more or less thickened at edges. *Neogene*, Eu.(Austr.); *Rec.*, Eu.(Medit.-Adriatic-Sp.).

Ceratozona Dall, 1882 [**Chiton guildingi* Reeve, 1847 (=**Chiton rugosus* Sowerby, 1841)] [=*Ceratophorus* Carpenter in Dall, 1882 (*non* Diesing, 1850); *Newcombia* Carpenter in Dall, 1882]. Oblong, rather convex, with back broadly arched, valves strong and somewhat beaked. Insertion plates of head valve long, sharp, rugose outside, thickened at slits; intermediate valves with similarly propped teeth; tail valve having teeth thick, shorter, rugose; sinus solid; slit formula 7 to 10-1-8 to 10. Girdle tough, bearing peculiar corneous spines, similar in substance to girdle, generally sparsely bunched at sutures, with larger ones not superficial but deeply imbedded. *Rec.*, Carib.-C.Am.

Family CHAETOPLEURIDAE Plate, 1899

[*nom. transl.* Bergenhayn, 1955 (*ex* Chaetopleurinae Plate, 1899] [=Chaetopleurae Rochebrune, 1881 *(partim)*; Chaetochitonidae Rochebrune, 1889 *(partim)*; Chaetopleuroidea Simroth, 1894]

Valve structure consisting of usual shell layers with addition of a well-developed mesostracum. Tegmentum with complicated microstructure and sculpture consisting generally of radial rows of pustules or nodules on end valves and lateral areas of intermediate valves. Jugal sinus provided with jugal plate across it between sutural laminae. Girdle covered with scales, spicules, or hairy processes. *Mio.-Rec.*

Chaetopleura Shuttleworth, 1853 [**Chiton peruvianus* Lamarck, 1819; SD Dall, 1879] [=*Choetopleura* Shuttleworth, 1856 *(nom. null.)*; *Hemphillia* Carpenter in Dall, 1879 (*non* Bland & Binney, 1872); *Pallochiton* Dall, 1879; *Arthuria* Carpenter in Dall, 1882; *Helioradsia* Thiele, 1893; *Variolepis* Plate, 1899; *Pristochiton* Clessin, 1903; *Chetopleura* Ashby, 1929 *(nom. null.)*]. Small to medium-sized, with valves somewhat as in *Ischnochiton*, ventral side porcelaneous, having rather long sharp teeth and squared sinus; eaves solid. Tegmentum usually sculptured with longitudinal beaded riblets on central areas, and pustules or pustulose ribs on lateral areas of intermediate and end valves, pustules being irregularly arranged in some groups. *Mio.*, USA(Md.); *Plio.*, USA(N.Car.-Fla.); *Pleist.*, USA(S.Car.-Calif.)-Mex.(BajaCalif.); *Rec.*, nearly all temperate and warm temperate seas.——Fig. 41,*9*. *C. apiculata* (Say), Pleist., USA(S.Car.), *9a,b*, intermed. valve, ×11 (9*).——Fig. 40,*2*. *C.*

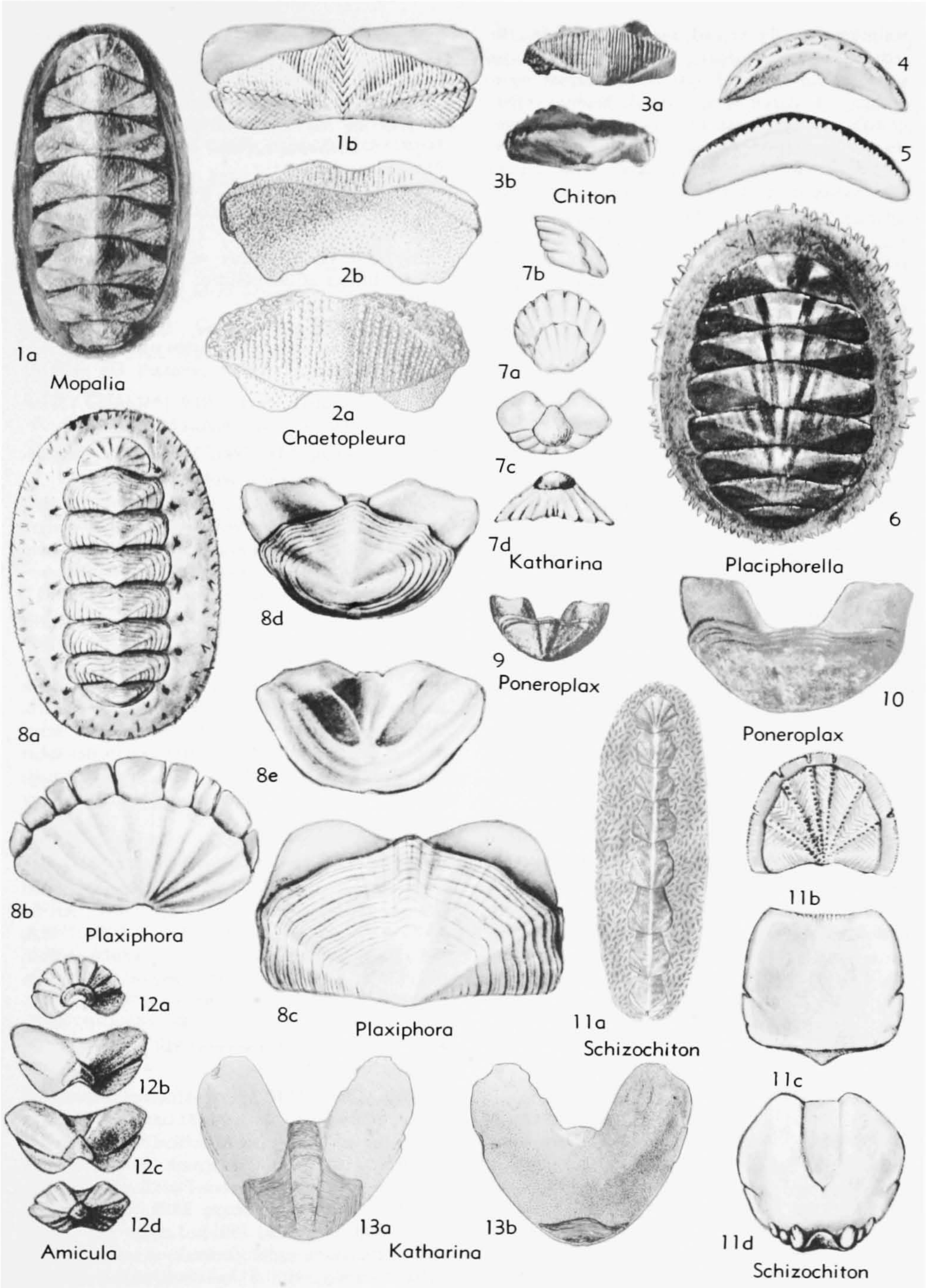

FIG. 40. Neoloricata; Ischnochitonina (Chaetopleuridae, Mopaliidae) (p. 160-163).

gemma CARPENTER in DALL, Pleist., USA(Calif.); *2a,b,* intermed. valve, dorsal, ventral, ×7 (10*).
Dinoplax CARPENTER in DALL, 1882 [**Chiton gigas* GMELIN, 1788]. Large oval chitons with thick, heavy valves, obtusely angled, lateral areas much elevated. Tegmentum without strongly marked

sculpture, usually eroded smooth in adults. Insertion-plate teeth sharp, smooth, those of tail valve directed forward, slits not corresponding to position of dorsal ribs; sutural laminae rather broadly united across jugal sinus by keystone-shaped lamina; eaves solid; mucro of tail valve posterior. Girdle thick, leathery, with minute scattered bunches of delicate spinelets. *Rec.,* S.Afr.

Calloplax THIELE, 1909 [**Chiton janierensis* GRAY, 1828]. Shell medium-sized, elevated, oblong and rather narrow; lateral areas strongly raised, sculptured with 4 coarse granose ribs; central areas having about 12 granose, acute threads on either side of jugum parallel with it; sutural laminae rounded, with shallow sinus between; slit formula 10-1-9, insertion teeth solid; eaves wide and solid. Girdle with rather wide, ribbed scales and individual spines accompanied by minute spicules. *Rec.,* W. Atl.

Family MOPALIIDAE Dall, 1889

[=Amiculidae DALL, 1889 *(partim);* Placophoridae DALL, 1889 *(partim);* Chaetochitonidae ROCHEBRUNE, 1889 *(partim);* Plaxiphoridae IREDALE, 1915; Mopalidae BERGENHAYN, 1930 *(nom. null.);* Katharinidae JAKOLEVA, 1952]

Small to large chitons with tegmentum divided into usual lateral and central areas, sculpture combining radial and longitudinal ribs or lirae that vary in strength from low to high relief. Insertion-plate slits in all valves generally corresponding in position with ends of external ribs, teeth not pectinated. Head valve normally with 8 slits but may be smaller or larger by fusion or splitting of one or more teeth, whereas in some forms slits are abnormally multiplied; intermediate and tail valves with single slit on each side, although in one group lacking in tail valve; tail valve with posteromedian sinus; sutural laminae well developed to very large. Girdle more or less hairy or bristly, never with scales, bristles simple or dendritic, in some species growing out of sutural pores, each of which bears one or more hairy bristles. *?U.Oligo., L.Mio.-Rec.*

Mopalia GRAY, 1847 [**Chiton hindsii* SOWERBY in REEVE, 1847; SD GRAY, 1847] [=*Molpalia* GRAY, 1857; *Osteochiton* DALL, 1886]. Valves normal in proportion, transverse, jugal angle acute or almost flat, not beaked; girdle somewhat encroaching at sutures between valves. Sculpture of tegmentum usually furrowed or netted in addition to radial ribbing. Insertion plate of head valve rather long, sharp, slit into nearly smooth teeth that are somewhat thickened at edges of slits, which are normally 8, corresponding in position to external ribs; intermediate valves single-slitted; sinus small; tail valve depressed, with mucro behind center and insertion plate sharp, smooth or roughened, having an oblique slit on each side (rarely doubled) and a larger sinus posteriorly. Girdle wider at sides than in front, leathery, more or less hairy, with or without sutural pores. *Pleist.,* USA(Calif.); Rec., N.Pac.(BajaCalif. to Alaska-Japan).

M. (Mopalia). *Pleist.-Rec.,* W.USA-N.Pac.——FIG. 40,*1.* **M. (M.) hindsii* (SOWERBY), Rec., Calif.; *1a,* whole animal, ×0.5 (25*); *1b,* intermed. valve, ×1 (25*). Other subgenera (classed by some authors as independent genera) include the following:

M. (Dendrochiton) BERRY, 1911 [**Mopalia (Dendrochiton) thamnopora*], *Rec.,* N.Am.(W. Coast).

M. (Semimopalia) DALL, 1919 [**Mopalia (Semimopalia) grisea*], *Rec.,* S.Am.(CapeHorn).

M. (Hachijomopalia) TAKI, 1954 [**M. (Hachijomopalia) integra*], *Rec.,* Japan.

Placiphorella CARPENTER in DALL, 1879 [**P. velata* DALL, 1879] [=*Euplacophora* VERRILL & SMITH, 1882; *Placophorella* FISCHER, 1885; *Placophora* DALL, 1889 (*non* FISCHER, 1885); *Placophoropsis* PILSBRY, 1893; *Langfordiella* DALL, 1925]. Medium-sized, with broadly rounded contour, valves very short and wide, middle ones much broader than those toward ends; head valve narrowly crescentic; tail valve much smaller, with shallow posterior sinus and posterior mucro. Tegmentum sculpture subobsolete, lateral areas distinct but very little raised. Insertion plates short and thick, teeth lobed or rugose; sinus small; slits 8 or more in head valve, single-slitted in intermediate valves, and 2 in tail valve (deep-water species with 20 or more slits in head valve and unslit tail valve); eaves spongy. Girdle wide and much extended in front, bearing sparse, scaled hairs or bristles. *Pleist.,* USA(Calif.); *Rec.,* Arctic-NW.Pac.(Japan)-NE.Pac.-NW.Atl. —— FIG. 40,*6.* **P. velata,* Rec., N.Am.(W.Coast), whole animal, ×1 (25*).——FIG. 40,*5. P. atlantica* (VERRILL & SMITH), Rec., NW.Atl.; head valve showing numerous teeth, ×1 (25*).——FIG. 40,*4. P. blainvillei* (BRODERIP), Rec., Peru; tail valve showing 9 teeth, ×1 (25*).

Plaxiphora GRAY, 1847 [**Chiton carmichaelis* GRAY, 1828 (=**Chiton auratus* SPALOWSKY, 1795)] [=*Euplaxiphora* SHUTTLEWORTH, 1853; *Placiphora* CARPENTER in DALL, 1879 *(nom. null.); Euplaciphora* DALL, 1879; *Plaxifora* FILHOL, 1880 *(nom. null.); Placophora* FISCHER, 1885 *(nom. van.); Euplacifora* JOHNSTON, 1891]. Large, oval chitons with tegmentum sculpture weak or lacking. Head valve normally with 8 indistinct radial ribs and concentric growth wrinkles; intermediate valves with similar indistinct ribs; tail valve with mucro slightly in front of posterior end; insertion plates well developed; head valve usually 8-slitted, intermediate valves single-slitted; tail valve with smooth insertion plate and unslit or with heavy callus and distinct median sinus. Girdle large, leathery, bearing simple scattered bristles or bristle tufts at sutures. *L.Mio.*, Austral.(Victoria); *Rec.*, Antarctic. [*Plaxiphora* = *Euplacophora* Fischer, 1885 (*non* Verrill & Smith, 1882)].

P. (Plaxiphora). *L.Mio.-Rec.*, Austral.-N.Z.-Antarctic.——Fig. 40,*8*. **P. (P.) aurata* (Spalowsky), Rec., N.Z.; *8a*, whole animal, ×0.3; *8b-e*, valves (*8b*, head; *8c*, intermed.; *8d,e*, tail), ×0.75 (45*). Other subgenera (treated by some authors as independent genera) include:

P. (Guildingia) Carpenter in Dall, 1882 [**Plaxiphora obtecta* Carpenter in Pilsbry, 1893; SD Pilsbry, 1893]. *U.Oligo.* or *L.Mio.*, *Rec.*, N.Z.

P. (Diaphoroplax) Iredale, 1914 [**Chiton biramosus* Quoy & Gaimard, 1835]. *Rec.*, N.Z.

P. (Poneroplax) Iredale, 1914 [**Chiton costatus* deBlainville, 1825], *L.Mio.-Rec.*, Austral.——Fig. 40,*9*. *P. (P.) gellibrandi* Ashby & Torr, L. Mio., Austral.(Victoria); tail valve, ×2 (11*).——Fig. 40,*10*. *P. (P.) concentrica* Ashby & Torr, L.Mio., Austral.(Victoria); tail valve ×2 (11*).

P. (Maorichiton) Iredale, 1914 [**Chiton caelatus* Reeve, 1847], *Rec.*, N.Z.-Ceylon-S.Afr.

P. (Aerilamma) Hull, 1924 [**A. primordia*] [=*Vaferichiton* Iredale & Hull, 1932], *Rec.*, Ceylon-Mozambique-Austral.(Queensl.)

P. (Mercatora) Leloup, 1942 [**Plaxiphora mercatoris* Leloup, 1936], *Rec.*, Easter I.

Fremblya H. Adams, 1866 [*nom. correct.* Dall, 1882 (*ex Frembleya* H. Adams, 1866)] [**Frembleya egregia*] [=*Fremblyia* Dall, 1879 *(nom. null.); Streptochiton* Carpenter in Dall, 1879 *(nom. nud.); Frembleyana* Ashby, 1919 *(nom. van.); Kopionella* Ashby, 1919]. Similar to *Plaxiphora* but smaller, egg-shaped, with more prominent sculpture, tail valve having strongly recurved mucro, concave behind; head valve 8-slitted, teeth grooved with fluted edges. Girdle with sutural tufts. *Rec.*, N.Z.

