Dipteropeltis CALMAN, 1912, p. 766 [**D. hirundo*; OD] [=*Talaus* MOREIRA, 1913; *Moreiriella* MELLA LEITÃO, 1914]. Antennules and antennae minute, imperfectly segmented, maxillules developed as suckers; preoral sting reduced; alae greatly elongate. *Rec.*, S.Am.

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CIRRIPEDIA

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CONTENTS

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[4] A *Treatise* chapter on the Cirripedia Thoracica was prepared (1953) by T. H. WITHERS. Following his death, this manuscript was revised and enlarged by NEWMAN and ZULLO. They also added sections on methods, anatomy of soft parts, life histories and evolution of the Thoracica, and sections on systematics of the remaining orders (Apoda, Ascothoracica, Acrothoracica and Rhizocephala), thus forming an integrated treatment of the entire class. The completed typescript and illustrations were received in December, 1967.—EDITOR.

ACKNOWLEDGMENTS

We have expressed our personal thanks and appreciation to many persons, and wish it were possible to do so again here. Regardless of limitation on space, we must mention our gratitude to our editor, Professor R. C. MOORE, for his relentless and high spirited encouragement, critical supervision and advice, and to his staff for careful attention to virtually all figures and other aspects of assembling the manuscript. We would also like to thank Mr. ARNOLD ROSS for his critical and helpful reading of the entire galley proof, Dr. J. T. TOMLINSON for allowing us to use his manuscript classification of the Acrothoracica and Drs. P. REISHMAN and J. BOCQUET-VÉDRINE for critically reviewing the classification of the Rhizocephala. We much appreciate the help of Drs. T. E. BOWMAN and A. G. HUMES in making decisions on certain quasi-rhizocephalans, and Drs. R. YANAGIMACHI and P. REISHMAN on the systematic position of *Thompsonia*. Many thanks are due Mrs. C. PLATT KOURTZ (SIO) for extensive and critical reference work, and for careful attention to countless details during the preparation of the manuscript. Support from the National Science Foundation is most gratefully acknowledged, W. A. N., GB-4937X; V. A. Z., GB-4507.

INTRODUCTION

HISTORICAL ACCOUNT

LINNÉ placed the Cirripedia in the class Testacea, along with most of the Mollusca. Cirripeds were not generally accepted as crustaceans until the discovery of the larvae and larval metamorphoses by J. VAUGHAN THOMPSON in 1829, even though their internal morphology was known to CUVIER, and though STRAUS had stressed their crustacean affinities as early as 1819.

It was CHARLES DARWIN who established the morphological nomenclature and systematic concepts upon which subsequent work was based. His two volumes on Recent cirripeds (1851,*38*; 1854,*39*) are among the finest morphological and systematic publications in zoological literature. Even after a lapse of more than a century, these works are still among the chief sources of reference.

Upon this basis, and the collections amassed by numerous biological expeditions of the turn of the century and early 1900's, a number of significant works appeared which refined and expanded our knowledge. Principal contributors include: ANNANDALE, AURIVILLIUS, BROCH, GRUVEL, KRÜGER, NILSSON-CANTELL, PILSBRY, WELTNER, and UTINOMI (=HIRO prior to 1939).

DARWIN also monographed the British fossil cirripeds *(37, 40)* but fossil representatives have not received nearly the attention given the extant fauna. Prior to 1928, the only other comprehensive works on fossil cirripeds were those of BOSQUET on Cretaceous fossils from Holland; SEGUENZA on Tertiary forms from Sicily and Italy; DE ALESSANDRI on Tertiary cirripeds from Italy; and WITHERS on Tertiary fossils from New Zealand.

Between 1928 and 1953 WITHERS published three monographs on fossil Cirripedia, including those of the Triassic and Jurassic (1928), the Cretaceous (1935) and the Tertiary (1953, exclusive of Balanomorpha and Verrucomorpha). Much of the data accumulated during the last twenty years on fossil Balanomorpha has come from the works of Davadie and Kolosvary. Significant papers on early cirripeds are those of Chernyshev (1930) on *Praelepas* (M.Carb., USSR), Wills (1963) on *Cyprilepas* (U.Sil., Estonia), and Tomlinson (1963) on *Trypetesa* (Penn., N.Am.).

Withers (1926) demonstrated the echinoderm affinities of the early Paleozoic Machaeridia, and thus removed these puzzling fossils from consideration as primitive cirripeds. Recently, Pope (1961) has shown the machaeridian family Lepidocoleidae to be cover plates of the brachial spines of carpoid echinoderms. Various Paleozoic fossils from the Silurian and Devonian of New York State have been attributed to the Cirripedia and proposed as ancestral stocks. These fossils, which include *Eobalanus* Ruedemann, *Eopollicipes* Ruedemann, *Palaeocreusia* Clarke, *Palaeopseudobalanus* Fisher, *Protobalanus* Whitfield, and *Strobilepas* Clarke, superficially resemble cirripeds, but on detailed examination exhibit no affinities with the group. For example, Ladd (1959) has shown that *Palaeocreusia* is not a cirriped, but more likely the shell of a fissurellid gastropod. Likewise, detailed examination of the shell of *Palaeopseudobalanus* reveals the stereome mesh structure characteristic of echinoderm plates. This structure, together with the arrangement of the imbricating whorls of plates suggests affinities with the machaeridians.

The present day has been described as the "Age of Barnacles," for these animals inhabit the shore line of every coast and are found from the surface to the greatest depths of the oceans. Explanation of the origins and development of this extant fauna requires detailed information on the fossil history of Cirripedia, and, conversely, an understanding of fossil cirripeds is best arrived at through knowledge of the living fauna. It is within this framework that the following synthesis is based. Additional references basic to cirriped systematics include the four monographs of Darwin *(37-40)* previously mentioned, the monographs by Gruvel (1905) and by Pilsbry (1907, 1916), and the synthesis of Krüger (1940) which includes a comprehensive bibliography to be consulted for many of the references cited herein.

Table 1. *Comparative segmentation of Malacostraca, Cephalocarida, Maxillopoda, and Ostracoda.*

			Maxillopoda				
	Malacostraca	Cephalocarida	Copepoda	Cirripedia	Mystacocarida	Ostracoda	
1	A′	A′	A′	A′	A′	A′	HEAD
2	A″	A″	A″	A″	A″	A″	
3	M	M	M	M	M	M	
4	M′	M′	M′	M′	M′	M′	
5	M″	M″	M″	M″	M″	?M″	
6	1P	1P	1P	1P ♀	1P	1P	THORAX
7	2P	2P	2P	2P	2P	2P	
8	3P	3P	3P	3P	3P	3P	
9	4P	4P	4P	4P	4P ⚥	4 ⚥	
10	5P	5P	5P	5P	5P	T+F	
11	6P ♀	6P ♂	6P	6P	6		
12	7P	7P	1 ⚥	1 ♂	1		
13	8P ♂	8P	2	2	2		
14	1P	1P ♀	3	3	3		ABDOMEN
15	2P	2	4	4	4		
16	3P	3	5T+F	5T+F	5T+F		
17	4P	4					
18	5P	5					
19	6P	6					
20	7	7					
21	8T+F	8					
22		9					
23		10					
24		11					
25		12T+F					

[Explanation: A′, first antenna; A″, second antenna; M, mandible; M′, first maxilla; M″, second maxilla; P, pod; T, telson; F, furca.]