Katharina Gray, 1847 [**Chiton tunicatus* Wood, 1815; SD Gray, 1847] [=*Katherina* Carpenter, 1857 *(nom. null.); Catharina* Dunker, 1882 *(nom. van.)*]. Large chitons with valves two-thirds covered by smooth black, leathery girdle. Exposed portion of tegmentum divided into jugal and lateral areas. Insertion plates, including sutural laminae, sharp, extremely long, projected forward. Head valve with 7 or 8 slits; tail valve with a wide caudal sinus and several slits on each side, commonly obsolete in part. *Plio.-Pleist.*, USA (Calif.); *Rec.*, NE.Pac.(Alaska to Calif.).——Fig. 40,*7*,*13*. **K. tunicata* (Wood); *7a-d* (Rec., Calif.), *7a,b*, head valve, *7c,d*, tail valve, ×0.75 (25*); *13a,b*, (Plio., Calif.), intermed. valve, ×1.4 (10*).

Amicula Gray, 1847 (June) [*non* Gray, 1840; *nec* Gray, 1843 (=*Cryptoconchus* Burrow, 1815)] [**Chiton vestitus* Broderip & Sowerby, 1829; SD Gray, 1847 (Nov.)] [=*Cryptochiton* Gray, 1847 (June) (*non* Middendorff, 1847); *Symmetrogephyrus* Middendorff, 1847; *Stimpsoniella* Carpenter, 1873; *Chlamydochiton* Dall, 1878; *Chlamydoconcha* Pilsbry, 1893 (*non* Dall, 1884)]. Medium-sized to large chitons with valves almost entirely buried in thick, pilose girdle, leaving very small, heart-shaped tegmentum area exposed at each apex; articulamentum produced backward in rounded sutural laminae at each side, separated by a posterior sinus with tegmentum at its apex; tail valve wtih posterior sinus and single slit on each side. *Pleist.*, Can.; *Rec.*, Arctic (circumboreal).——Fig. 40,*12*. **A. vestita* (Broderip & Sowerby), Rec., Alaska; *12a*, head valve; *12b,c*, intermed. valves; *12d*, tail valve; ×0.75 (25*).

Family SCHIZOCHITONIDAE Dall, 1889

[=Prochitonidae Rochebrune, 1889; Loricidae Iredale & Hull, 1923; Aulacochitonidae Cotton & Godfrey, 1940]

Much elongated or ovate, medium-sized chitons with well-developed tegmentum bearing sculpture of flattened riblets along which are rows of eyes; head valve with 6 to 10 slits; tail valve with deep caudal sinus. Girdle spiculose or scaly. *L.Mio.-Rec.*

Schizochiton Gray, 1847 [**Chiton incisus* Sowerby, 1841]. Much elongated, valves bearing large eyes along tops of diagonal ribs on all except tail valve; insertion-plate slits in articulamentum correspond in position to ends of diagonal ribs; sinus narrow; head valve wtih 6 to 8 slits; tail valve with deep posterior fissure accompanied by several slits on each side. Girdle bearing small calcareous spinelets, slit behind. *Rec.*, Philippines-N.Austral.——Figs. 40,*11*; 41,*1*. **S. incisus* (Sowerby), SW. Pac.; 40,*11a*, entire animal, ×1; 40,*11b-d*, valves, ca. ×2 (25*); 41,*1*, tail valve, ×2 (25*).

Lorica Adams & Adams, 1852 [**Chiton cimolius* Reeve, 1847] [=*Aulacochiton* Shuttleworth, 1853; *Protolorica* Ashby, 1925; *Zelorica* Finlay, 1927]. Large, elongate-oval, elevated, carinated chitons; tail valve small, with recurved mucro; sculpture of small erect pustules forming radial ribs; eyes small, subobsolete, appearing on intermediate valves only; articulamentum of head valve 8-slitted, slits not corresponding with dorsal ribs, teeth obsoletely pectinated; intermediate valves single-slitted; sutural laminae extending nearly across valves, sinus appearing as small deep gap at jugum only; insertion plates of tail valve reduced to striated callus interrupted by deep

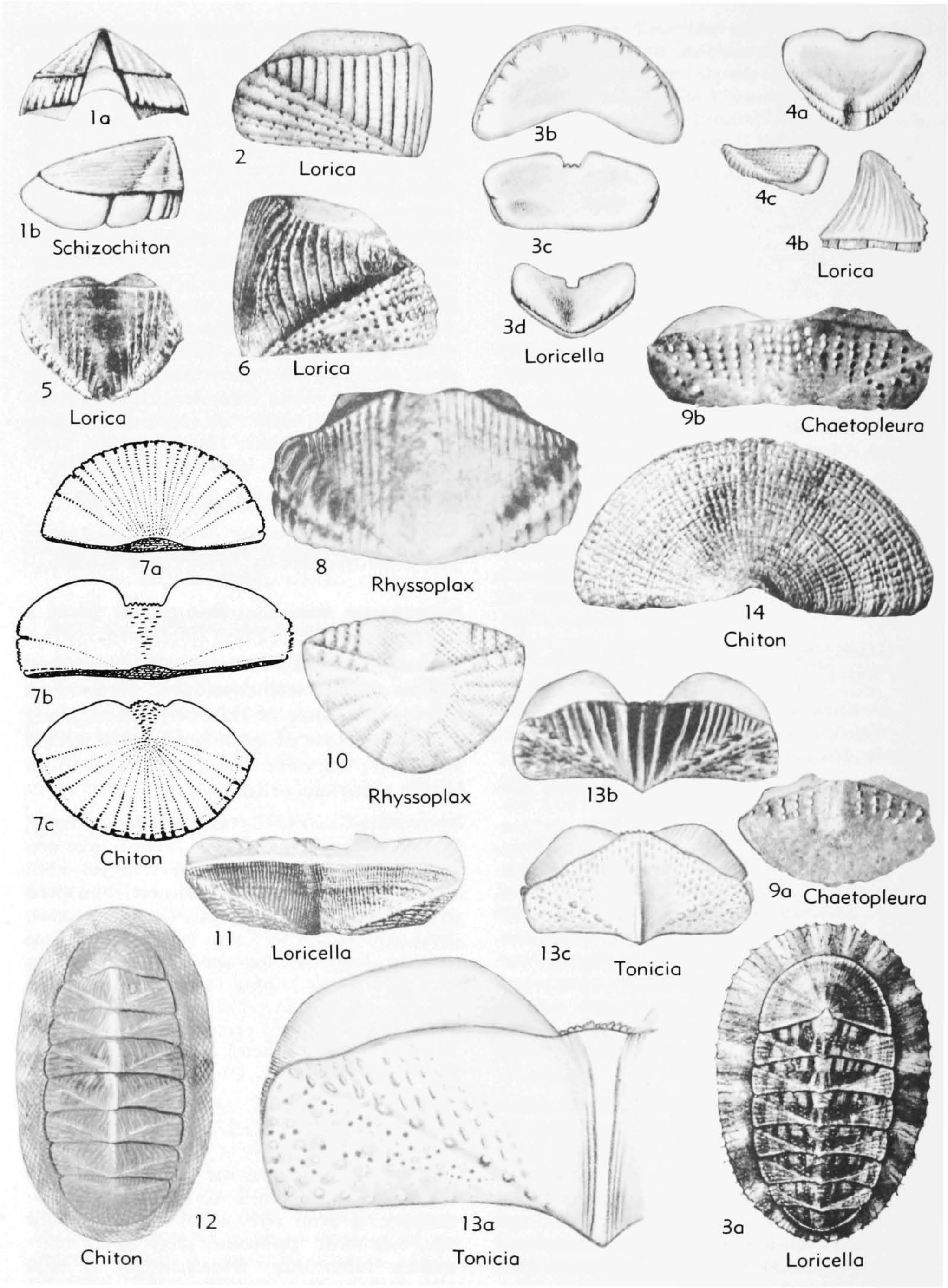

Fig. 41. Neoloricata; Ischnochitonina (Schizochitonidae, Chitonidae) (p. *163-166*).

sinus below recurved mucro. Girdle scaly, with slit behind. *L.Mio.*, Tasmania; *M.Mio.*, Austral. (Victoria); *Rec.*, S.Austral.-N.Z.——Fig. 41,*2,4*. **L. cimolia* (Reeve), Rec., Austral.; *2*, half of intermed. valve, ×1 (20*); *4a-c*, form described as *Chiton volvox* Reeve, 1847 (=*L. cimolia*), Rec., Austral., head and tail valves, ×1 (25*).——Fig. 41,*5*. *L. atkinsoni* (Ashby), L.Mio., Tasmania; tail valve, ×2 (1*).——Fig. 41,*6*. *L. cudmorei* Ashby, L.Mio., Tasmania, intermed. valve, ×2 (1*).

Loricella Pilsbry, 1893 [**Lorica angasi* H. Adams & Angas, 1864] [=*Squamophora* Nierstrasz, 1905; *Pseudoloricella* Ashby, 1925]. Like *Lorica* but head valve abnormally large. Sutural laminae continuous across intermediate valves in one group but normally with narrow gap under jugum filled with pectinated, spade-shaped forward extension of articulamentum. Tail valve small, with sinuate callus having 2 obscure lateral slits. Girdle also decorated with small spicules. *L.Mio.*, Tasmania; *L.Plio.*, Austral.(Victoria); *Rec.*, Austral.-Celebes. ——Fig. 41,*3*. **L. angasi* (Adams & Angas), Rec., Austral.; *3a*, whole animal, ×1 (20*); *3b-d*, valves (ventral views), ×1 (25*).——Fig. 41,*11*. *L. sculpta* Ashby, L.Mio., Tasmania; intermed. valve, ×1.5 (1*).

Family CHITONIDAE Rafinesque, 1815

[*nom. correct.* Gray, 1834 (*pro* family Chitonia Rafinesque, 1815), validation proposed, L. R. Cox, ICZN pend.] [=Gymnoplacidae Gray, 1821; Chitones Férussac, 1821; Chitonacea Menke, 1830; Chitonina MacGillivray, 1843; Chaetopleurae Rochebrune, 1881 *(partim)*; Chaetochitonidae Rochebrune, 1889 *(partim)*; Placophoridae *(partim)*, Lophyridae *(partim)* Dall, 1889; Toniciinae, Chitoninae (*non* Adams & Adams, 1858), Liolophurinae Pilsbry, 1893; Acanthopleurinae Thiele, 1910, Rhyssoplacinae, Amaurochitoninae, Sypharochitoninae, Onithochitoninae Iredale & Hull, 1932; Tonicinae Bergenhayn, 1930]

Small to large chitons with sculpture of tegmentum varying considerably in strength and character; articulamentum consisting of strong insertion plates and sutural laminae. Differ from all other chiton families in well-developed pectination on outside of insertion plates, which ranges from coarsely grooved to fine and comblike. Girdle may be scaly, with short bristles, spines, or spicules, or nude and leathery. *Cret.-Rec.*

The family includes the more highly specialized chitons comprising several diverse groups of species. The well-marked pectination of the insertion plates is considered at present to be the common family character that appears to have developed at least in the Cretaceous and possibly earlier.

Authors have divided the Chitonidae into several subfamilies based largely on type of tegmentum sculpture and variations in girdle ornamentation. As such a division at present can only be provisional in view of the limited knowledge of species relationships within the family, it is not attempted here. Subfamily usage is indicated in the synonymy, the approach to a modern classification dating from Pilsbry, 1893.

Chiton Linné, 1758 [**C. tuberculatus;* SD Dall, 1879] [=*Scuterigulus* Meuschen, 1787; *Lophyrus* Poli, 1791; *Gymnoplax* Gray, 1821; *Lepidopleurus* Leach in Risso, 1826; *Radsia* Gray, 1847; *Trachyodon* Dall, 1892; *Chondroplax, Diochiton, Georgus* Thiele, 1893; *Typhlochiton* Dall, 1921]. Mostly medium-sized to large, usually rather low-arched; intermediate valves with one or more slits and the end valves multiple-slitted; lateral areas generally raised and fairly prominent, their surface smooth to radially or concentrically ribbed, or combining these; central areas may be longitudinally lirated or smooth, or with only jugal area smooth. Girdle usually covered by smooth, large, imbricating scales. [Prior to the work of Dall (1879, 1882) and to some extent subsequently, nearly all polyplacophorans were classified in the genus *Chiton*. This is true of a great many fossil species, a large number of which have been inadequately described and imperfectly or improperly figured because of understandable lack of attention to now-known significant differences in the structure and configuration of chiton shells. Thus, it is impossible to place many fossil species described as *Chiton* in a modern classification without a thorough study of original materials. In the arrangement of Chitonidae here given, only those fossil records are cited that can be referred with some confidence to *Chiton* or other genera of the family group. Other fossil records must be left in the status of *incertae sedis* until relationships of such species can be worked out.] *U.Cret.*, USA(Md.-Tenn.); *Eoc.*, Fr.(Paris Basin)-USA(Ala.); *Mio.-Plio.*, Eu.(Fr.-Aus.-Italy-Eng.); *Pleist.*, Sicily; *Rec.*, cosmop. (nearly all temperate and tropical seas). [*Chiton squamosus* Linné, 1758, herein designated by A. G. Smith as type of *Scuterigulus* Meuschen, 1787.]

C. (Chiton). *U.Cret.-Rec.*, cosmop.——Fig. 41,*12*. **C. (C.) tuberculatus*, Rec., W.Indies; whole animal, ×1 (25*).——Fig. 41,*7*. *C. (C.) albolineatus* Broderip & Sowerby, Rec., Gulf of Calif.; *7a-c*, head, intermed., tail valves showing pectination of insertion plates, ×2 (35*).——Figs. 40,*3*, 41,*14*. *C. (C.) cretaceus* C. T. Berry, U. Cret.; 40,*3a,b*, head valve (holotype), USA(Md.), ×2.7; 41,*14*, intermed. valve (paratype), USA (Tenn,). ×2.6 (9*). The following names for species groups closely related to *Chiton* as now restricted have been used by recent authors in a sectional or subgeneric sense, and by some as having full generic status. The forms so designated differ from typical *Chiton* in size, characters of tegmentum sculpture, girdle ornamentation, and in what appear to be minor variations in the type of slitting and other feaures of the articulamentum. For convenience they are here treated as having subgeneric rank.

C. (Rhyssoplax) Thiele, 1893 [**Chiton janierensis* Gray, 1821; SD Iredale, 1914] [=*Clathropleura* Thiele, 1893 (*non* Tiberi, 1877); *Antho-*

chiton Thiele, 1893]. *Oligo.*, N.Z.; *L.Mio.*, Austral.(Victoria); *Plio.*, Austral.-N.Z.; *Rec.*, Austral.-N.Z.-S.Afr.——Fig. 41,*10*. *C.* *(R.)* *macdonaldensis* (Ashby & Cotton), L.Plio., Victoria (referred to *Anthochiton* by authors); tail valve, ×8.5 (5*).——Fig. 41,*8*. *C.* *(R.)* *relatus* (Ashby & Cotton), U.Plio., S.Austral.; intermed. valve, ×7.5 (11*).

C. (Amaurochiton) Thiele, 1893 [**Chiton olivaceus* Frembly, 1827 (*non* Spengler, 1797), =**Chiton magnificus* Deshayes, 1832; SD Iredale & Hull, 1926] [=*Poeciloplax* Thiele, 1893]. *Rec.*, N.Z.-Tasm.-W.S.Am.

C. (Sypharochiton) Thiele, 1893 [**Chiton pelliserpentis* Quoy & Gaimard, 1835] [=*Triboplax* Thiele, 1893; *Sympharochiton*, Oliver, 1915 *(nom. null.)*]. *Rec.*, N.Z.-E.Austral.

C. (Squamopleura) Nierstrasz, 1905 [**Chiton miles* Carpenter in Pilsbry, 1893; SD Pilsbry, 1893] [=*Sclerochiton* Carpenter in Dall, 1882 (*non* Kraatz, 1859); *Sklerochiton* Nierstrasz, 1905 *(nom. null.)*; *Slerochiton* Thiele, 1910 *(errore)*]. Similar to *C. (Chiton)* but teeth of tail valve projecting forward, blunt; sinus smooth, not denticulate. Girdle scales striated and separated, not imbricating. *Rec.*, Ceylon-Indonesia-New Guinea-W.Austral.-N.Caledonia.

C. (Delicatoplax) Iredale & Hull, 1926 [**Chiton translucens* Hedley & Hull, 1909]. *Rec.*, Austral. (NSW-S.Queensl.).

C. (Tegulaplax) Iredale & Hull, 1926 [**Chiton howensis* Hedley & Hull, 1912]. *Rec.*, Red Sea-Ceylon-Maldive Arch.-Molucca I.-N.Austral.

C. (Mucrosquama) Iredale & Hull, 1926 [**Chiton carnosus* Angas, 1867]. *Rec.*, S.Austral.

Tonicia Gray, 1847 (June) [**Chiton elegans* Frembly, 1827 (*non* deBlainville, 1825, *nom. inquir.*); SD Gray, 1847 (Nov.)] [=*Tonichia* Gray, 1840 *(nom. nud.)*; *Conicia* Sowerby, 1852 *(nom. null.)*; *Fannyia* Gray, 1857; *Fannettia* Dall, 1882 (*pro* *Fannia* Dall, 1882, *non* Robineau-Desvoidy, 1830); *Tonica* Odhner, 1917 *(nom. null.)*; *Tonicea* Ashby, 1926 *(nom. null.)*]. Medium-sized (length 1 to 2 in.), surface of tegmentum generally relatively smooth; valve *ii* tending to be noticeably larger than valves *iii* to *viii* and with different sculpture on jugal area; end valves and forward part of lateral areas of intermediate valves with radiating rows or bands of small black eye dots scattered among granules of surface sculpture; eaves not very spongy; insertion-plate teeth pectinated, end valves multiple-slitted, intermediate valves usually with single slit but some with more; sutural laminae separated by squared, denticulate sinus. Girdle leathery, nude or sparsely hairy. *Eoc.-Plio.*, Fr.; *Rec.*, cosmop. (nearly all seas except along W. N.Am. N. of Mex.). [The fossil records are based on the somewhat problematical identifications of Rochebrune, 1883.]——Figs. 41,*13*; 42,*1*. **T. elegans* (Frembly), Rec., W.S.Am.; 41,*13a-c*, intermed. valves, dorsal view showing eye dots; 42, *1a-c*, head, intermed., tail valves, ventral views; all ×2 except 41,*13a*, ×4 (25*).

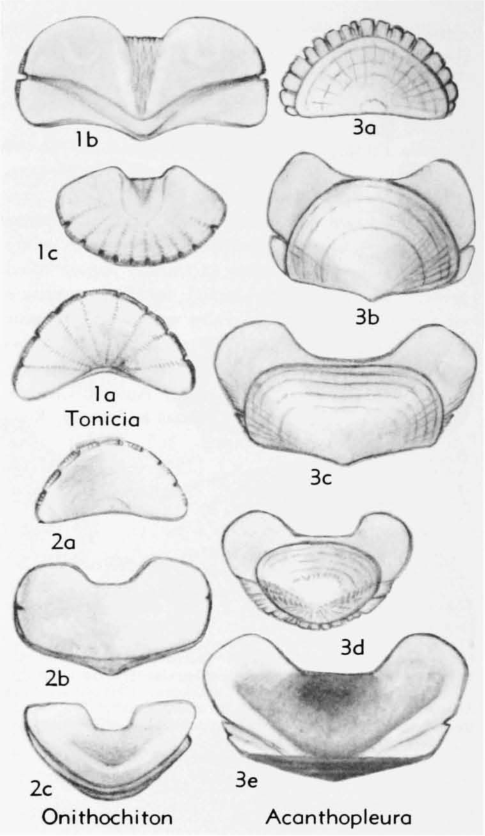

Fig. 42. Neoloricata; Ischnochitonina (Chitonidae) (p. *166-167*).

Lucilina Dall, 1882 [**Chiton confossus* Gould, 1846] [=*Lucia* Gould, 1862 (*non* Swainson, 1833); *Toniciopsis* Thiele, 1893; *Onithoplax* Thiele, 1910]. Small to medium-sized, elongate-oval, elevated, round-backed or carinated; tegmentum sculpture consisting of pits and nodules; tail valve with prominent, elevated mucro; insertion plates and sutural sinus finely pectinated, posterior insertion plate projecting somewhat forward; slit formula usually 8-1-12. Girdle fleshy, finely spiculose. *Rec.*, Austral.-E.Pac.

Onithochiton Gray, 1847 (June) [**Chiton undulatus* Quoy & Gaimard, 1835 (*non* Wood, 1828) =**Onithochiton neglectus* Rochebrune, 1881] [=*Onythochiton* Gray, 1847 (Nov.) *(nom. null.)*; *Ornithochiton* Carpenter in Dall, 1882 *(nom. null.)*; *Onitochiton* Rochebrune, 1884 *(nom. null.)*; *Pristochiton* Clessin, 1903; *Onithella* Mackay, 1933]. Small to large oval, elevated, round-backed, polished, somewhat beaked; dorsal sculpture of low nodules and fine longitudinal lirae; tail valve depressed, triangular, with posterior terminal and marginal mucro; eyes well developed in ray on forward part of each lateral area and in numerous rays on head valve; articulamentum as in *Tonicia* but insertion plate of tail valve not slit and reduced to low, smooth, narrow callus; head valve with 8 slits; intermediate valves with single slit; interior of valves porcelaneous. Girdle fleshy, decorated with minute chaffy hairs or spicules, or microscopic scales. *Rec.*, S.Afr.-Austral.-N.Z.——Fig. 42,*2*. *O. lyelli* (Sowerby), Austral.; *2a-c*, head, intermed., tail valves, ventral views, showing unslit callused insertion plate of tail valve, ×1.5 (25*).

Acanthopleura Guilding, 1830 [**Chiton spinosus* Bruguière, 1792] [=*Canthapleura* Swainson, 1840 (*nom. null.*); *Corephium* Gray, 1847 (*non* Brown, 1827); *Maugeria* Gray, 1857; *Franciscia* Carpenter in Dall, 1882; *Rhopalopleura* Thiele, 1893; *Mesotomura, Amphitomura* Pilsbry, 1893; *Acanthozostera* Iredale & Hull, 1926]. Large, round-backed, depressed, oval, beaked; subobsolete sculpture usually too eroded to be discerned except at valve edges; tegmentum broadly inflexed at posterior valve margins; mucro posterior; eyes small, situated on forward part of lateral areas and scattered among surface granules, usually seen only where unworn new shell growth appears. Valves thick, heavy, generally colored inside; insertion plates deeply grooved and coarsely pectinated, projecting forward. Long teeth of tail valve (more than half length of tegmentum) projecting forward instead of outward, and multiple slitting of intermediate valves characterize genus. Girdle thick and muscular, with dense covering of small to large calcareous spines of varying length. *Pleist.*, S.Am.(Bol.); *Rec.*, E.Afr.-IndoPac.-Austral.-W.S.Am.——Fig. 42,*3*. **A. spinosa* (Bruguière), *Rec.*, Austral.; *3a*, head valve; *3b,c*, intermed. valves; *3d*, tail valve; all dorsal views, ×1.5; *3e*, intermed. valve, ventral view, ×1.5 (25*).

Liolophura Pilsbry, 1893 [**Chiton japonicus* Lischke, 1873] [=*Liolopleura* Cox, 1893 (*nom. null.*); *Clavarizona* Hull, 1923]. Like *Onithochiton,* except exterior of valves dull as well as eroded; somewhat raised instead of marginal mucro; distribution of eyes on sides of central areas instead of band on forward part of lateral areas; girdle ornamentation consisting of densely crowded calcareous spines of varying sizes. *Rec.*, Japan-Austral.

Enoplochiton Gray, 1847 [**Chiton niger* Barnes, 1824]. Like *Onithochiton* except lateral areas of intermediate valves and head valve irregularly studded with minute oval instead of round eyes; articulamentum minutely laminated and punctured in unusual patterns. Girdle fleshy, bearing extremely broad and short, blunt, separately spaced, striated scales. ?*Eoc.*, Fr.(Paris Basin); *Rec.*, W.S.Am.

Suborder ACANTHOCHITONINA Bergenhayn, 1930

[=Opsichitonia Dall, 1889 (*partim*); Mesoplacophora Pilsbry, 1893 (*partim*); Chitonina Thiele, 1910 (*partim*); Isoplacophora Cotton & Weeding, 1939 (*partim*)]

Chitons varying in size from small to largest known, with valves partially to completely buried in girdle; valve coverage ranging from complete to none at all for several posterior valves. Tegmentum surface reduced in area relative to articulamentum, which is highly developed; tegmentum on head valve with anterior area only (Fig. 43,*2a*); on intermediate valves with jugal area having tip at apex of each valve, flanked on both sides by lateropleural areas (Fig. 43,*2b*); tail valve with small triangular jugal area and 2 adjacent subtriangular pleural areas all radiating forward from mucro, and relatively large posterior area behind these (Fig. 43,*2c*). *Oligo.-Rec.*

Family ACANTHOCHITONIDAE Pilsbry, 1893

[*nom. correct.* Simroth, 1894 (*pro* Acanthochitidae Pilsbry, 1893)] [=?Acanthochitae Rochebrune, 1881; Amiculidae Dall, 1889 (*partim*); Cryptoplacidae, Mopaliidae (*partim*) Dall, 1889; Lophyrochitonidae Rochebrune, 1889 (*partim*); Acanthochitinae, Cryptochitoninae Pilsbry, 1893; Cryptoplacinae Thiele, 1910; Cryptoconchidae Iredale, 1914; Acanthochitoninae Ashby, 1925; Pseudotonicinae Ashby, 1928]

This family contains a number of superficially different groups of chitons, all of which seem to be related through division of the tegmentum, when present, into specific shell areas described for the suborder. Encroachment of the girdle over the valves ranges from partial to complete in one genus, which has valves completely buried and no tegmentum layer. Slitting of the insertion plate in the tail valve is an important character and varies from a single slit on each side of a wide, shallow, posterior sinus to multiple-slitted. The head valve in some groups is without dorsal radiating ribs and in others has five such ribs with a correspondingly lobed margin. *L.Oligo.-Rec.*

Recent authors divide this assemblage into subfamilies, which are not recognized here since no approach to unanimity in defining them yet exists. Many genera have been assigned to the family, the tendency having been to raise the status of groups originally

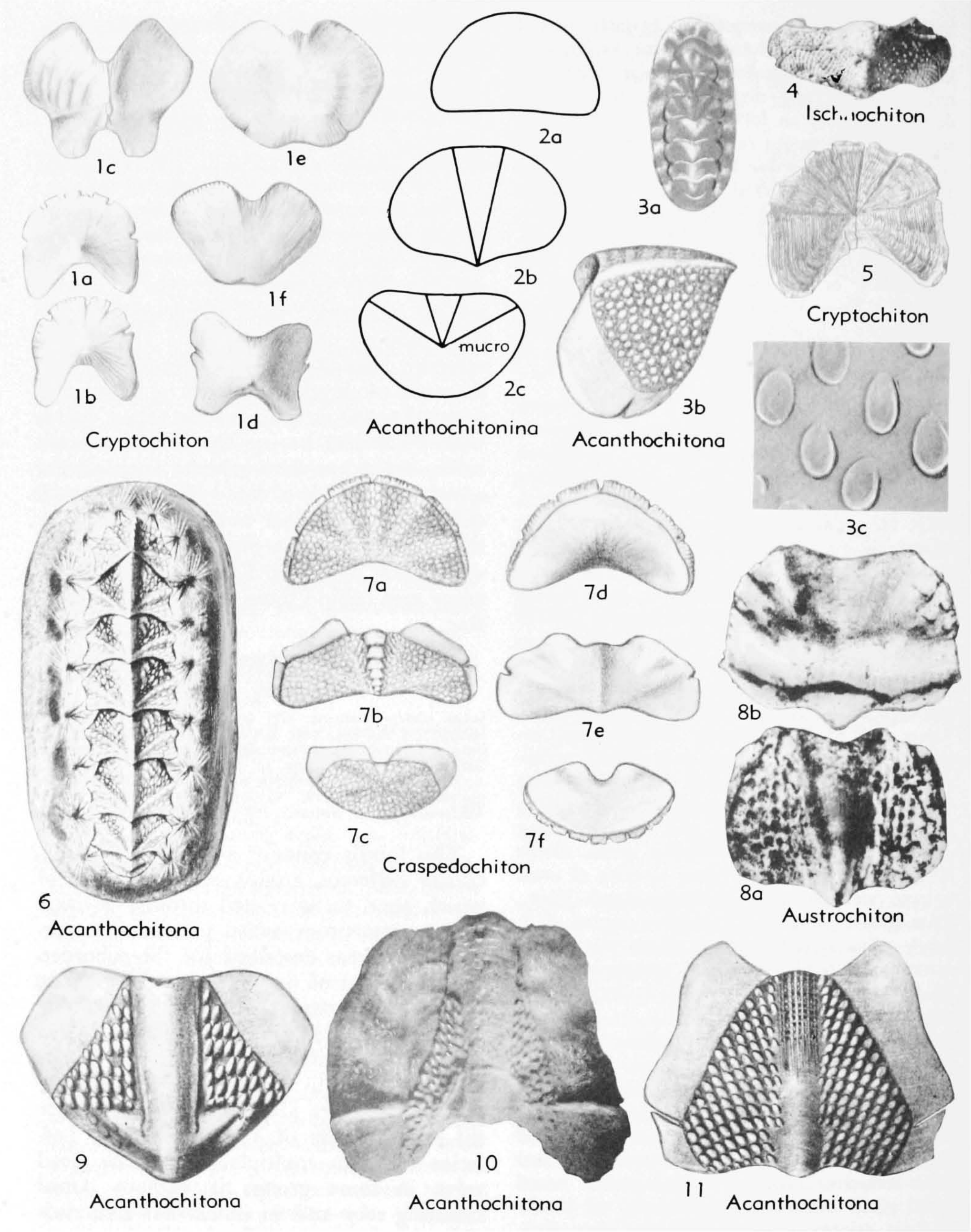

FIG. 43. Neoloricata; Acanthochitonina (Acanthochitonidae) (p. 167-170).

believed to be only of sectional or subgeneric importance. Because many of these have been segregated on the basis of small differences in tegmentum sculpture and girdle characters, only those appearing to be major generic groups are described in the *Treatise,* what seem to be closely allied group designations being cited in synonymy. Although this arrangement may be regarded by neontologists as somewhat drastic, the classification is materially simpler for paleontologists, who deal usually only with occasionally found fossil chiton valves.