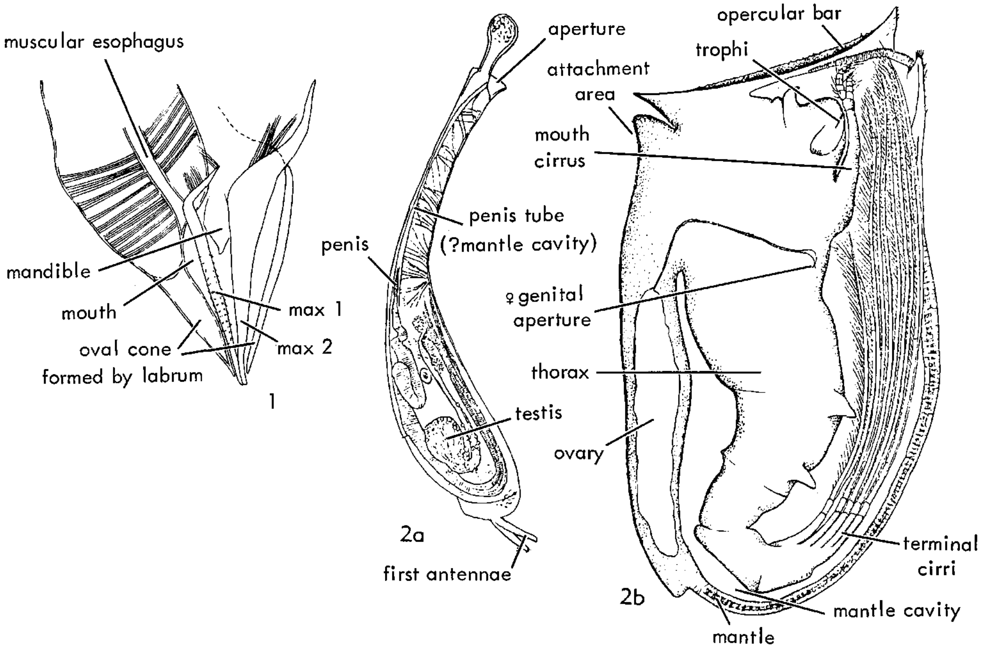

FIG. 80. Morphology of cirripeds.

1. Arrangement of biting mouth parts in female ascothoracican, *Synagoga metacrinicola* OKADA, ×50 (after Okada, 1939).

2. General anatomy of acrothoracican, *Berndtia purpurea.*——*2a.* Male, ×47 (after *103a*).——*2b.* Female, ×20 (*105,* mod.).

DEFINITION OF CIRRIPEDIA

The Cirripedia comprise a diverse and conspicuous group of sedentary marine Crustacea. The fundamental body plan is that of the Maxillopoda[1] (DAHL, 1956): five head and six thoracic appendage-bearing somites; and five abdominal somites, the last bearing a furca (Table 1). Parasitism has evolved in four of the five orders, and in one has resulted in appendageless forms unrecognizable as cirripeds except for their characteristic naupliar and cyprid larval stages.

Attachment in cirripeds occurs during the cyprid stage and is effected initially by the first antennae. The bivalved cyprid carapace is homologous with the so-called mantle of the adult, and it forms the mantle cavity enclosing the appendage-bearing portions of the body of the adult. The mantle itself is either membranous, armed with chitinous spines, or more or less covered with calcareous plates. Food is obtained by setose feeding with the thoracic appendages in nonparasitic forms. Parasitic forms feed by piercing mouth parts; by absorption through cephalic or derived root systems; or through the surface of the carapace.

Sexes are separate or combined. The male genital apertures open on the first abdominal somite, or the last thoracic somite when the abdomen is reduced. The female genital apertures open on the first thoracic somite, near the basis of the first cirri, and this is the most anterior position occupied by genital apertures in any known crustacean. Eggs are laid and retained in the mantle cavity of the female or hermaphrodite, where they develop before being released, usually as planktonic nauplius larvae.

Five orders are generally recognized as Cirripedia: 1) Acrothoracica, 2) Rhizocephala, 3) Ascothoracica, 4) Thoracica, 5) Apoda. The placing of the last among the cirripeds appears to be questionable, however.

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[1] Not recognized in *Treatise* classification. According to DAHL (1963, p. 1) includes Mystacocarida, Copepoda, Branchiura, and Cirripedia, but branchiurans are omitted in Table 1 of this chapter.—Ed.

GENERAL FEATURES OF ORDERS

1) The Acrothoracica are free-living, burrowing cirripeds. Extant species are found in shells of bivalve and gastropod mollusks, living and dead corals, and limestone. Fossils are known only by their burrows that occur in a variety of invertebrate skeletons (see "Fossil Traces"), the earliest having been found in Pennsylvanian pelecypod shells. The anatomically most primitive or unmodified living genus is *Weltneria* BERNDT.

Sexes are separate in all known Acrothoracica. Females excavate individual burrows where they are usually accompanied by one or more minute males (Fig. 80,*2a,b*).