Acanthochitona Gray, 1821 [*_Chiton fascicularis_ Linné, 1766] [=_Chitonellus_ deBlainville, 1825 (_non_ Lamarck, 1819); _Acanthochites_ Leach in Risso, 1826; _Phakellopleura_ Guilding, 1830; _Phacellopleura_ Agassiz, 1846; _Phacelopleura_ Lovén, 1847 _(nom. null.); Platysemus, Hamachiton_ Middendorff, 1848; _Amycula, Strecochiton_ A. Adams in Tapparone-Canefri, 1874; _Stectoplax_ Carpenter in Dall, 1882; _Stretochiton_ Pilsbry, 1893 _(nom. null.); Meturoplax_ Pilsbry, 1894; _Acanthochiton_ Iredale, 1915 _(nom. van.); Pseudoacanthochiton_ Šulc, 1934; _Eoplax_ Ashby & Cotton, 1936; _Crocochiton_ Cotton & Weeding, 1939; also various misspellings or emendations of _Acanthochites_ Leach in Risso, 1826: _Acanthochetes_ Leach, 1819 (MS.); _Acanthochistes_ Costa, 1841; _Acanthochaetes_ Gray, 1843; _Acanthochitus_ Philippi, 1844; _Acanthochiton_ Herrmannsen, 1846 (_non Acanthochitona_ Gray, 1821); _Acantoctites_ Gregorio, 1889; _Acanthocites_ Johnston, 1891; _Acantochiton_ Sacco, 1897; _Acanthochoetes_ Iredale & Hull, 1930]. Small to medium-sized chitons, rather narrow and elongated, tegmentum sculpture consisting of separated nodules or pustules of round to tear-drop shape, generally arranged in radial lines or rows. Valve coverage complete. Tail valves with submedian mucro and no dorsal ribs. Insertion plates generally with 5 slits in head valve, one on each side of intermediate valves, and in tail valve one on each side with a wide shallow sinus between; all teeth sharp and nearly smooth; sutural laminae large. Girdle varying from nude to densely hairy, but invariably with series of bristle-bearing pores (normally 18), situated around head valve with single row on each side at valve sutures. _Mio.,_ Eu.(Eng.-Fr.-Aus.) - E. Afr.(Mafia I.) - Austral.(Victoria; _Plio.,_ Eu.(Eng.-Fr.-Italy) - USA(Fla.-N. Car.) - Austral.; _Pleist.,_ Eu.(Eng.-Sicily)-USA(Calif.); _Rec.,_ cosmop. (nearly all seas except N.Pac.).——Fig. 43,_3_. *_A. fascicularis_ (Linné), Rec., Medit.; _3a,_ whole animal, ×1; _3b,_ intermed. valve, ×3; _3c,_ detail of sculpture, ×30 (25*).——Fig. 43,_6_. _A. crocodilus debilior_ Iredale & Hull, Rec., Austral. (NSW); whole animal, ×2 (20*).——Fig. 43,_9_. _A. pilsbryoides_ Ashby & Cotton, M.Mio. Austral. (Victoria); intermed. valve, ×14 (11*).——Fig. 43,_11_. _A. trianguloides_ Ashby & Cotton, L.Plio., Victoria; intermed. valve, ×10 (11*).——Fig. 43, _10_. _A. adelaidae_ (Ashby & Cotton), U.Plio., S. Austral. (referred by authors to _Eoplax_); intermed. valve, ×2.8 (11*).——Fig. 43,_4_. _A. spiculosa_ (Reeve), Plio., USA(N.Car.); intermed. valve, ×10 (9*).

Craspedochiton Shuttleworth, 1853 [*_Chiton laqueatus_ Sowerby, 1841] [=_Notoplax_ H. Adams, 1862; _Phacellopleura, Macandrellus_ Carpenter in Dall, 1879; _Leptoplax, Spongiochiton, Angasia_ (_non_ White, 1863) Carpenter in Dall, 1882; _Augasia_ Scudder, 1882 _(nom. null.); Loboplax_ Pilsbry, 1893; _Mecynoplax_ Thiele, 1893; _Phacellozona_ Pilsbry, 1894 (_pro Angasia_ Carpenter in Dall, 1882, _non_ Bate, 1864); _Thaumastochiton, Aristochiton_ Thiele, 1909; _Glyptelasma_ Iredale & Hull, 1925; _Craspedoplax_ Iredale & Hull, 1925; _Amblyplax, Lophoplax_ Ashby, 1926; _Bassethullia_ Pilsbry, 1928 (_pro Glyptelasma_ Iredale & Hull, 1925; _non_ Pilsbry, 1907); _Pseudotonicia_ Ashby, 1928; _Ikedaella_ Taki & Taki, 1929]. Small to large, generally similar to _Acanthochitona_ but nodular sculpture of tegmentum usually more pronounced, head valve having low to prominent ribs, intermediate valves with single rib, and tail valve with or without ribs and subcentral mucro. Animal more or less elongate and tending to be vermiform in some species as result of sponge-living habitat. Insertion plate of head valve 5-slitted, of intermediate valves single-slitted, and of tail valve irregularly with 6 to 10 slits, in some species tending toward replacement with age through degeneration into a callus ridge without slits. Girdle variously spiculose or minutely scaly in addition to sutural tufts (asymmetrical in some species), wider in front than behind. [The genus includes a number of species groups varying in details of surface sculpture, articulamentum structure, and girdle characters, all of which seem to bear close relationship to each other. The dorsal ribbing on the head valve and the multiple-slitted insertion plate of the tail valve seem to be common features that distinguish this genus from _Acanthochitona_.] _L. Oligo.,_ N.Z.; _?Mio.,_ Eu.(Austr.); _U.Plio.,_ N.Z.; _?Tert.,_ Eu.(Italy); _Rec.,_ IndoPac.-Austral.-N.Z.——Fig. 43,_7_. *_C. laqueatus_ (Sowerby), Rec., Philippines; _7a-c,_ head, intermed., and tail valves, dorsal views; _7d-f,_ same, ventral view; ×2 (25*).

Choneplax Carpenter in Dall, 1882 [*_Chiton strigatus_ Sowerby, 1840 (=*_Chitonellus latus_ Guilding, 1829)] [=_Chitoniscus_ Carpenter in Dall, 1882 (_?ex_ Herrmannsen, 1846); _Chnoeplax_ Pilsbry, 1894 _(nom. null.)_]. Small to medium-sized, body somewhat vermiform, living in coral holes. Valves subequal in size, with complete valve coverage; mucro of tail valve projecting far backward; insertion plates and sutural laminae all strongly projecting forward, head valve with 3 to 5 shallow slits, others with single slit on each side or none. Girdle minutely setose; sutural tufts may be obsolete. _Rec.,_ W.Indies.

Cryptoconchus deBlainville in Burrow, 1815 [*_Chiton porosus_ Burrow; SD Gray, 1847 (Nov.)] [=_Cryptoconctus_ Sowerby, 1852; _Cryptochoncus_ Clessin, 1903]. Large, elongate chitons with valves almost completely buried in large, fleshy girdle, only a very small jugal area being exposed. Valves large, valve coverage complete, uncovered tegmentum practically linear in intermediate valves, minute subcircular spot on head valve, and long line on tail valve. Dorsal sculpture consisting of a few small, flattened, somewhat rounded pustules. Articulamentum strong and solid, head valve 5-slitted, intermediate valves single-slitted, tail valve multiple-slitted between 2 major side slits, total number ranging from 5 to 7. Girdle with usual 18 sutural tufts, which grow out of sizeable elevated, rounded pockets. *Rec.*, N.Z.

Cryptochiton Middendorff, 1847 [**Chiton (Cryptochiton) stelleri;* SD Dall, 1879]. Largest of the chitons, with length up to 10 inches or more. Valves completely buried in tough, thick girdle, lacking tegmentum layer, more or less thinned at edges and crenulated by radial striae, their posterior margins produced backward in a deep lobe on each side, lobes united across median line causing their apices to be removed inward from posterior edge. Head valve with 4 to 7 slits; intermediate valves having subobsolete slits or none; tail valve with slit on each side of deep sinus, mucro posterior or near posterior third. Girdle covered with myriad fascicles of minute spinelets. *Plio.*, USA(Calif.); *Pleist.*, Calif.-Mex.(BajaCalif.); *Rec.*, N.Pac.(N.Japan to Aleutian I. and Calif.).——Fig. 43,*1,5*. **C. stelleri* (Middendorff); *1a,b,* head valves; *1c,d,* intermed. valves; *1e,f,* tail valves; all dorsal views, ×0.5, Rec., Calif. (25*); 43,*5*, ventral view of delaminated head valve, ×0.5, Pleist., Calif. (10*). [*Cryptochiton*=*Cryptochiton* Gray, 1847 *(partim)*].

Austrochiton Bergenhayn, 1945 [**Acanthochites rostratus* Ashby & Torr, 1901]. Tegmentum of single intermediate valve decorated with oval tubercles arranged in longitudinal rows on lateropleural areas, posterior margin strongly beaked. Maximum width of jugal area about equal to that of lateropleural areas. Articulamentum represented only by sutural laminae, which reach almost to anterior margin of long apical area. *M. Mio.*, Austral.(Victoria).——Fig. 43,*8*. **A. rostratus* (Ashby & Torr); *8a,b,* intermed. valve (holotype), dorsal and ventral, ×6 (42*).

Cryptoplax deBlainville, 1818 [**Chiton larvaeformis* Burrow, 1815; SD Herrmannsen, 1852] [=*Chitonellus* Lamarck, 1819; *Crytoplax* Gray, 1821; *Chitonella* Deshayes, 1830 *(nom. null.); Oscabrella* Broderip, 1835; *Chitoniscus* Herrmannsen, 1846 (*pro Chitenellus* Lamarck, 1819) *(nom. van.); Ametrogephyrus, Phaenochiton, Dichachiton* Middendorff, 1848; *Dibachiton* Paetel, 1875 *(nom. null.)*]. Medium-sized to large, elongate, almost vermiform chitons with valves well buried in thick, fleshy girdle; valves all in contact in juveniles but with increasing age they tend to separate, separation becoming very wide in valves *v* to *viii*. Tegmentum of head valve circular or more than semicircle; of valve *ii*, irregularly orbicular; of valve *iii*, roundly oval; and of remainder, elongate-oval. Dorsal sculpture granulose, granules forming longitudinal or radiating lozenge-chains or massing into irregular lines. Jugal area linear, narrow, generally smooth; lateropleural areas not separated. Mucro of tail valve terminal. Articulamentum with large insertion plate in head valve, obsoletely 3-slitted; intermediate valves with large sutural laminae and unslit insertion plates; tail valve also with unslit insertion plate, which generally projects strongly forward but may be directed backward. Girdle densely spiculose, with small sutural tufts, most prominent in living animal. *?L.Mio.(Burdigal.)*, Eu. (Austr.); *U.Mio.*, E.Borneo; *Plio.*, Austral.; *Rec.*, Japan-Indo Pac.-Austral.-N. Z.-Tasm. —— Fig. 44, *1a-f*. **C. larvaeformis* (Burrow), Rec., Austral.; *1a,b,* juvenile and adult animals, ×1 (20*); *1c-f,* valves (*1c,* head; *1d,e,* tail, *1f,* juvenile tail), ×2 (20*).——Fig. 44,*1g*. *C. numicus* Ashby & Cotton, L.Plio., Victoria; intermed. valve, ×12 (11*).——Fig. 44,*1h*. *C. pritchardi* Hall, L.Plio., Austral.(Victoria); intermed. valve, ×6.5 (11*).

Suborder AFOSSOCHITONINA Bergenhayn, 1955

Shell areas of tegmentum similar to those in Lepidopleurina, sculpture somewhat resembling *Acanthochitona;* articulamentum represented by sutural laminae only. *M.Mio.*

Family AFOSSOCHITONIDAE Ashby, 1925

[*nom. transl.* Bergenhayn, 1945 (*ex* Afossochitoninae Ashby, 1925)]

Characters of the suborder. *M.Mio.*

Afossochiton Ashby, 1925 [**A. cudmorei*] [?=*Telochiton* Ashby & Cotton, 1939]. Small chitons having intermediate valves with tegmentum sculpture of large subtriangular tubercles arranged in distinct rows running anteriorly and laterally from posterior margin; sculpture of jugal area undetermined; apical area very narrow; articulamentum as in suborder. Head and tail valves unknown but the latter assumed to have sutural laminae as in intermediate valves. *M.Mio.*, Austral.(Victoria).——Fig. 44,*7*. **A. cudmorei;* intermed. valve, ×6 (42*).

Incertae Sedis

Suborder Uncertain

Family LLANDEILOCHITONIDAE Bergenhayn, 1955

Chitons with shell lacking articulamentum layer. Shape of intermediate valves subquadrate, tegmentum surface divided into 7 areas consisting of 2 side slopes of valve on either side of a peculiarly shaped jugal

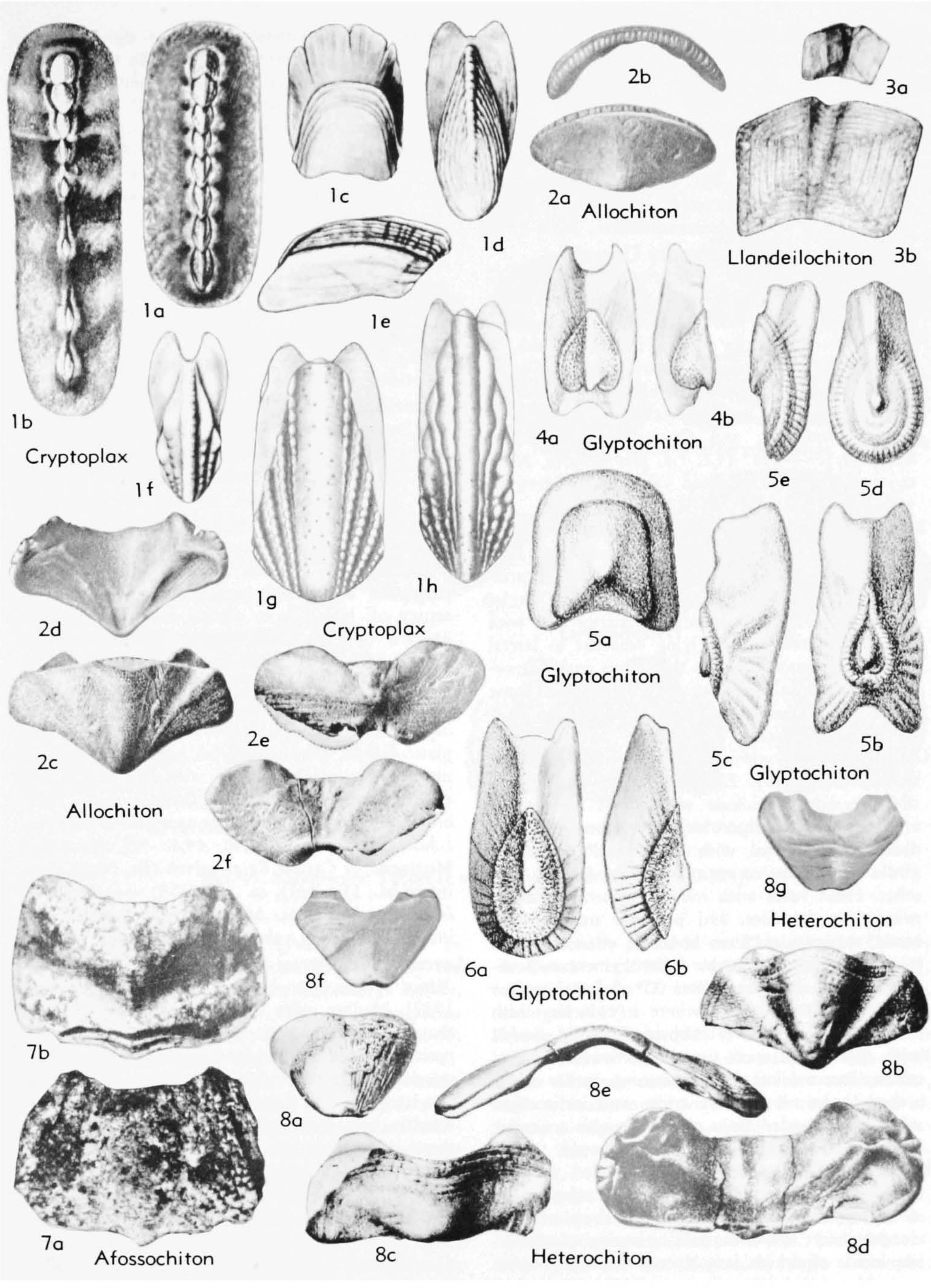

FIG. 44. Neoloricata; Acanthochitonina (Acanthochitonidae); Afossochitonina (Afossochitonidae); Incertae Sedis (Llandeilochitonidae and others) (p. I70-I72).

area, which is formed like the lower half of an expanding tube, very narrow posteriorly and gradually enlarging to give the valve a concave dip at middle of the anterior edge; from approximate center of valve 4 indistinct ribs or structural breaks radiate to each of its corners, thus dividing it into 2 anterior, 2 lateral, and 2 posterior areas, but this division does not affect the channel-like jugal area. _M.Ord._

Llandeilochiton Bergenhayn, 1955 [_*L. ashbyi_]. Characters of the family. End valves unknown. _M.Ord.,_ Austral.——Fig. 44,_3_. _*L. ashbyi,_ Llandeilo., Austral., _3a,_ intermed. valve (type), ×1.8; _3b,_ schematic view of intermed. valve, ×3.6 (8*).