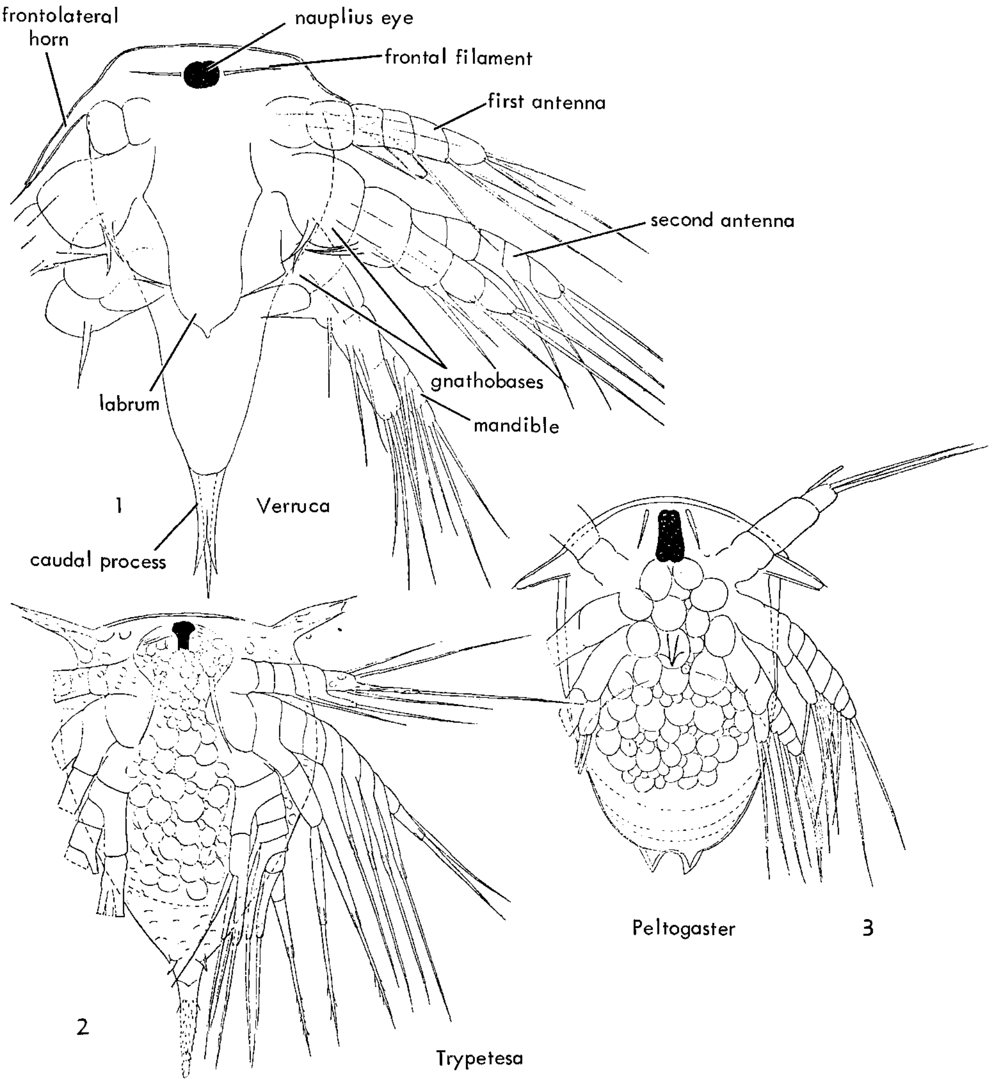


FIG. 81. Morphology of cirripeds; nauplius larvae (mod. from *61*).

1. Thoracican, *Verruca (Verruca) stroemia* (MÜLLER), stage 1 nauplius, ×267.
2. Acrothoracican, *Trypetesa lampas* (HANCOCK), ×107.
3. Rhizocephalan, *Peltogaster sulcatus* LILLJEBORG, ×189.

The male consists of little more than a sac of gametogenic material, sometimes provided with a visible copulatory apparatus. The life cycle includes nauplius and cyprid stages, although the former may be passed through in the egg. The female cyprid settles and initially becomes attached by its first antennae. In general, while in the process of metamorphosis, the cyprid begins to burrow mechanically into the substratum. The first antennae are left at the exterior attachment point, as the burrow becomes occupied.

In the adult, the mantle sac lines the burrow and opens to the exterior through an aperture at the entrance. The sac commonly is cemented to the wall of the burrow by the anterior end (attachment disc). The animal resides within the cavity formed by the mantle. The mouth field is made up of the labrum, the usual three pairs of mouth parts, and the first pair of cirri (mouth cirri) which are reduced in size and situated along the posterolateral margins of the oral cone. A maximum of five pairs of cirri are situated in a group at the posterior end of the thorax, and a pair of anal or caudal appendages may be present. The abdomen, present in the cyprid, is completely wanting. The most complete recent anatomical studies have been made on *Berndtia* by UTINOMI (1957, 1960, 1961).

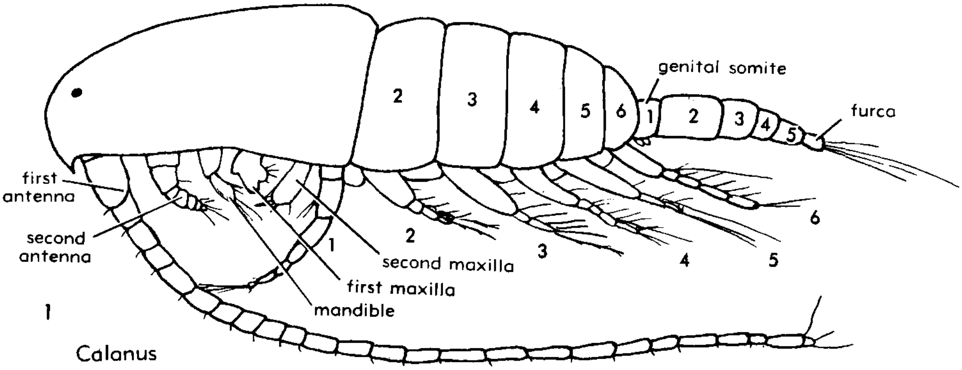
2) The Rhizocephala are parasites primarily of decapod crustaceans. In general, the cyprid seeks out and attaches itself to the host. Metamorphosis proceeds and a larval form known as kentrogon is developed that invades and ramifies through the tissues, usually resulting in parasitic castration of the host. Reproductive structures appear on the surface of the host after the nutritive structures have become well developed. The mantle, mantle cavity or brood chamber, ovaries and nervous elements of the reproductive body of the rhizocephalan are considered homologous with these structures in other cirripeds. However, the Rhizocephala are so modified that virtually no characteristics identify them as arthropods, much less crustaceans, other than their larval forms which are comparable to those of the acrothoracican and thoracican Cirripedia (Fig. 81,*3*).

Recent work has demonstrated that some species previously thought to be hermaphroditic have separate sexes. The female parasitizes the host while the male exists as a mass of spermatogenic material delivered to the female by the male cyprid larva (YANAGIMACHI, 1961). Another recently investigated rhizocephalan has been found to lack kentrogon and consequently to be externally parasitic (BOCQUET-VÉDRINE, 1961). BOSCHMA (1925 to date) can be consulted for taxonomic details of the group. A comprehensive bibliography is given in Zool. Meded. *39:* xli-xlvi, 1964.

3) The Ascothoracica are parasitic on hexacorals and echinoderms. The order is ranked by some workers among the Cirripedia, and by others as a separate subclass of crustaceans, the Ascothoracida WAGIN. The least specialized forms have separate sexes, a life cycle including nauplius and cyprid larvae, a head reduced in the same manner as in ordinary cirripeds, an initial attachment by prehensile first antennae, and the same unique position of the female genital aperture as in other cirripeds (Fig. 82). Differences that have been utilized to separate them from the cirripeds are for the most part secondary and therefore of no great weight in a diagnosis of a separate subclass. We therefore have retained the Ascothoracica as an order of the Cirripedia.

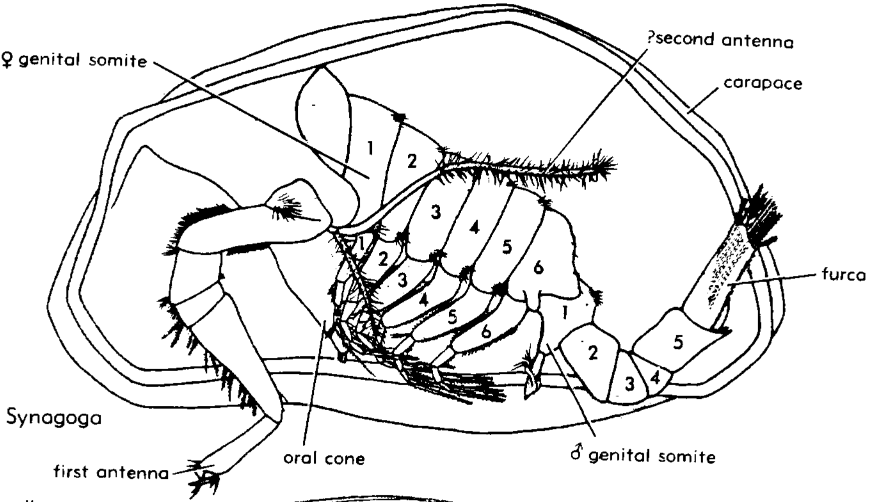
The adult consists of a bivalved carapace gaping ventrally, permeated by gastric ceca, and provided with a postoral adductor muscle. The prosoma supports the prehensive first antennae, succeeded by a pair of filamentary appendages which have been interpreted as rudiments of the second antennae. The second antennae are usually lost in ordinary barnacles, appearing only in the nauplius and as rudiments in certain cyprids.

The mouth field is produced into an oral cone formed by the labrum, mandibles and two pairs of maxillae, and is apparently adapted to piercing and sucking (Fig. 80, *1*). The thorax supports six biramous, natatory appendages. The abdomen of five somites is well developed in many species; the first somite supporting a penis or rudiment thereof, the last the furca. This is



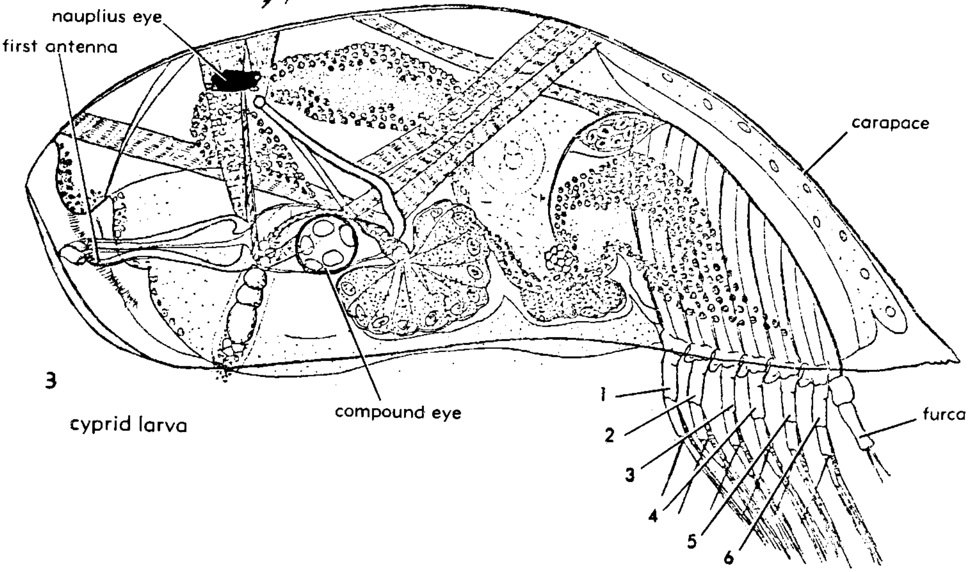
1

Calanus



2

Synagoga



3

cyprid larva

the most generalized somite pattern found in the cirripeds and corresponds to that of the unspecialized Copepoda (cf. Fig. 82, *1-3*). Hermaphroditism is apparently secondarily acquired. There are no fossils, although VOIGHT (1959) has described cysts in a Cretaceous octocoral; and MADSEN & WOLFF (1965) describe scars in an Upper Cretaceous echinoid they suggest were caused by ascothoracicans. WAGIN (1946) and BRATTSTRÖM (1947, 1948) can be consulted for systematic and biological aspects of the order.

4) Most Thoracica are free-living or commensal cirripeds found attached to a variety of living and inanimate substrata. They gain their greatest diversity in shallow waters but representatives are found at all depths. The earliest undoubted fossils *(Cyprilepas)* are found in the Silurian, but it is not until the Mesozoic that fossils become numerous. These are stalked forms belonging to the suborder Lepadomorpha (Fig. 83,*1,3a,b*). The Cenozoic marks the advancement of the sessile barnacles of the suborder Balanomorpha, an expansion that has continued through to the present time (Fig. 83,*2*).

Most of the Thoracica are hermaphroditic, with internal fertilization. There is evidence for self-fertilization, but cross fertilization is generally the rule. The Scalpellidae and Iblidae, among the Lepadomorpha, have species in which sexes are separate or combined; reduced attached males occurring with females; or complemental males with hermaphrodites; or all individuals are hermaphrodites. The Balanomorpha were thought to be exclusively hermaphroditic. Recently, however, complemental males were discovered in a species of *Balanus* (HENRY & MCLAUGHLIN, 1965).

The life cycle of the Thoracica is comparable to that of the Acrothoracica, including nauplius and cyprid stages. Anatomically the adult differs primarily in having the cirri nearly evenly distributed along the thorax, the mandibular palp associated more closely with the lateral margin of the labrum than with the mandible, and in not molting the exterior of the mantle along with the exoskeleton lining the mantle cavity and covering the appendages. This last feature is correlated with the ability to build up a permanent calcareous armament. Further details of structure will be taken up in the following section.

5) The Apoda was established by DARWIN to accommodate a curious parasite, *Proteolepas bivincta* DARWIN, found in the mantle cavity of the pedunculate barnacle *Heteralepas cornuta* (DARWIN) from the West Indies (Fig. 84). *Proteolepas* has not been seen since DARWIN described it. Because its segmentation can be interpreted as that of a copepod, or possibly a malacostracan (epicaridean), rather than that of a cirriped, it is presently considered to be an organism of unknown affinities. Therefore, the Apoda, and the larval forms attributed to it by HANSEN, STEUER, and MCMURRICH, are retained *incertae sedis* in the Cirripedia only as a matter of convenience.

MORPHOLOGY OF THORACICA

GENERAL FEATURES

Thoracican cirripeds are sedentary animals. When at rest, the body and appendages are enclosed within a "mantle" formed by bilateral folds of the carapace. The mantle is usually protected externally by a number of calcified plates (Fig. 83, 85). In the adult stage, the animal is attached to the substratum by the anterior part of the cephalic region. The first antennae and their associated cement glands form the

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(See facing page.)

FIG. 82. Comparison of maxillopodan body plan of copepod with that of ascothoracan and thoracican cyprid larva.

1. Male *Calanus*, ×32 *(23)*.
2. Male *Synagoga metacrinicola* OKADA, ×25 (after Okada, 1939).
3. Cyprid larva, *Trypetesa lampas* (HANCOCK), ×233 (after Kühnert, 1935, in *61*).