Suborder and Family Uncertain

Allochiton Fucini, 1912 [_*A. gemmellaroi;_ SD A.G. Smith, herein]. Shell not very elongate, tail valve rather large, almost smooth, bilobate, with rounded and beaked posterior apex; insertion plate of head valve with numerous coarse slits, similar in size to those of intermediate valves. [Fucini states that the genus has some aspects of the Mopaliidae, Acanthochitonidae, and Cryptoplacidae.] _L.Jur.,_ Eu.(Sicily).——Fig. 44,_2_. _*A. gemmellaroi,_ Montagna di Casale; _2a,b,_ head valve; _2c,d,_ intermed. valve; _2e,f,_ tail valve; all ×2 (15*).

Beloplaxus Oehlert, 1881 [_*Chiton sagittalis_ Sandberger, 1853]. Chitons with triangular valves having sloping lateral areas, wide median depression, and anterior end with projecting angles and deep indentation at edge; posterior end with narrow insertion surface lying adjacent to lateral edges. [Oehlert compares this genus with _Sagmaplaxus,_ which in the _Treatise_ is assigned with some doubt to the Chelodidae.] _Dev.,_ Eu.(Villmar-Prussia in Hesse-Nassau).

Glyptochiton deKoninck, 1883 [_*Chiton? cordifer,_ deKoninck, 1844]. Elongate, rather small, possibly vermiform chitons with small tegmentum area and much larger articulamentum area, indicating an animal with valves well buried in girdle and almost or entirely separated from each other. Head valve with rounded anterior margin, nearly straight sides, and posterior margin with broad semicircular sinus bounded on either side by rounded marginal valve ends; tegmentum similar in shape, occupying inner 0.7 of dorsal surface except at posterior edge where it coincides with articulamentum; valve subpyramidal in profile with mucro-like apex situated somewhat behind center. Intermediate valves narrow, rather high-arched, twice as long as wide, anterior margin with deep rounded sinus, posterior with a similar but squared sinus, sides somewhat waved, widest about 0.3 of distance behind rounded anterior shell tips, whole valve configuration subquadrate in aspect; tegmentum area of tear-drop or very elongate heart shape, marked by strong crenulated rib, inside of which is a smooth depression with a sizable, raised, elongate pustule at center, and radiating from this rib are rather weak, closely spaced riblike striae that become obsolete at valve margin but do not appear on posterior 0.3 of articulamentum area. Supposed tail valve narrower in front than behind, with somewhat truncated anterior edge, posterior end oval; tegmentum set off by a similar crenulated ovate rib that occupies more than 0.7 of dorsal area, smooth inside area with prominent subcentral mucro, back of which anterior end slopes away sharply; articulamentum projecting forward from front edge of tegmentum, sloping away from it quite deeply at anterior end of shell and marked with similar radiating striae. Ventral aspect of valves unknown. _L.Carb.,_ Eu.(Belg.-Scot.). —— Fig. 44,_4_. _G. subquadratus_ (Kirkby & Young), Scot.(Ayrshire); _4a,b,_ intermed. valve, ×8 (43*).——Fig. 44,_5_. _*G. cordifer_ (deKoninck), Belg.; _5a-e,_ valves (_5a,_ head, _5b,c,_ intermed., _5d,e,_ tail) enlarged (23*).——Fig. 44,_6_. _G. youngianus_ (Kirkby & Young), Scot.(Ayrshire); _6a,b,_ tail valve, ×4 (43*).

Heterochiton Fucini, 1912 [_*H. giganteus;_ SD A.G.Smith, herein]. Shell not very elongate, valves fairly thick and heavy. Tegmentum well developed, sculptured with granules or ribs, or both. Head valve about as long as wide, subpyramidal, widest at anterior edge and narrowing sharply backward; intermediate valves short and wide, generally thrown forward from rounded, projecting apex, with well-marked diagonal rib setting off lateral from pleural areas, which slope upward over rounded jugum. Tail valve solid, shaped like head valve except for fairly deep, rounded sinus anteriorly, apical area extending considerably on to ventral side. Articulamentum of all valves well developed, calloused; insertion plate of head valve slit, of tail valve unslit, and of intermediate valves usually with 2 slits forming rude, rounded teeth; sutural laminae thick, fairly broad, with semicircular or squared sinus between. _L.Jur.,_ Eu.(Sicily).——Fig. 44,_8_. _*H. giganteus,_ Montagna di Casale; _8a-g,_ valves (_8a,_ head; _8b-e,_ intermed.; _8f,g,_ tail), ca. ×2 (15*).——Fig. 45,_4_. _H. vinassai_ Fucini, Montagna di Casale; _4a,b,_ intermed. and tail valves, ca. ×2 (15*).

Lavenachiton Cotton & Godfrey, 1940 [_*Ischnochiton (Radsiella) cliftonensis_ Ashby & Cotton, 1939]. Median valve differs from _Ischnochiton_ in shape, absence of differentiated lateral areas, and position of sutural laminae; posterior valve characterized by same unique sculpture; bridging of flat irregular ribs forms oblong pits that tend toward a somewhat cuneiform pattern. [The authors think that this genus may belong to the Chitonidae.] _M.Mio.,_ Austral.(Victoria).——Fig. 45,_7_. _*L. cliftonensis_ (Ashby & Cotton); intermed. valve, ×3.4 (11*).

Lirachiton Ashby & Cotton, 1939 [_*Acanthochiton (Lirachiton) inexpectus_ Ashby & Cotton, 1931] [=_Molachiton_ Ashby & Cotton, 1939]. Pleural areas decorated with narrow, widely spaced ribs instead of granular ornamentation; in type species sculpture behind mucro and in area corresponding to lateral area of median valve is formed of triangular flat grains; near apex of each is an

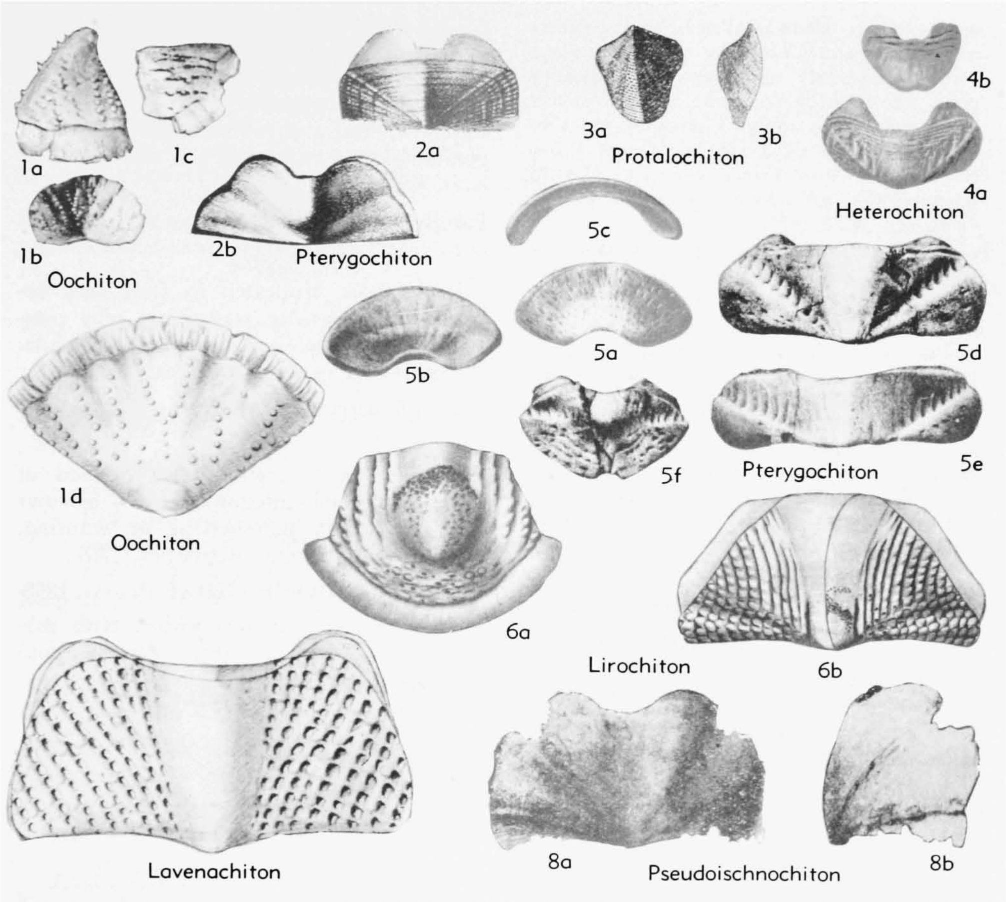

FIG. 45. Neoloricata; Suborder and Family Uncertain (p. 172-174).

ocellus or sense organ. [Possibly classed in Acanthochitonidae, as provisionally placed by the authors, or in the A'fossochitonidae.] *L.Plio.*, Austral.(Victoria).——FIG. 45,*6*. **L. inexpectus* (ASHBY & COTTON); *6a*, head valve, ×7; *6b*, intermed. valve, ×6.5 (11*).

Oochiton ASHBY, 1929 [**O. halli*]. Very small, high-arched, carinated chitons; valves with steep side slopes. Sculpture of erect, ovate pustules arranged in irregular rows or widely scattered over dorsal surface, each with a minute aperture at summit. Head valve with tegmentum unfolded at apex and well-produced insertion plate with irregularly spaced, broad, and short slits, outside closely grooved but leaving a sharp, beveled edge; intermediate valves with single, broad, deep slit on each side of pectinated insertion plate, sutural laminae joined across median line; tail valve unique, with upturned, greatly thickened extremity and deep sinus immediately behind mucro, tegmentum having an extended fold into sinus. [Provisionally placed in the Chitonidae by COTTON & GODFREY (1940).] *M.Mio.*, Austral.(Victoria).——FIG. 45,*1*. **O. halli*; *1a-d*, valves (*1d*, head), enlarged (11*).

Protalochiton ROCHEBRUNE, 1883 [**P. settlensis* (*pro Chiton?* sp. nov. KIRKBY, 1862)]. Shell ovate-elliptical, carinate, head valve semicircular, tail valve elevated; valve *ii* subtriangular, with anterior edge undulate, jugum acute, and posterior edge umbonate; other intermediate valves narrow, elevated, and concave anteriorly. Tail valve cap-shaped, with abruptly acute posterior, reflected apex. Articulamentum, if any, not defined. *L.Carb.*, Eu.(Eng.).——FIG. 45,*3*. **P. settlensis*, L.Scar Ls., Yorkshire; *3a,b*, ?intermed. valve, ×3 (47*).

Pseudoischnochiton ASHBY, 1930 [**P. wynyardensis*]. Only median valve known, its shell extremely thin and unsculptured except for a strongly raised rib and weak radial ribbing; pleural area unusually broad, tegmentum well bowed forward on either side of jugal sinus; sutural laminae reduced to narrow extension of articulamentum bordering anteriorly bowed tegmentum; insertion plates absent wholly or in part. [ASHBY considers *Pseudoischnochiton* to be a primitive genus belonging either in the Lepidopleuridae or Ischnochitonidae.] *L.Mio.*, Tasmania.——FIG. 45,*8*. **P. wynyardensis; 8a,b,* intermed. valve, top and side views, ×2, ×3.5 (41*).

Pterygochiton ROCHEBRUNE, 1883 [**Chiton terquemi* DESLONGCHAMPS, 1859; SD A.G.SMITH, herein]. Shell ovate, carinate, strongly arched; valves broad, anterior edge more or less emarginate, sutural laminae broad, rounded, very prominent, and separated by a subquadrate sutural sinus; tail valve elliptical, with very prominent, pointed, straight mucro. *L.Jur.*, Fr.-?Sicily.——FIG. 45,2. **P. terquemi* (DESLONGCHAMPS), Fr.(Calvados); *2a,b,* intermed. valve and internal cast, ×? (44*).——FIG. 45,*5*. *P.? busambrensis* FUCINI, Sicily(Montagna di Casale); *5a-f,* valves (*5a-c,* head; *5d,e,* intermed., *5f,* tail), ca. ×2 (15*).

Doubtful Genera

Several genera considered to represent fossil remains of chitons have been omitted from the systematic account of Polyplacophora because of doubt as to their nature. They include the following:

Duslia JAHN, 1893 [**D. insignis*]. *L.Sil.*, Bohemia.

Permochiton IREDALE & HULL, 1926 [**P. australianus*]. Permo-Carb., Austral.(NSW).

Solenocaris YOUNG & YOUNG, 1868 [**S. solenoides*]. *Sil.*, Scot.

Sulcochiton RYCKHOLT, 1862 [**S. grayi*]. *L.Carb.*, Belg.

Trachypleura JAECKEL, 1900 [**T. triadomarchica*]. *Trias.*, Ger.

Subclass APLACOPHORA von Ihering, 1876

[Treated by VON IHERING as "class" in "phylum" Amphineura of the Vermes] [=Telobranchia KOREN & DANIELSSEN, 1877; Solenogastres GEGENBAUR, 1878; Scolecomorpha LANKESTER, 1883]

Wormlike animals with spiculose integument, adults without covering of shelly plates. *Rec.*

Order NEOMENIIDA Simroth, 1893

[*nom. correct.* A.G.SMITH, herein (*pro* Neomeniina SIMROTH, 1893)] [=Neomeniomorpha PELSENEER in LANKESTER, 1906]

Spiculose integument with distinct longitudinal ventral groove; bisexual, with paired genital glands and lacking a differentiated liver. *Rec.*

Family NEOMENIIDAE von Ihering, 1876

[*nom. correct.* SIMROTH, 1893 (*pro* Neomeniadae VON IHERING, 1876)]

Body short, truncated in front and behind; cloacal orifice transverse; gills present; rather thin integument; no radula. [Contains 43 genera, 96 species.] *Rec.*

Family PRONEOMENIIDAE Simroth, 1893

Body elongate, cylindrical, rounded at both ends; thick integument with acicular spicules; radula polystichous or wanting. [Contains 12 genera, 40 species.] *Rec.*

Family LEPIDOMENIIDAE Pruvot, 1890

Body slender, tapering behind, with subvental cloacal orifice; cuticle thin, without papillae; spicules flattened; no gills.

[Contains 11 genera, 23 species.] *Rec.*

Family GYMNOMENIIDAE Odhner, 1921

Cuticle thin, epidermis a single multicellular layer without papillae; no spicula. [Contains single genus and species.] *Rec.*

Order CHAETODERMATIDA Simroth, 1893

[*nom. correct.* A.G.SMITH, herein (*pro* Chaetodermatina SIMROTH, 1893)] [=Chaetodermorpha PELSENEER in LANKESTER, 1906]

Animals without distinct ventral or pedal groove; gonad unpaired, unisexual; liver differentiated; posterior cloacal chamber with two bipectinate gills. *Rec.*

Family CHAETODERMATIDAE von Ihering, 1876

[*nom. correct.* SIMROTH, 1893 (*pro* Chaetodermata VON IHERING, 1876)]

Characters of the order. [Contains 4 genera, 27 species.] *Rec.*

REFERENCES

POLYPLACOPHORA

The following publications relating to the Polyplacophora have been selected from a much longer list. They are considered to be the ones most helpful in any study of living and particularly of fossil forms. Some contain extensive reference lists to systematic work on the group that should be consulted for a complete picture of it.

Ashby, Edwin

(1) 1925, *Monograph on Australian fossil Polyplacophora (chitons):* Roy. Soc. Victoria, Proc., new ser., v. 37, pt. 2, p. 170-205, pl. 18-22 (Melbourne).

(2) 1929, *Notes and additions to Australian fossil Polyplacophora (chitons):* Same, v. 41, pt. 2, p. 220-230, pl. 24.

(3) 1929, *New Zealand fossil Polyplacophora (chitons):* New Zealand Inst., Trans. Proc., v. 60, pt. 2, p. 366-369, pl. 32, fig. 1-13a,b (Wellington).

(4) 1939, *Fossil chitons from Mornington, Victoria:* Linn. Soc. London, Proc., 151st session (1938-39), pt. 3, p. 186-189, pl. 3, fig. 1-4.

———, & Cotton, B. C.

(5) 1936, *South Australian fossil chitons:* South Australian Mus., Records, v. 5, pt. 4, p. 509-512, text fig. (Adelaide).

(6) 1939, *New fossil chitons from the Miocene and Pliocene of Victoria:* Same, v. 6, pt. 3, p. 209-242, pl. 19-21.

Bergenhayn, J. R. M.

(7) 1930, *Kurtze Bemerkungen zur Kenntnis der Schalenstruktur und Systematik der Loricaten:* Kungl. Svenska Vetenskapsak., Handl., ser. 3, v. 9, no. 3, p. 1-54, pl. 1-10 (Stockholm).

(8) 1955, *Die fossilen schwedischen Loricaten nebst einer vorlaüfigen Revision des Systems der ganzen Klasse Loricata:* Lunds Univ. Årssk., new ser., 2, v. 51, no. 8 (Kungl. Fysiogr. Sallskapets, Handl., new ser., v. 66, no. 8), p. 1-41, pl. 1-2.

Berry, C. T.

(9) 1940, *Some fossil Amphineura from the Atlantic Coastal Plain of North America:* Acad. Nat. Sci. Philadelphia, Proc., v. 91 (1939), p. 207-217, pl. 9-12.

Berry, S. S.

(10) 1922, *Fossil chitons of western North America:* California Acad. Sci., Proc., ser. 4, v. 11, no. 18, p. 399-526, pl. 1-16, text fig. 1-11 (San Francisco).

Cotton, B. C. & Godfrey, F. K.

(11) 1940, *Australian fossil chitons:* Handbook, Molluscs of South Australia, South Australia Mus., pt. 2, p. 569-590, text figs. 577-589 (Adelaide).

Dall, W. H.

(12) 1879, *Report on the limpets and chitons of the Alaskan and Arctic regions, with descriptions of genera and species believed to be new:* U. S. Natl. Mus., Proc., v. 1 (1878), p. 281-344, pl. 1-5; also published, 1879, as Scientific Results, Explor. Alaska, art. 4, p. 63-126, pl. 1-5 (Washington).

(13) 1882, *On the genera of chitons:* U. S. Natl. Mus., Proc., v. 4 (1881), p. 279-291 (Washington).

Dechaseaux, Colette

(14) *Classe des Amphineures:* in Piveteau, J., Traité de Paléontologie, v. 2, p. 210-215, fig. 1-4, Masson (Paris).

Fucini, A.

(15) 1912, *Polyplacophora del Lias Inferiore della Montagna di Casale in Sicilia:* Paleontographica Italica, Pisa, v. 18, p. 105-127, pl. 18-19.

Gray, J. E.

(16) 1847, *On the genera of the family Chitonidae:* Zool. Soc. (London), Proc., 1847, p. 63-70.

(17) 1847, *Additional observations on Chitones:* Same, pt. 15, no. 178, p. 126-127.

(18) 1847, *A list of the recent Mollusca, their synonymy and types:* Same, Family Chitonidae, no. 179, p. 168-169.

Hoffman, H.

(19) 1929-30, *Amphineura (Polyplacophora):* in Bronn, H. G., Klassen und Ordnung des Thier-Reichs, v. 3, pt. 1, suppl. 2, p. 135-368 (1929); suppl. 3, p. 369-382, fig. 81-195 (1930); contains long list of references, continuing the list of Simroth (in Bronn), 1892-94. (Ref. No. 31).

Iredale, Tom, & Hull, A. F. B.

(20) 1926, *Paleoloricata:* A monograph of the Australian loricates, VIII, App. B, Australian Zool., v. 4, pt. 5, p. 324-328, pl. 45; reprinted, 1927, Roy. Zool. Soc. New South Wales, p. 130-143, pl. 18.

Knorre, Heinrich von

(21) 1925, *Die Schale und die Rückensinnesorgane von Trachydermon (Chiton) cinereus L. und die ceylonischen Chitonen der Sammlung Plate. (Fauna et Anatomica ceylonica, III, nr. 3):* Jenaische Zeitschr. Naturwiss., v. 61 (new ser., v. 54), p. 469-632, pl. 18-35, text fig. 1-17 (Jena).

Koninck, L. G. de

(22) 1857, *Observations on two new species of Chiton from the Upper Silurian 'Wenlock Limestone' of Dudley:* Acad. roy. Sci. Belgique, Bull., ser. 2, v. 3, p. 190-199, pl. 1 (Bruxelles); reprinted in English translation by Baily, W. H., 1860, Ann. & Mag. Nat. Hist., ser. 3, v. 6, p. 91-98, pl. 2, fig. 1a-d, 2a-c (London).

(23) 1883, *Faune du calcaire carbonifère de la Belgique, pt. 4, Gastéropodes (suite et fin):* Mus. roy. d'Hist. nat. Belgique, Ann., sér. paléont., v. 8, pt. 4, p. 198-213, pl. 50-53 (Bruxelles).

Lindström, G.

(24) 1884, *On the Silurian Gastropoda and Pteropoda of Gotland:* Kungl. Svenska Vetenskap-

sak., Handl., v. 19, no. 6, p. 48-52, pl. 2, fig. 1-28 (Stockholm).

Pilsbry, Henry A.

(25) 1892-94, *Monograph of the Polyplacophora:* Manual of Conchology, v. 14 (1892-93), xxiv+350 p., 68 pl.; v. 15 (1893-94), 133 p., 17 pl. (Philadelphia).

(26) 1900, *Polyplacophora:* in Zittel, K. A., Text-book of Palaeontology (Eastman transl.), p. 433-436, fig. 792-793, Macmillan (London & New York).

Plate, L.

(27) 1897-1901, *Die Anatomie und Phylogenie der Chitonen:* Fauna Chilensis, v. 1, pt. 1, p. 1-243, pl. 1-12 (1897); v. 2, pt. 1, p. 15-216, pl. 2-11 (1899); v. 2, pt. 2, p. 281-600, pl. 12-16 (1901); Zool. Jahrb., Suppl., v. 4 (1898), v. 5 (1902).

Quenstedt, Werner von

(28) 1932, *Die Geschichte der Chitonen und ihre allgemeine Bedeutung:* Paläont. Zeitschr., v. 14, no. 1-2, p. 77-96, fig. 1 (Berlin).

Rochebrune, A. T. de

(29) 1883, *Monographie des espèces fossiles appartenant à la Classe des Polyplaxiphores:* Ann. Sci. géol., v. 14, art. no. 1, p. 1-74, pl. 1-3 (Paris). (The figures are misleading and should be disregarded.)

Ryckholt, Philip de

(30) 1845, *Résumé géologique sur le genre Chiton Lin.:* Acad. roy. Sci. et Belles Lettres, Bull., v. 12, no. 7, pt. 2, p. 36-62, 4 pl. (Bruxelles).

Simroth, H.

(31) 1892-94, *Amphineura:* in Bronn, H. G., Klassen und Ordnung des Thier-Reichs, v. 3 (Mollusca), pt. 1, sec. 1-21, p. 128-355, pl. 1-22, 51 text figs.; excellent bibliography, continued by Hoffman (in Bronn), 1929-30 (Ref. no. 19).

Šulc, Jaroslav

(32) 1936, *Studie über die fossilen Chitonen—I. Die fossilen Chitonen im Neogen des Wiener Beckens und der angrezenden Gebiete:* Naturhist. Mus. Wien, Ann., v. 47, p. 1-31, text fig. 1-4, pl. 1-2.

Thiele, Johannes

(33) 1893, *Polyplacophora:* in Troschel, F. H., Das Gebiss der Schnecken zur Begründung einer natürlichen Classification, v. 2, p. 353-401, pl. 30-32 (Berlin).

(34) 1909-10, *Revision des Systems der Chitonen:* Zoologica, v. 22, no. 56, p. 1-132, pl. 1-10.

(35) 1929, *Classis Loricata:* Handbuch der systematischen Weichtierkunde, v. 1, pt. 1, p. 1-12, fig. 1-12.

APLACOPHORA

Heath, Harold

(36) 1911, *Reports on the scientific results of the expedition to the tropical Pacific, in charge of Alexander Agassiz, by the U. S. Fish Commission Steamer* Albatross, *from August 1899 to June 1900, Commander Jefferson F. Moser.–XIV.–The Solenogastres:* Mus. Comp. Zool., Harvard Coll., Mem., v. 45, p. 1-182, pl. 1-40 (Cambridge).

(37) 1918, *Solenogastres from the eastern coast of North America:* Same, v. 45, pt. 2, p. 183-260, pl. 1-14.

Hoffman, H.

(38) 1929, *Aplacophora:* in Bronn, H. G., Klassen und Ordungen des Thier-Reichs, v. 3, pt. 1, p. 1-134, text figs. 1-80 (Leipzig); bibliography of 41 titles.

Pilsbry, H. A.

(39) 1898, *Order Aplacophora v. Ihering:* Man. Conch., Acad. Nat. Sci. Philadelphia, v. 17, p. 281-310.

Simroth, H.

(40) 1893, *Aplacophora:* in Bronn, H. G., Klassen und Ordnungen des Thier-Reichs, v. 3, pt. 1, p. 128-233, pl. 1-4, text figs. 1-12 (Leipzig); bibliography of 40 titles.

SOURCES OF ILLUSTRATIONS

The sources of illustrations for various species in the Polyplacophora are indicated by numbers which in most instances correspond to those assigned to the "List of References" that carry numbers 1-40. Where it has been necessary to select illustrations from sources outside the basic list, these have been assigned numbers above 40, as indicated below. An asterisk(*) associated with an index number signifies that the original figure has been reproduced without alteration except for a possible change in scale.

(41) **Ashby, Edwin**
(42) **Bergenhayn, J. R. M.**
(43) **Etheridge, R., Jr.**
(44) **Eudes-Deslongchamps, J. A.**
(45) **Iredale, Tom & Hull, A. F. B.**
(46) **King, William**
(47) **Kirkby, J. W.**
(48) **Leloup, Eugène**
(49) **Pompeckj, J. F.**
(50) **Richardson, E. S. Jr.**
(51) **Salter, J. W.**
(52) **Sandberger, Guido**
(53) **Wilson, Alice E.**

MONOPLACOPHORA

By J. Brookes Knight[1] and E. L. Yochelson[2]

Class MONOPLACOPHORA Wenz in Knight, 1952

Mollusks with a single shell, cap-shaped, or spoon-shaped to arched, in some groups bilaterally symmetrical, in others longitudinally curved and deviating from symmetry. *L.Cam.-Rec.*

The reader is referred to the general account of the Mollusca prepared by C. M. Yonge, herein, for the basis of erecting this sixth class of mollusks. Briefly, it is based primarily on the absence of torsion in the soft anatomy of a living representative, the pairing of the ctenidia, muscles and other anatomical structures, and the presence of a single shell. The fossil monoplacophorans lived in epicontinental seas, whereas Recent representatives of the class, in contrast, occur in deep oceanic waters, as indicated by specimens obtained at depths ranging from 1,963 to 3,201 fathoms.

Order TRYBLIDIOIDEA Lemche, 1957

Mollusks with a single bilaterally symmetrical shell showing evidence of bilateral symmetry of the soft parts. *L.Cam.-Rec.*

In fossil species there was a more or less elaborate system of shell muscles as evidenced by the symmetrically paired muscle scars in the family Tryblidiidae, where there are five to eight pairs. Tending to support a possible relationship to the Polyplacophora are the numerous fine, branching tubules through the shell of *Tryblidium reticulatum* Lindström. These suggest rather strongly the very similar tubules that carry the aesthetes, or shell eyes, in a number of polyplacopheran genera. It is possible that these extremely fine tubules have been found only in *T. reticulatum* because of its thick shell and the perfect preservation of specimens from Gotland.

Superfamily TRYBLIDIACEA Pilsbry in Zittel-Eastman, 1899

[*nom. transl.* Knight, herein (*ex* Tryblidiidae Pilsbry, 1899)]

Shell cap-shaped, spoon-shaped or slightly arched; with 5 to 8 symmetrical pairs of dorsal muscles. *L.Cam.-Rec.*

Family PALAEACMAEIDAE Grabau & Shimer, 1909

[=Scenellinae Wenz, 1938]

Aperture of shell subcircular; apex commonly subcentral, but position variable among individuals; with several strong rugosities between apex and margin of aperture. *L.Cam.-U.Cam.*

?**Scenella** Billings, 1872 [**S. reticulata*] [=*Parmorphella* Matthew, 1886]. Low cap-shaped shell with moderately strong concentric wrinkles and fine radiating threads; an early Middle Cambrian species shows 6 (or 7) pairs of dorsal muscle scars. *Cam.*, N.Am.-NE.Asia.——Fig. 46,*1*. **S. reticulata,* L.Cam., Can.(Newf.); *1a,b,* individuals showing extremes in variation, ×2.7.——Fig. 46,*2*. *S. sp.* (Rasetti), M.Cam., Can.(B.C.); interior showing muscle scars, ×3.5.

Palaeacmaea Hall & Whitfield, 1872 [**P. typica*]. Low conical shell with subcentral apex; strong concentric rugae; muscle scars unknown. *U.Cam.*, N.Am.-NE.Asia.——Fig. 46,*4*. **P. typica,* N.Y.; steinkern oblique from above, ×1.3.

Family TRYBLIDIIDAE Pilsbry in Zittel-Eastman, 1899

Most genera with aperture elongate oval; apex distinctly anterior; muscle scars well developed where known. *U.Cam.-Rec.*

Subfamily PROPLININAE Knight & Yochelson, 1958

Shell with apex distinctly overhanging anterior margin; 6 pairs of muscles arranged approximately normal to margin of aperture. *U.Cam.-U.Ord.*

Proplina Kobayashi, 1933 [**Metoptoma cornutaforme* Walcott, 1879]. Apex strongly overhanging anterior end but with no coiling; exterior of shell smooth; 6 muscle scars in shell. *U.Cam.-L.Ord.*, N.Am.-NE.Asia.——Fig. 46,*3*. **P. cornutaformis* (Walcott); *3a,* U.Cam., N.Y., left side, ×4; *3b,* L.Ord., Mo., steinkern showing muscle scars, ×1.3.

?**Vallatotheca** Foerste, 1914 [**V. manitoulini*]. Shell relatively deep; ornament sharp concentric lamellae with fine superimposed radiating threads;

---

[1] Honorary Research Associate, Smithsonian Institution, Washington, D.C.; Longboat Key, Florida.

[2] U.S. Geological Survey, Washington, D.C.