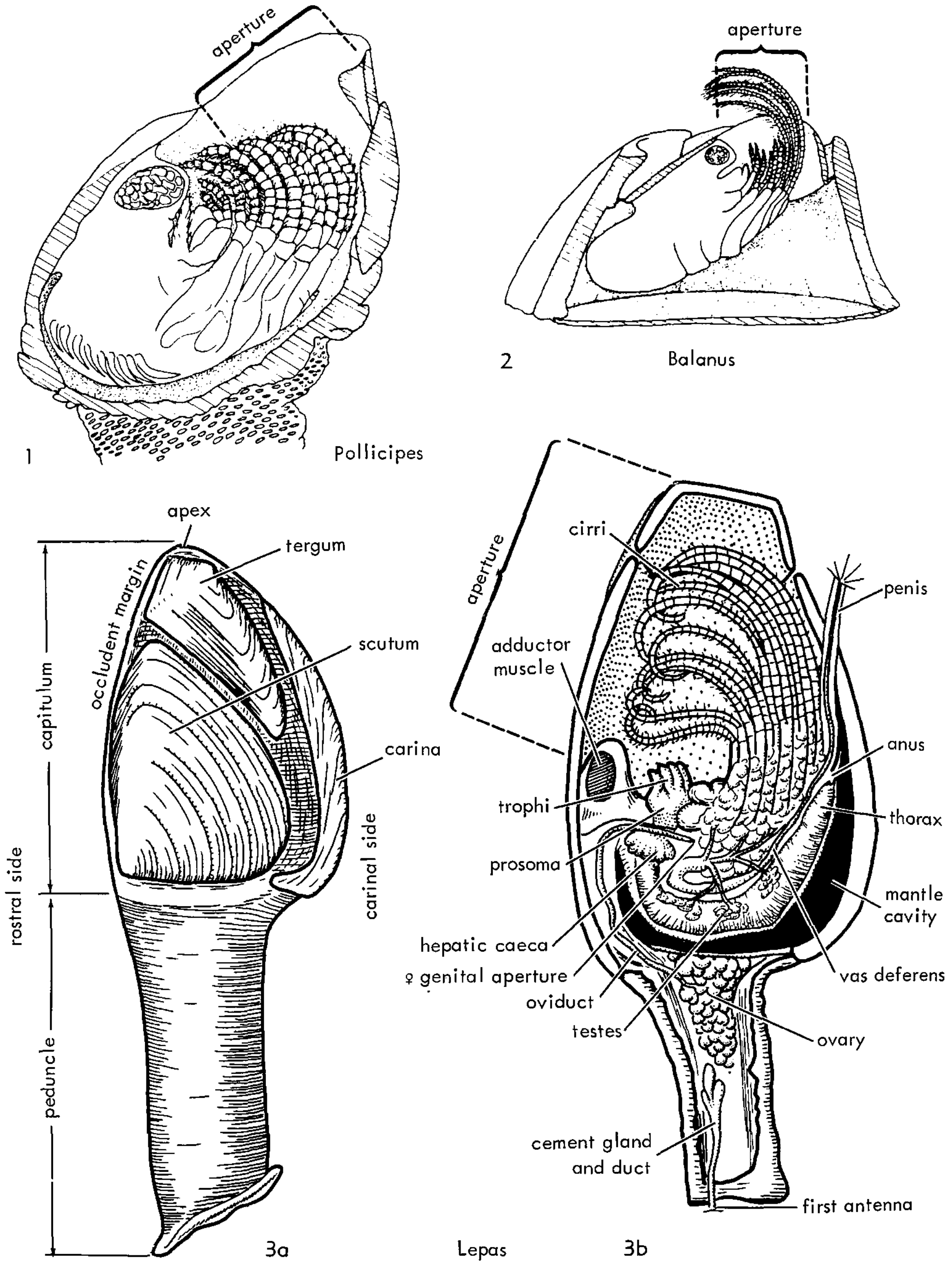

FIG. 83. Morphology of cirripeds; body plan of lepadomorphs compared with that of balanomorph.

1. Lepadomorph (Scalpellidae), *Pollicipes polymerus* SOWERBY, with right side of capitulum removed, ×2.4 (Newman, n).
2. Balanomorph (Balanidae), *Balanus (Balanus) amphitrite* DARWIN, with right side of wall and lining of mantle cavity removed, ×2.4 (Newman, n).
3. Lepadomorph (Lepadidae), *Lepas.——3a. L. (L.) hillii* LEACH, outer view of individual from right side, ×2 (after Darwin).——*3b. L. (L.)* sp., dissection from right side, ×2.5 (after Claus).

initial attachment of the free-living cyprid larva. After metamorphosis, the base of the peduncle in the Lepadomorpha, or where the margin of the wall meets the basis in Verrucomorpha and Balanomorpha, take over the function of attachment and cement the animal in place.

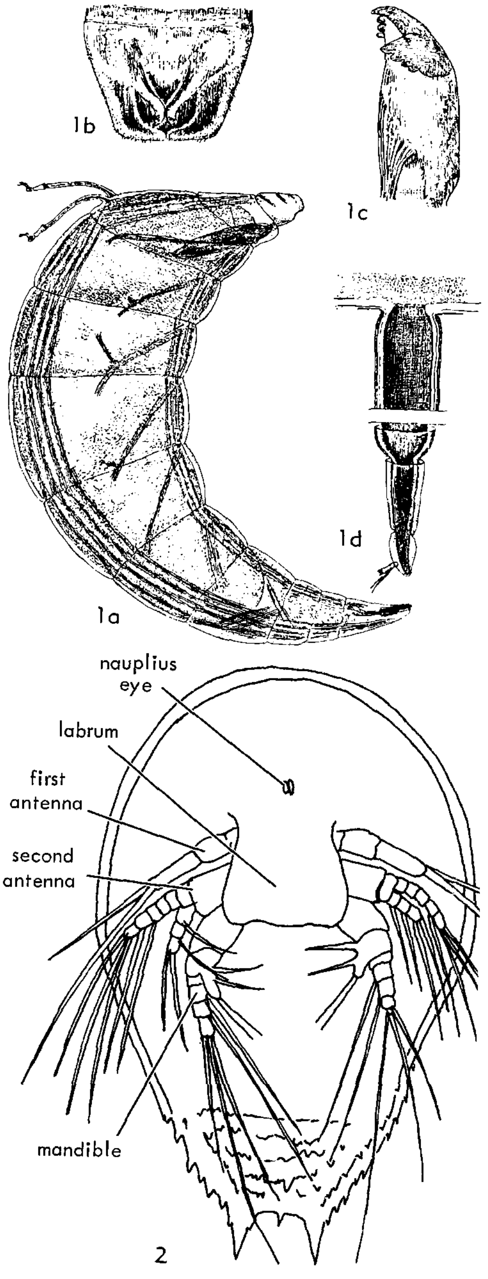

FIG. 84. Morphology of Apoda.——*1. Proteolepas bivincta* DARWIN; *1a,* hermaphrodite, ×17; *1b,* mouthfield, enl.; *1c,* "compound mandibular organ," greatly enl.; *1d,* "first antenna," greatly enl. (after Darwin).——*2.* HANSEN'S "Y" larva, supposed larva of the Apoda, ×240 (after *51*).