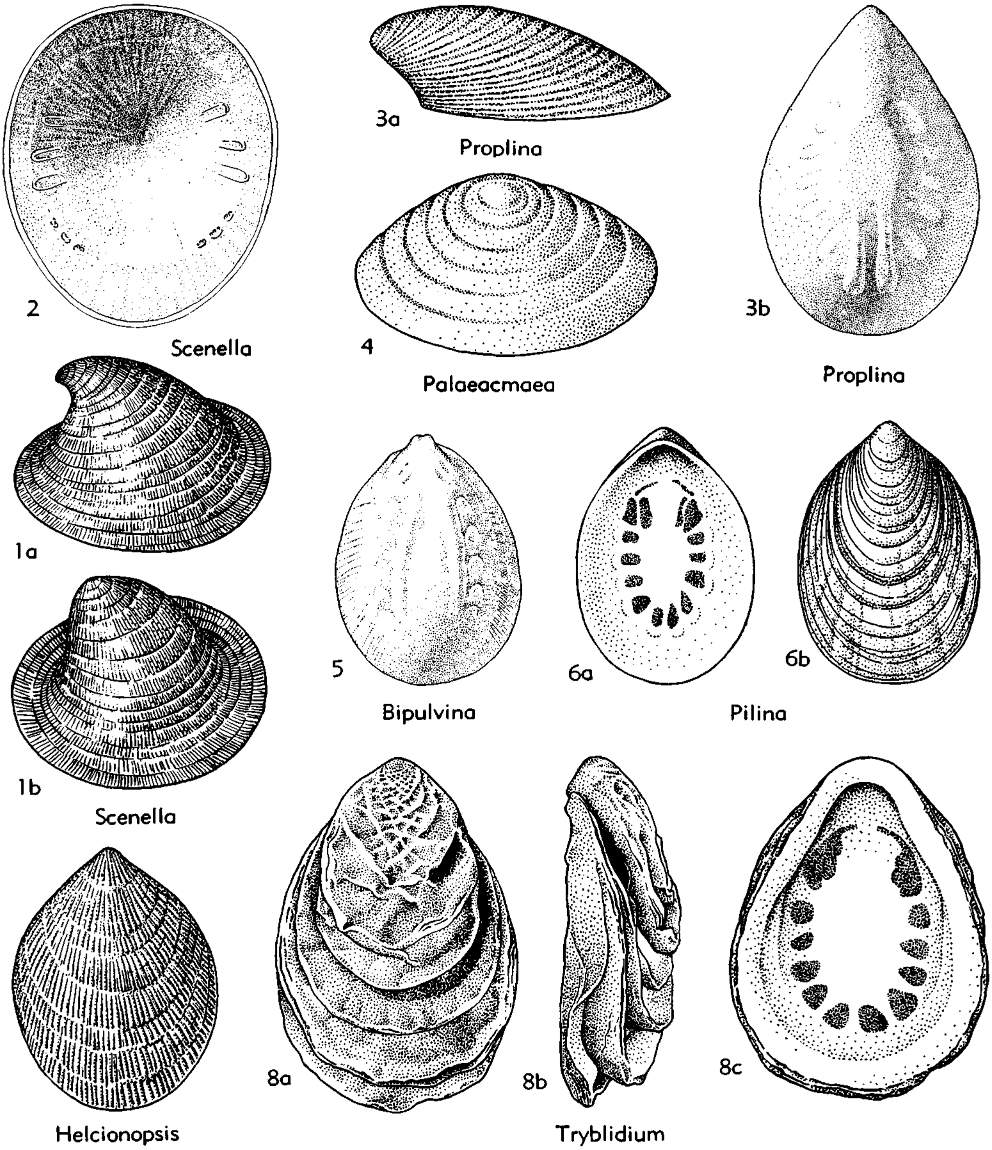

Fig. 46. Tryblidioidea; Tryblidiacea (Tryblidiidae) (p. I77-I79).

muscle scars unknown. _U.Ord._, N.Am.——Fig. 47. *_V. manitoulini_, Can.(Ont.); left side, ×2.

Subfamily TRYBLIDIINAE Pilsbry in Zittel-Eastman, 1899

[_nom. transl._ Knight, herein (_ex_ Tryblidiidae Pilsbry, 1899)]

Shell shallow spoon-shaped, with slight arching of margin about 0.3 of distance posteriorly from anterior; with 5 to 8 pairs of muscles, those in front commonly more elaborate. _L.Ord.-M.Sil._

Bipulvina Yochelson, 1958 [*_B. croftsae_]. Shell thick, thinning abruptly at margin; at least 5 pairs of muscle scars present; interior of shell flattened for about half its length; ornament unknown. _L.Ord._, N.Am.——Fig. 46,_5_. *_B. croftsae_, Mo.; steinkern showing muscle scars, ×1.3.

Tryblidium Lindström, 1880 [*_T. reticulatum;_ SD S.A.Miller, 1889] [=_Triblidium_ Grabau &

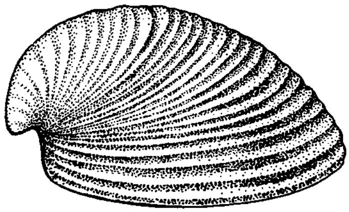

FIG. 47. Tryblidioidea; Tryblidiacea (Tryblidiidae)—*Vallatotheca manitoulini* Foerste, U.Ord., Can. (Ont.); left side, ×2.

SHIMER, 1909]. Shell interior divided into 4 concentric zones converging under apex, outermost rather thick and rounded around posterior 0.75 of aperture, next inner zone narrow, smooth and gently arched, third zone roughened by muscle scars, and innermost zone smoothed by secondary deposits that cover first-formed parts of muscle scars; scars comprising 6 symmetrical pigmented pairs with scars of anterior pair seemingly compounded of 3 parts; ornament (of type species) consisting of broad, high, thin, frilled lamellae that arise alternately from opposite sides so as to make a reticulate pattern; shell punctured by many microscopic perforations that branch on approaching outer surface in manner suggesting minute openings that carry nerves for aesthetes (or shell eyes) in many Polyplacophora. *?Ord., M.Sil.,* N. Am.-Eu.——FIG. 46,*8*. **T. reticulatum,* M.Sil., Gotl.; *8a,b,* dorsal and left sides; *8c,* interior showing paired muscle scars (compound scars above); all ×1.3.

Pilina KOKEN, 1925 [**Tryblidium unguis* LINDSTRÖM, 1880]. Like *Tryblidium* in shape and nature of muscle scars but with thinner shell; ornament consisting of concentric growth lines and faint, widely spaced radiating grooves. [A specimen illustrated by LINDSTRÖM (1880, pl. 1, fig. 36) shows a small anterior pit internally, which appears to be the open end of a partially filled protoconch.] *M.Sil.,* Eu.——FIG. 46,*6*. **P. unguis* (LINDSTRÖM), Gotl.; *6a,* interior showing paired muscle scars; *6b,* dorsal view; ×0.7.

?**Helcionopsis** ULRICH & SCOFIELD, 1897 [**H. striatum* ULRICH in ULRICH & SCOFIELD, 1897]. Shell with rather wide radiating threads that cross widely spaced growth lines; muscle scars unknown. *U.Ord.,* N.Am.-Eu.——FIG. 46,*7*. **H. striatum,* Ky.; ×1.3.

Subfamily ARCHAEOPHIALINAE Knight & Yochelson, 1958

Shell deeply cup-shaped, with apex not quite central, offset toward anterior extremity; 6 or 8 muscle scars in shell, anterior ones differentiated from those behind. *M. Ord.-L.Dev.*

Archaeophiala PERNER, 1903 [**Patella antiquissima* HISINGER, 1837; SD KOKEN, 1925] [=*Scapha* HEDSTRÖM, 1923 (*non* HUMPHREY, 1797, *nec* MOTSCHULSKY, 1845, *nec* GRAY, 1847) (obj.); *Scaphe* HEDSTRÖM, 1923 (obj.); *Patelliscapha* TOMLEN, 1929, and *Paterella* HEDSTRÖM, 1930 (*pro Scapha* HEDSTRÖM, 1923) (obj.)]. Shell externally sugarloaf-shaped, with slightly anterior blunt apex; interior cup-shaped, with 6 pairs of pigmented dorsal muscle scars, those of anterior pair being compounded of 3 elements; each principal scar (except anterior) with supplementary shadow scar slightly in front and toward margin; ornament concentric lamellae. *Ord.,* Eu.——FIG. 48,*4*. **A. antiquissima* (HISINGER), U.Ord., Swed.; *4a,* right side view, ×1.3; *4b,* interior, showing paired muscle scars, compound scars at top, shadow scars outside main circle, ×1.8.

?**Micropileus** WILSON, 1951 [**M. obesus*]. Shell high cap-shaped, apex rather blunt, slightly anterior; muscle scars and ornament unknown. *M. Ord.,* N.Am.——FIG. 48,*2*. **M. obesus,* Can. (Ont.); side view of steinkern, ×1 (150).

?**Calloconus** PERNER, 1903 [**Palaeoscurria (Calloconus) humilis;* SD KNIGHT, 1937]. Shell cap- or cup-shaped, apex subcentral, blunt, pointing anteriorly; muscle scars unknown; ornament, many concentric imbricating lamellae. *L.Dev.,* Eu.——FIG. 48,*1*. **C. humilis* (PERNER), Czech.; left side, ×1.3.

Subfamily DRAHOMIRINAE Knight & Yochelson, 1958

Shell low, spoon-shaped; 7 pairs of elongate muscle scars in shell, situated at a high angle to apertural margin. *U.Sil.*

Drahomira PERNER, 1903 [**Tryblidium glaseri* PERNER, 1903]. Like *Trybilidium* and *Pilina* in shape but having 7 pairs of muscle scars, anterior pair larger than others and shaped somewhat like tadpole with tail to the rear and curving inward, next 5 pairs linear and arranged radially on each side of dorsum, posterior pair close together and of irregular pustulose shape; ornament broad, low undulating ribs radiating from the apex (114, p. 23). *U.Sil.,* Eu.——FIG. 48,*3*. *D. glaseri* (PERNER), Czech.; ×2.7.

Subfamily NEOPILININAE Knight & Yochelson, 1958

Shell low; aperture oval; apex just projecting over anterior margin; 5 or 6 pairs of muscle scars; ornament fine radial striae and growth lines. *Rec.*

Neopilina LEMCHE, 1957 [**N. galatheae*]. Shell exceedingly thin; aperture oval; asymmetrical, coiled protoconch; with bilaterally symmetrical paired muscles and gills, anterior mouth and posterior anus; circular, poorly muscled foot (9, p. 414). [This remarkable living representative of

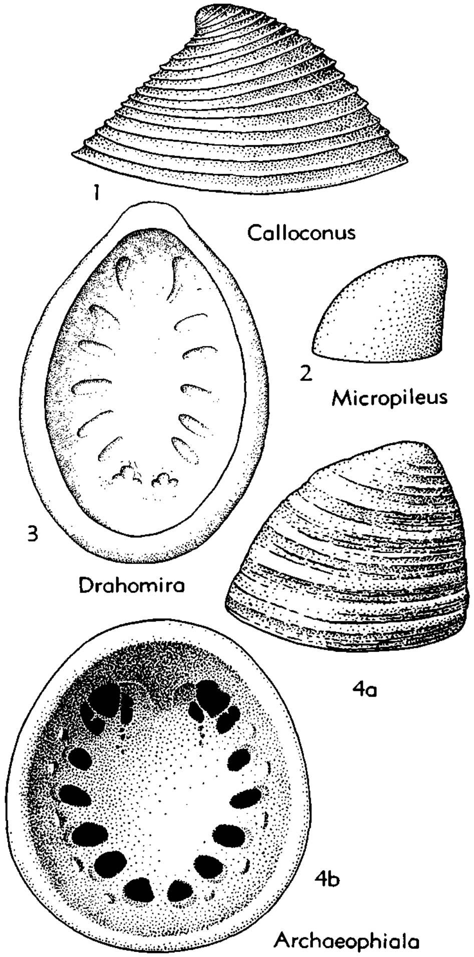

FIG. 48. Tryblidioidea; Tryblidiacea (Tryblidiidae) (p. 179).

a group supposedly extinct since early Devonian time will be described in detail by LEMCHE and co-workers in the *Galathea* reports. The asymmetrically coiled protoconch is considered a larval adaptation with little taxonomic significance.] *Rec.*, off W. coast of S.Am.

N. (Neopilina). Shell exceedingly thin, smooth and fairly low; protoconch asymmetrically coiled; with anterior mouth and posterior anus, five pairs of gills, and a poorly muscled foot. *Rec.*, off W. coast of C. Amer.——FIG. 48A*1*. **N. (N.) galatheae: 1a,* apical part of larval shell, ×3.5; *1b,c,* dorsal and ventral views of holotype, ×1, ×1.6; *1d,* ant. part of body, ×1.65 (9).

N. (Vema) CLARKE & MENZIES, 1959 [**N. (Vema) ewingi*]. Shell moderately thin, compressed and fairly high in early growth stages, more similar to typical subgenus at maturity, but lacking coiled protoconch and ornamented by numerous fine radial striae; with 6 pairs of gills (*Science*, 17 April 1959, p. 1026). *Rec.* off W. coast of Peru.——FIG. 48A,*2*. **N. (Vema) ewengi; 2a-c,* dorsal, lateral, ventral views of paratypes, ×5.3; *2d,* apical part of shell, enlarged (CLARKE & MENZIES, 1959).

Superfamily CYRTONELLACEA Knight & Yochelson, 1958

Shell strongly arched, but not completing one full whorl; apex and anterior margin of shell symmetrical with reference to main body of shell; at least 2 pairs of crescent-shaped shallow muscle scars present in shell. *L.Ord.-M.Dev.*

Family CYRTONELLIDAE Knight & Yochelson, 1958

With the characters of the superfamily. *L.Ord.-M.Dev.*

Cyrtonellopsis YOCHELSON, 1958 [**C. huzzahensis*]. Like *Cyrtonella* in overall shape, but lacking median dorsal crest; muscle scars unknown. *L.Ord.*, N.Am.——FIG. 49,*1*. **C. huzzahensis,* Mo.; *1a,b,* anterior and left side of steinkern, ×1.3.

Cyrtonella HALL, 1879 [**Cyrtolites? mitella* HALL, 1862; SD S.A.MILLER, 1889]. Shell cap-shaped, with apex extending forward about a half circle and marked by an obscure median dorsal crest; ornament rather small concentric lamellae with fine radiating threads between them; 2 symmetrical pairs of dorsal muscle scars are accompanied by 2 pairs of "shadow scars," as in *Archaeophiala,* but presence of other scars anterior to these not established; scars dorsal and quite unlike the single pair of lateral scars on the columella of bellerophonts. *Sil.-Dev.*, N.Am.——FIG. 49,*2*. **C. mitella* (HALL), *M.Dev.*, N.Y.; *2a,* right side; *2b,* dorsal view of steinkern showing 2 pairs of muscle scars with "shadow scars"; ×1.3.

?TRYBLIDIOIDEA INCERTAE SEDIS

Macroscenella WILSON, 1951 [**Metoptoma superba* BILLINGS, 1865]. Shell large, subconical; apex slightly excentric; aperture with slight invagination; muscle scars unknown; ornament cancellate. Shell not a smooth cone, locally with slight indentations and irregularities (150, p. 18). *M.Ord.*, N.Am.