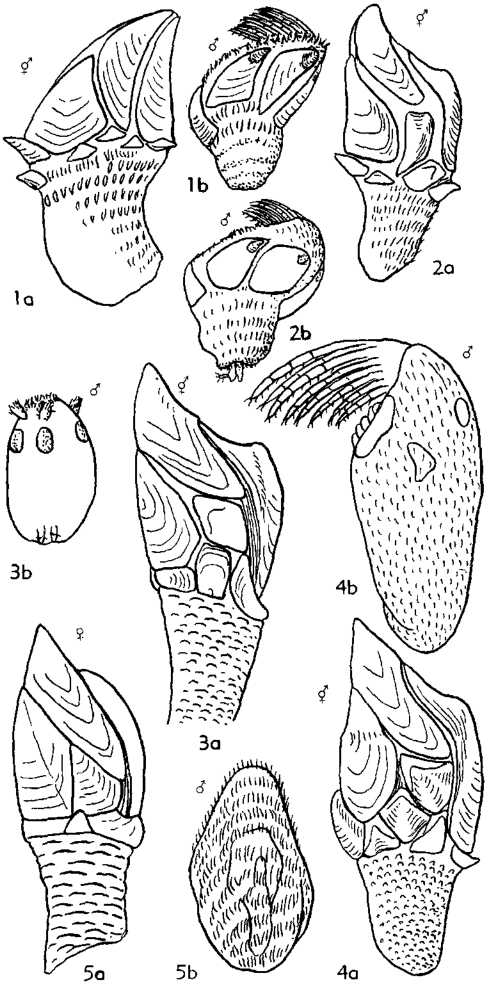

FIG. 85. Morphology of cirripeds. Sexuality in scalpellid genera, individuals viewed from right side, hermaphrodites *(1a-4a)* and their complemental males *(1b-4b)* and a female *(5a)* with dwarf male *(5b)* (males greatly enl.) (from Pilsbry, after Withers).——*1a,b. Calantica (Calantica) villosa* (LEACH).——*2a,b. Smilium peroni* GRAY.——*3a,b. Scalpellum scalpellum* (LINNÉ).——*4a,b. Euscalpellum rostratum* (DARWIN).——*5a,b. Acroscalpellum velutinum* (HOEK).

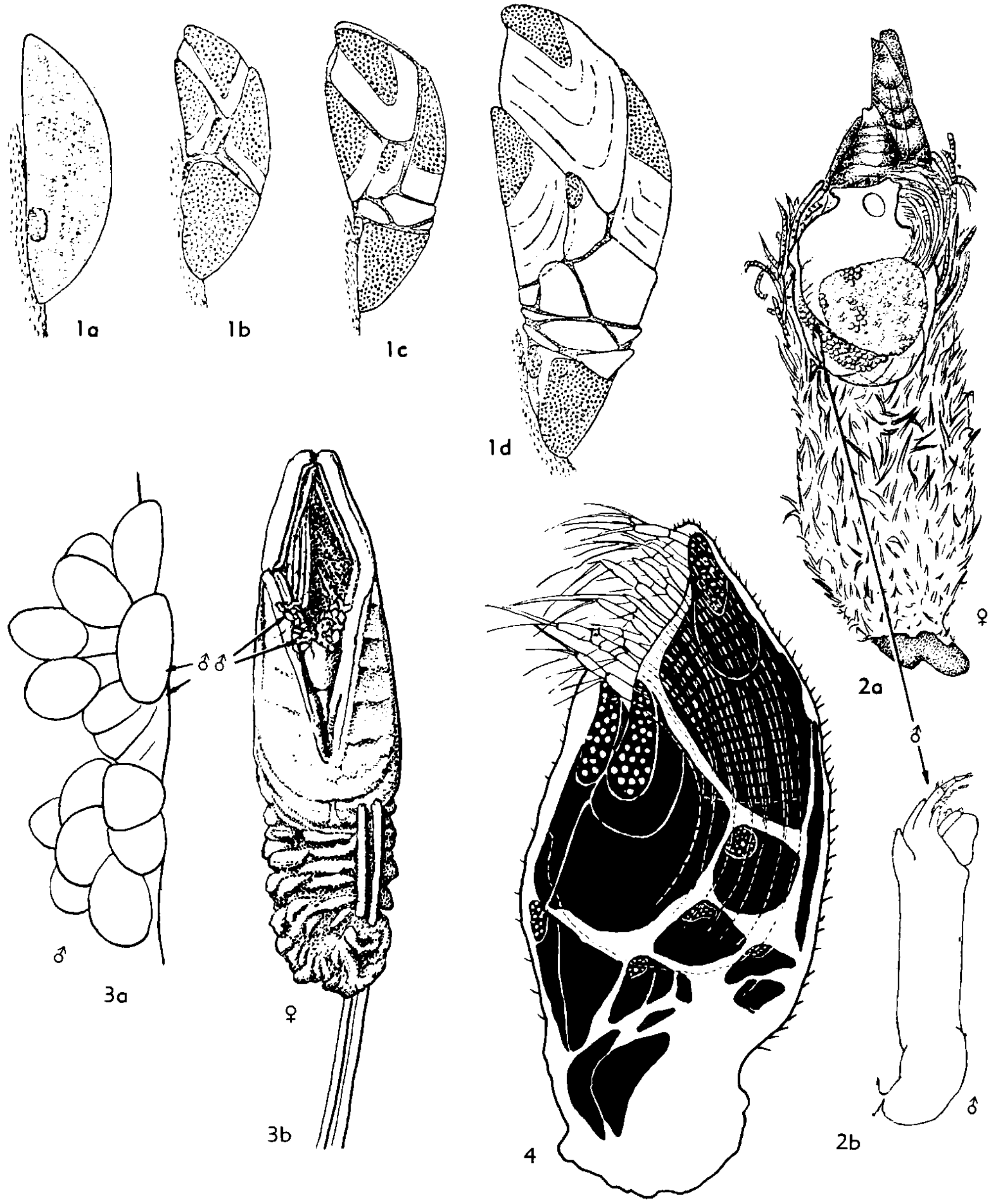

FIG. 86. Morphology of cirripeds. Ontogeny and sexuality.

1. Ontogeny of *Arcoscalpellum balanoides* (HOEK), illustrating appearance of additional primordia over basic number of five, ×50 (after *22*).——*1a.* Newly settled cyprid larva.——*1b.* Cyprid shell cast, six primordia visible including that for upper latus and one each for dorsal and ventral peduncular scales, inframedian latus and carinal latus appearing as calcified plates without primordial precursor.——*1c.* Later stage, rostral latus appearing without primordial precursor.——*1d.* Still later stage showing appearance of additional peduncular plates and continuing calcification of capitular plates, carrying primordia apically at their umbones.
2. *Ibla cumingi* DARWIN.——*2a.* Female, ×4.5 (right side of capitulum cut away, male and ovigerous lamellae seen *in situ*).——*2b.* Dwarf male, viewed from left side, ×18 (Newman, 1960).

The cephalic region in Lepadomorpha is developed into a more or less flexible stalk or **peduncle**. In the sessile forms Balanomorpha and Verrucomorpha, the anterior region is represented by a flattened disc or **basis**. The homology of these two regions in pedunculate and sessile forms was demonstrated by DARWIN (1851-54), who observed in both groups that initial attachment was made by the first antennae of the cyprid larva, and that traces of these appendages were located centrally, embedded in the cement of the attachment disc.

In the pedunculate cirripeds, the mantle, with or without its protective plates, is termed the **capitulum** (Fig. 83,*3a*). The body occupies the cavity formed by the capitulum, where it lies attached at the scutal margin in a curved position. The long axis of the body is curved, but for the most part, it is oriented at right angles to the long axis of the animal when at rest. Because of this distortion in the relationship of one part of the animal to the other, confusion arises if ordinary terms of orientation are followed. It therefore has been customary in describing cirripeds to use the arbitrary terminology established by DARWIN. By convention, pedunculate cirripeds are illustrated in an upright position, with the capitulum above and the peduncle below, so that the animal is effectively "standing on its head." In this position, what would be anatomically equivalent to the ventral surface, including the occludent margin, is termed **rostral**, and what would be dorsal is termed **carinal**, names being derived from the unpaired calcified plates that occur on these margins in many species. The body lying within the capitulum is reflexed toward the carinal margin from the prosoma. When extended during feeding, it assumes a position more parallel to the long axis of the entire animal, so that its ventral and dorsal surfaces more closely correspond to the dorsal (carinal) and ventral (rostral) surfaces of the capitulum.