Order ARCHINACELLOIDEA Knight & Yochelson, 1958

Shell shape varied but with apex presumed to be anterior; muscle scar (where known) ring-shaped or an incomplete ring and single pair of discrete muscle scars. *U.Cam.-L.Sil.*

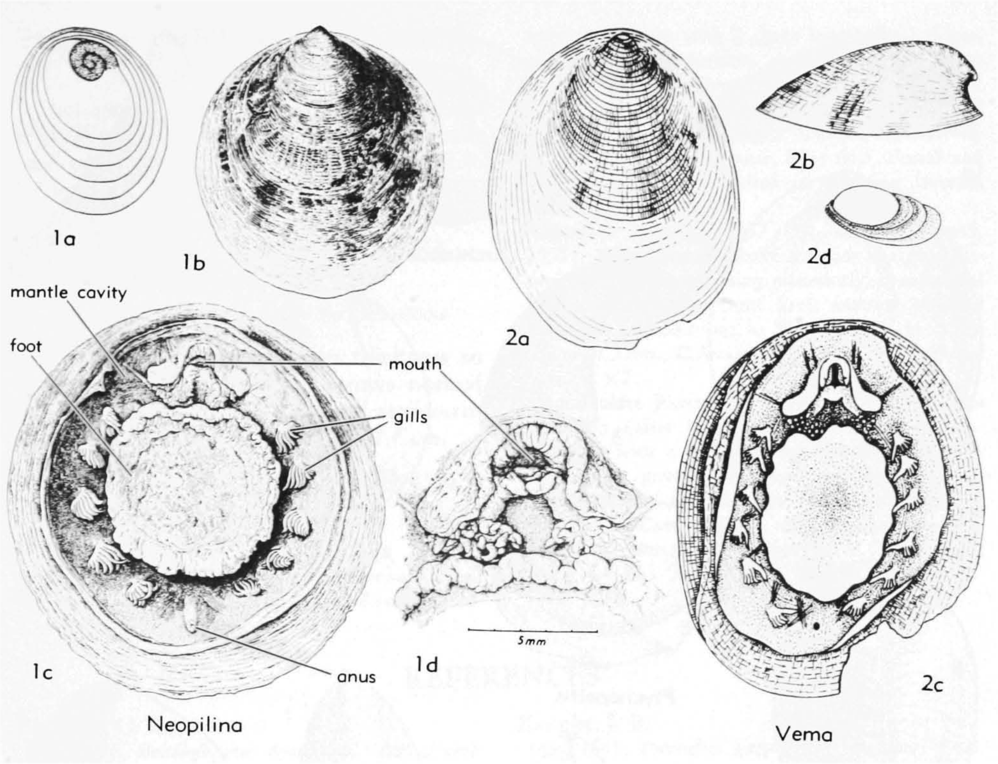

FIG. 48A. Tryblidioidea; Tryblidiacea (Tryblidiidae)—Neopilina, Rec., E.Pac., from deep water (p. *I*80).

Superfamily ARCHINACELLACEA Knight, 1956

With characters of the order. *U.Cam.-L.Sil.*

Family ARCHINACELLIDAE Knight, 1956

Shell low, spoon-shaped, apex strongly anterior, just overhanging margin of aperture. *M.Ord.-L.Sil.*

Archinacella ULRICH & SCOFIELD, 1897 [**A. powersi*]. Shell form as in *Pilina* but with muscles forming a continuous scar below apex, possibly open posteriorly with pair of discrete muscles located in the opening; surface marked by widely spaced growth lines. *M.Ord.-L.Sil.*, N.Am.-Eu.——FIG. 50,*1*. **A. powersi*, M.Ord., Wis.; *1a*, left side; *1b*, apertural view; *1c*, posterior side looking obliquely toward aperture; all ×1.3.——FIG. 50, *4*. *A. patelliformis* (HALL), *M.Ord.*, N.Y.; steinkern showing muscle scar, ×1.3.

?Ptychopeltis PERNER, 1903 [**P. incola*]. Shell thin, saddle-shaped, with greatly convex longitudinal profile and strongly convex transverse profile; apex small, blunt, presumably anterior; musculature unknown; steinkerns show numerous fine radiating threads near aperture where shell probably is thinnest. *M.Ord.*, Eu.——FIG. 50,*7*. **P. incola*, Czech.; ?left side steinkern, ×1.3.

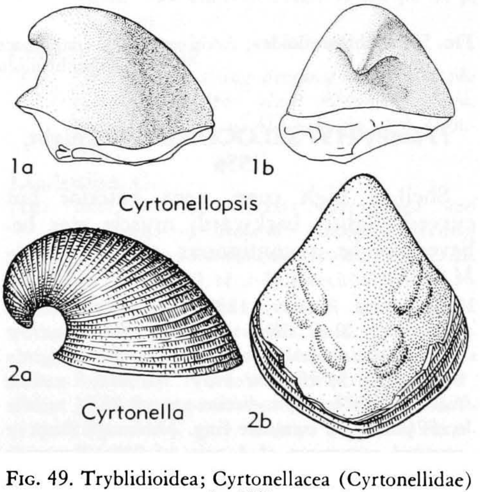

FIG. 49. Tryblidioidea; Cyrtonellacea (Cyrtonellidae) (p. *I*80).

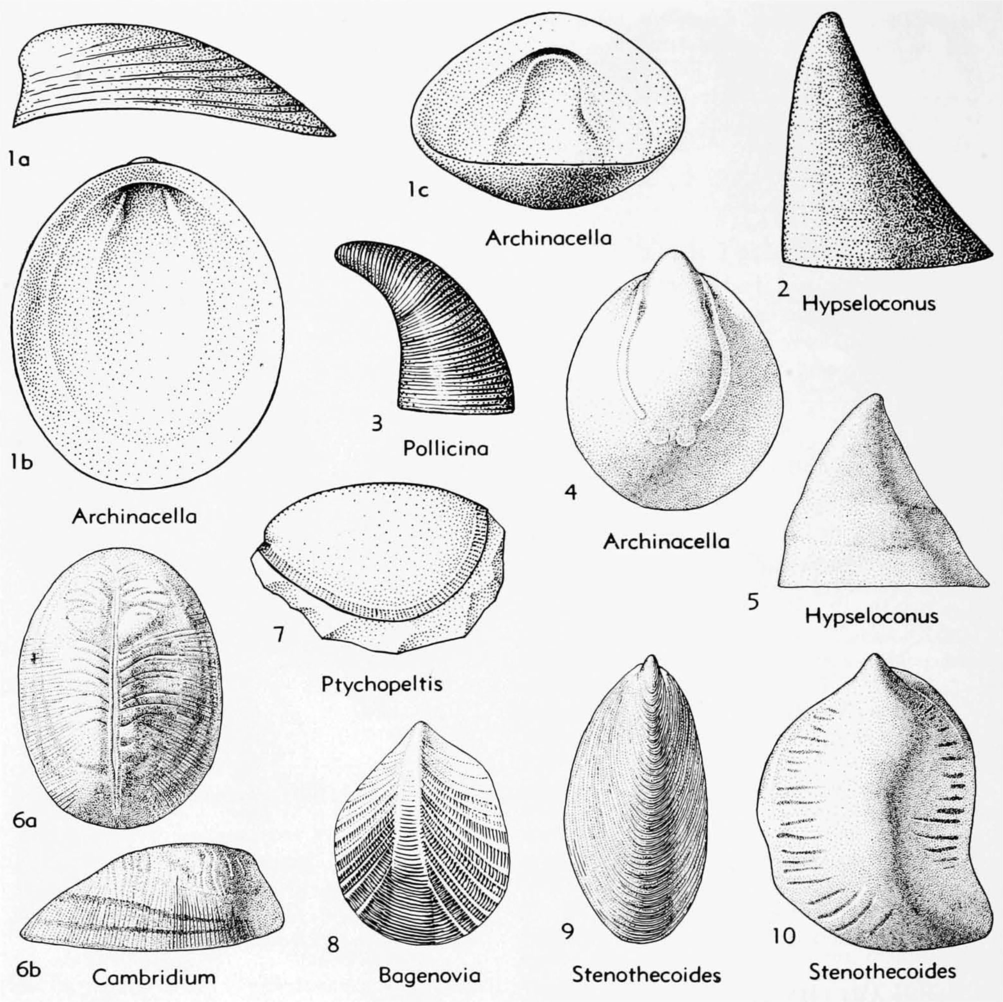

Fig. 50. Archinacelloidea; Archinacellacea (Archinacellidae, Hypseloconidae). Cambridioidea; Cambridiiacea (Cambridiidae) (p. *1*81-*1*83).

?Family HYPSELOCONIDAE Knight, 1956

Shell a high cone, apex anterior but curved slightly backward; muscle scar believed to be a continuous ring. *U.Cam.-M.Ord.*

Hypseloconus Berkey, 1898 [**H. recurvus* var. *elongatus*]. Shell thin, with apex above narrow (presumed anterior) extremity and curved slightly backward; form extremely variable; surface marked only by faint, distant growth lines; muscle scars possibly a complete ring. [Although Berkey reported occurrence of 6 pairs of scars, Knight's examination of his specimens, including those figured as showing muscle scars, fails to confirm this.] *U.Cam.-L.Ord.*, N.Am.——Fig. 50,*2*. **H. elongatus*, U.Cam., Wis.; ?left side, ×0.7.——50,*5*. *H.* sp., L.Ord., Mo.; steinkern showing supposed muscle scar, ×1.3.

?**Ozarkoconus** Heller, 1954 [1956] [**O. prearcuatus*]. With high, conical slightly curved, cap-shaped shell; aperture oval; ornament longitudinal costae or threads. Muscle scars unknown. *L.Ord.*, N.Am.

?**Pollicina** Holzapfel, 1895 [**Cyrtolithes corniculum* Eichwald, 1860 (*pro Cyrtoceras laeve* Murchison in Eichwald, 1842 (*non* Sowerby, 1839)]. Shell with rather blunt apex; surface marked by fine concentric threads; muscle scars unknown. *M.Ord.*, Eu.——Fig. 50,*3*. **P. corniculum* (Eichwald), Russ.; ?left side, ×1.

?Order CAMBRIDIOIDEA Horný, in Knight & Yochelson, 1958

Shell elongate, with strongly pointed apex, presumably anterior; some shells with marked deviation from bilateral symmetry. *L.Cam.-M.Cam.*

Superfamily CAMBRIDIACEA Horný, 1957

[*nom. transl.* Knight & Yochelson (*ex* Cambridiidae Horný, 1957)]

Interior of shell varying in thickness so that numerous ridges and furrows normal to edges of aperture appear on steinkern; muscle scars unknown. *L.Cam.-M.Cam.*

Family CAMBRIDIIDAE Horný, 1957

With characters of superfamily. *L.Cam.-M.Cam.*

Cambridium Houný, 1957 [**C. nikiforovae*]. Shell symmetrical to asymmetrical, aperture suboval; interior of dorsum with 2 sharp longitudinal ridges, end ridges and furrows curving outward from median part of these ridges; numerous finer ridges and furrows near edges of margin, and essentially normal to margin. *L.Cam.*, N.Asia.——Fig. 50,*6*. **C. nikiforovae,* Sib.; *6a,b,* dorsal and right side views of steinkern showing internal markings, ×2.

?**Bagenovia** Radugin, 1937 [**B. sajanica* Horný, 1957]. Apex directly above anterior margin; distinct dorsal keel widening posteriorly, ornamented by costae radiating from keel; interior of shell unknown. [According to Horný, may be a bivalve.] *L.Cam.*, C.Asia.——Fig. 50,*8*. **B. sajanica* Horný, ×2.

Stenothecoides Resser, 1938 [**Stenotheca elongata* Walcott (after Horný)]. Shell distinctly asymmetrical; with a sharp median dorsal crest; ornamented by growth lines only; interior of shell bearing ridges and furrows normal to edges of aperture. *L.Cam.-M.Cam.*, N.Am., Asia.——Fig. 50,*9*. **S. elongata* (Walcott), M.Cam., Nev.; ×5.3.——Fig. 50,*10*. *S.* sp., M.Cam., Can., steinkern, ×3.3.

REFERENCES

Boettger, C. R.

(1) 1956, *Beiträge zur Systematik der Urmollusken (Amphineura):* Zool. Anzeiger, Suppl. Band, v. 19, p. 223-256 (Leipzig).

Eichwald, Edouard d'

(2) 1842, *Die Urwelt Russlands, durch Abbildungen erläutert:* Nat- und Heilkunde K. med. chirur. Akad. St. Petersburg, Zeitschr., Heft 2, p. 115-210.

Heller, R. L.

(3) 1956, *Stratigraphy and paleontology of the Roubidoux Formation of Missouri:* Missouri Bur. Geol. Survey & Water Resources, ser. 2, v. 35, 118 p., 19 pl. (Rolla). [Heller's publication did not appear in 1954 as shown on the title page. It was delivered to the Missouri State Geologist on December 20, 1955, but distribution was not begun until January, 1956—J. B. Knight.]

Horný, Radvan

(4) 1955, *Tryblidiinae Pilsbry, 1899 (Gastropoda) from the Silurian of central Bohemia:* Sborník Uštředního ústavu geologického oddíl paleontologický [Service géologique de Tchecoslovaquie, Sec. de paléontologie], v. 22, p. 73-88 (Czech), 90-96 (Russ.), 97-102 (Eng.), pl. 9-12 (Praha).

(5) 1957, *Problematic molluscs (?Amphineura) from the Lower Cambrian of south and east Siberia (U.S.S.R.):* Same, v. 24, p. 397-413 (Czech), 414-422 (Russ.), 423-432 (Eng.), pl. 20-23.

Knight, J. B.

(6) 1941, *Paleozoic gastropod genotypes:* Geol. Soc. America, Spec. Paper 32, 510 p., 96 pl., 32 fig. (New York).

(7) 1952, *Primitive fossil gastropods and their bearing on gastropod classification:* Smithson. Misc. Coll., v. 117, no. 13 (Publ. 4092), 56 p., 2 pl. (Washington).

———, & Yochelson, E. L.

(8) 1958, *A reconsideration of the Monoplacophora and the primitive Gastropoda:* Malac. Soc. London, Proc., v. 33, pt. 1, p. 37-48, pl. 5.

Lemche, Henning

(9) 1957, *A new living deep-sea mollusc of the Cambro-Devonian class Monoplacophora:* Nature, v. 179, p. 413-416, fig. 1-4 (London).

Lindström, G.

(10) 1884, *On the Silurian Gastropoda and Pteropoda of Gotland:* Kungliga Svenska Vetenskaps-Akademiens Handlinger, v. 19, no. 6, p. 1-250, pl. 1-21 (Stockholm).

Perner, Jaroslav

(11) 1903, *Bellerophontidae:* in Barrande, Joachim, Système silurien du centre de la Bohême, p. 1-164, pl. 1-89 (Praha).

(12) 1907, Same, v. 2, text, p. 1-380, pl. 90-175.

(13) 1911, Same, v. 3, text, p. i-xvii, 1-390, pl. 176-247.

Rasetti, Franco

(14) 1954, *Internal shell structures in the Middle*

Cambrian gastropod Scenella and the problematic genus Stenothecoides: Jour. Paleont., v. 28, no. 1, p. 59-66, pl. 11-12 (Tulsa).

Rusconi, Carlos

(15) 1954, *Fosiles Cambricos y Ordovicos de San Isidro:* Bull. paleontologico de Buenos Aires, no. 30, 4 p.

Wenz, Wilhelm

(16) 1940, *Ursprung und frühe Stammesgeschichte der Gastropoden:* Arch. Molluskenkunde, v. 72, p. 1-10 (Frankfurt a.M.).

(17) 1938-44, *Gastropoda. Allgemeiner Teil und Prosobranchia:* in O. H. Schindewolf, ed., Handbuch der Paläozoologie, v. 6, pt. 1-7, 1639 p. (Berlin).

Wilson, A. E.

(18) 1951, *Gastropoda and Conularida of the Ottawa Formation of the Ottawa-St. Lawrence Lowland:* Geol. Survey Canada, Bull. 17, 149 p. (Ottawa).

Yochelson, E. L.

(19) 1958, *Some Lower Ordovician monoplacophoran mollusks from Missouri:* Washington Acad. Sci., Jour., v. 48, no. 1, p. 8-14, fig. 1-13.

GASTROPODA

GENERAL CHARACTERISTICS OF GASTROPODA

By L. R. Cox[1]

CONTENTS

---

[1] British Museum (Natural History), London, England.