The relationship of the body to the mantle wall is basically the same in the pedunculate and sessile cirripeds (cf. Fig. 83,*1-3*). However, the body is reflexed even more in the latter, so that when the animal is at rest, the body tends to lie almost parallel to the substratum. When feeding, however, the body is rotated and extended posteriorly, so that the same general relationships hold for sessile forms as for the lepadomorphs. Further similarities and homologies between these two basic forms will be taken up under the section on evolution.

The majority of the extant thoracican cirripeds are hermaphroditic. However, some species produce relatively small males (Fig. 85, 86,*2-3*). Following DARWIN, the male is referred to as a **complemental male** when it occurs with a hermaphrodite, and as a **dwarf male** when it occurs with a female. In Recent forms, the males are considerably smaller than the female or hermaphrodite and are always attached either externally or within the mantle cavity. Usually the armature, trophic structures and digestive system of such males are degenerate or nonexistent.

Among Recent scalpellids (e.g., *Scalpellum ornatum, Mesoscalpellum gruvelii,* Fig. 86,*3*) a depression or pocket occurs internally in the scuta, above the attachment for the adductor muscle closing these plates, and accommodates one or more minute males. A similar depression is seen in the scutal plates of *Arcoscalpellum* from the Upper Cretaceous, suggesting the presence of dwarf or complemental males in Mesozoic times. (See Addendum to Cirripedia, p. *R*628.)

It is assumed that fossil lepadomorphs are large females or hermaphrodites. Presently, however, there is no way of knowing that free-living separate sexes did not occur. The trend seen in Recent forms suggests that they did, and if such were the

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FIG. 86. *(Continued from facing page.)*

3. Mesoscalpellum gruvelii (ANNANDALE).——*3a.* Dwarf males, enl.——*3b.* Female with males *in situ,* viewed from rostral end, ×2 (Annandale, 1907-1908).

4. Primordial plates (possibly more than basic number of five) in *Euscalpellum bengalense* (ANNANDALE), ×48 (after Stubbings, 1936).

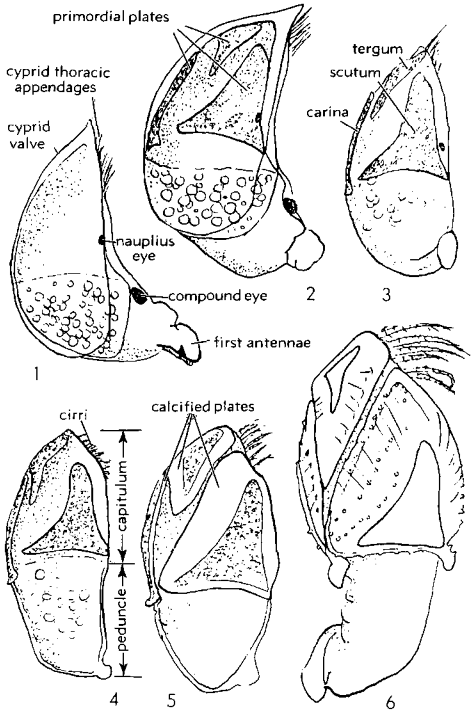


FIG. 87. Morphology of cirripeds. Metamorphosis of *Lepas (Lepas) anatifera* LINNÉ, ×16 (Newman, n).——*1.* Recently settled cyprid larva beginning metamorphosis.——*2.* Primordial plates appearing beneath cyprid shell, compound eyes being shed.——*3.* Cyprid shell shed, nauplius eye still visible near middle of occludent margin of scutal primordium.——*4.* Further differentiation of capitulum and peduncle, cirri but not calcareous plates having appeared.——*5.* Calcification beginning beneath and progressing away from primordial plates.——*6.* Juvenile stage having much the same proportions as adult.

case, it seems likely that the males would have been smaller than the females of the same species.

HARD PARTS

A fundamental characteristic of the Arthropoda is molting of the exoskeleton during growth and development. Among the Crustacea, only the Conchostraca, certain fossil supposed Ostracoda and the thoracican Cirripedia, all forms with a basically bivalved carapace, have developed the ability to retain and build up portions of the exoskeleton of the carapace with calcium carbonate, while frequently molting the chitinous exoskeleton of the rest of the body. Among Cirripedia, the Thoracica, but not the Ascothoracica, Acrothoracica, or Rhizocephala, produce a shell of calcium carbonate.

According to CLARKE & WHEELER (1917), the barnacle shell differs from that of other crustaceans in containing very little phosphate or organic material. CHAVE (1954) reported the shell of various forms to be predominantly calcite, to contain no aragonite and to have a magnesium carbonate fraction ranging between 1.35 and 4.60 percent, varying proportionally to the temperature at which it was laid down.

The calcareous portion of the thoracican shell appears during the metamorphosis of the cyprid larva into a young barnacle. In the Lepadomorpha and Verrucomorpha the appearance of certain of the calcified plates or valves is preceded by the appearance of so-called **primordial valves** or **plates,** which are presumably chitinous and for which the function is unknown. The primordial valves appear attached to the hypodermis, beneath the cyprid shell (Fig. 87-89). In the Lepadidae *s.l.* there are five primordia, corresponding to the five calcified plates that will develop beneath them as metamorphosis progresses. In the Scalpellidae there are also usually five primordia, associated with the same centers of calcification as in the Lepadidae, but in certain species additional primordia may be present as well (Fig. 86,*1c,d*).

The shape and size of a primordial plate is apparently determined when it is formed and it appears that it becomes physiologically isolated from the hypodermis after calcification sets in. In the adult barnacle, it resides at the umbo of the calcified plate with which it is associated, and although small, it can be found, unless eroded away. Primordial plates have been found on the umbones of certain fossil scalpellids from the Middle Carboniferous and Jurassic (Kimmeridgian).

Interpretations of the phylogenetic significance of the primordial plates will be taken up in the section on phylogeny. Suffice it to say at this point that primordial

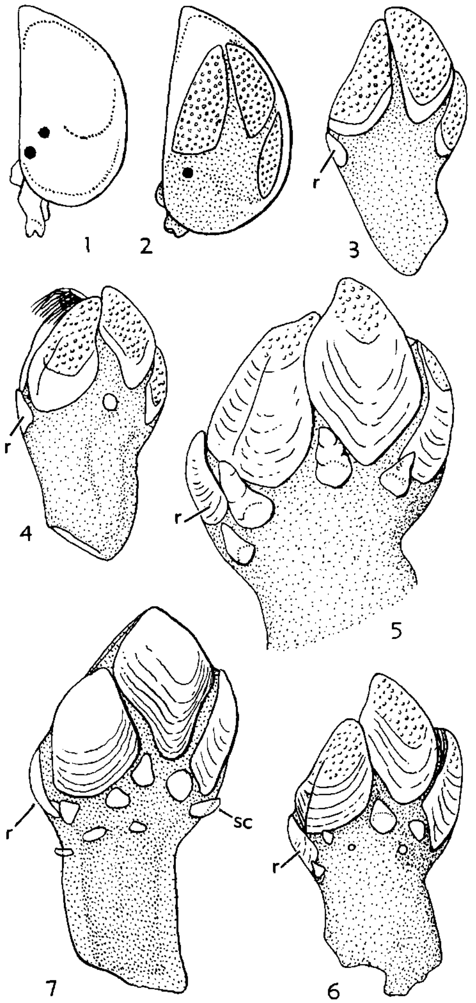


FIG. 88. Morphology of cirripeds. Ontogenetic development of *Pollicipes polymerus typica* BROCH, Rec. (not to scale) (Broch, mod.).——*1.* Cyprid just attached.——*2.* Cyprid with primordial plates. ——*3.* Cyprid shell shed, calcification around primordia and rostrum developing.——*4.* Specimen with upper latus.——*5.* Somewhat aberrant specimen with three latera and subrostral latus.——*6.* Normal specimen with two lower latera developed. ——*7.* Specimen with subcarina well developed, and first peduncle scale appearing below rostrum. [Explanation; *r,* rostrum; *sc,* subcarina.]

plates, while found in Lepadomorpha and Verrucomorpha, are unknown in the Balanomorpha.

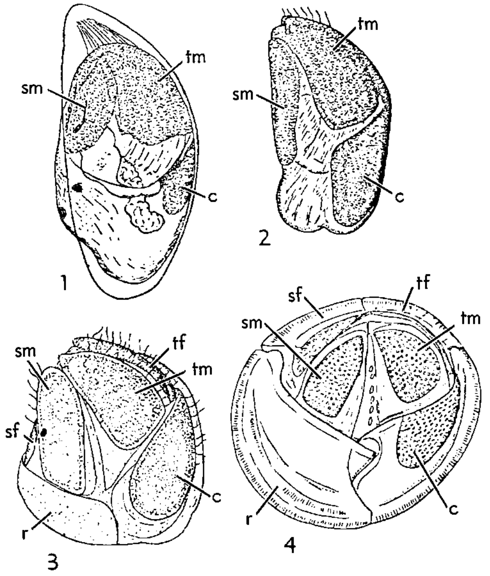


FIG. 89. Morphology of cirripeds. Metamorphosis in *Verruca (Verruca) stroemia* (O. F. MÜLLER), all enl. (after Runnström, 1926, from *61*).——*1.* Attached cyprid with primordial plates of movable scutum, movable tergum and carina visible.——*2.* Cyprid shell cast, carina rotated somewhat to right side.——*3.* Calcification beginning—movable scutum, movable tergum, fixed scutum, fixed tergum and rostral plate visible.——*4.* Juvenile resembling adult. [Explanation: *c,* carina; *r,* rostrum; *sf,* scutum (fixed); *sm,* scutum (movable); *tf,* tergum (fixed); *tm,* tergum (movable).]

LEPADOMORPHA

The armature of the capitulum consists of a distinct number of principal calcareous plates formed and arranged in a definite manner, depending on the species, genus, and generally the family. Therefore, the number of relative positions of the plates are of systematic, ontogenetic, and phylogenetic significance. For descriptive purposes, it has been found necessary to name not only each principal capitular plate, but also various conspicuous features of most of them.

The principal plates seem to be fundamentally six in number, in the Scalpellidae, namely the paired **scuta** and **terga,** a **carina** and a **rostrum** (Fig. 90,*1a*). During meta-

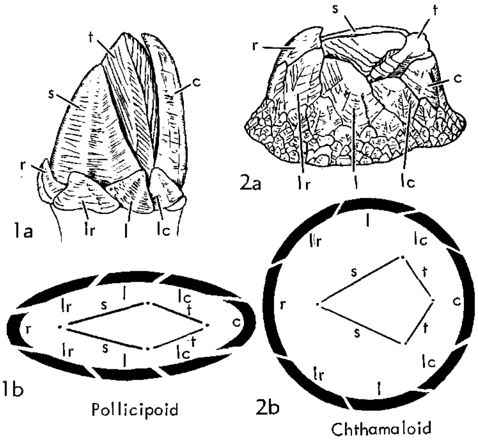


FIG. 90. Morphology of cirripeds. Comparison of *(1)* pollicipoid form comparable to *Calantica (Scillaelepas) dorsata* (STEENSTRUP), U.Cret.(Dan.), Denmark, but with relationship of latus to other latera altered and *(2)* the chthamaloid *Catophragmus (Catomerus) polymerus* DARWIN, Rec., Tasm.; *1a, 2a,* ×2.2 *(1a,* after *118, 120)*; *1b, 2b,* plan views of principal plates (Newman, n). [Explanation: *c,* carina; *l,* latus; *lc,* latus (carinal); *lr,* latus (rostral); *r,* rostrum; *s,* scutum; *t,* tergum.]

morphosis from the cyprid larva to the adult, in the Verrucomorpha, as well as the scalpellid Lepadomorpha, all but the last, or rostral plate, is preceded by a primordial plate (Fig. 88, 89). In the Lepadidae, there are basically only five capitular plates, the rostrum being completely absent (Fig. 87). The carina forms the dorsal margin of the capitulum. In *Praelepas,* one of the oldest known thoracicans, and in the Lepadomorpha *s.l.,* the carina extends between both the terga and the scuta (cf. Fig. 83,*3,* see Fig. 114,*10*). However, in the scapellids, it borders on the terga alone, and this is another fundamental difference between the two groups. The scuta, usually larger than the terga in lepadids and equal or smaller in the scalpellids, serve to protect the ventrolateral part of the animal while the terga form the ventral or posteroventral aperture through which the cirri are protruded during feeding. A free scutum can often be recognized by the presence of an adductor muscle pit or scar on the interior.

The terga are usually large and flat, adjoin the scuta, and serve to protect the posterior part of the animal. These plates are not provided with muscles, but are affected by opening and closing movements of the scuta. The rostrum, present in the scalpellids, commonly resembles the carina in shape, but is usually much smaller and adjoins the rostral angles of the scuta. This plate can usually be distinguished by the greater development of growth ridges on the apical part of the inner surface.

Only the principal six plates are present in the Carboniferous *Eolepas,* and they form a single whorl (see Fig. 115,*1*). *Archaeolepas* has the same basic arrangement of plates, but the peduncle has become armed with successive whorls of uniform additional plates (see Fig. 115,*6*). In *Calantica (Scillaelepas),* the scuta, terga and carina form an upper whorl, whereas the rostrum and basal portion of the carina, in conjunction with a number of secondary plates, form a secondary basal whorl, the margins of which overlap one another (Fig. 91,*6*). This secondary whorl has nine parts—the **rostrum,** three pairs of **latera** (sing., **latus**) known as the **rostral, median** and **carinal latera,** the **carina** and a **subcarina.** Eight of the nine can be compared with the wall plates of *Catophragmus* spp., forms intermediate between pedunculate and sessile barnacles to be taken up later (Fig. 90).

In genera such as *Arcoscalpellum* (see Fig. 115,*8*), the median latus, rather than forming part of the basal whorl, is located up between basal portions of the scutum and tergum, where it is known as the **upper latus,** the plate below it being termed the **inframedian latus.** The subcarina is highly developed in the Cretaceous *Cretiscalpellum* (see Fig. 115,*4*) and the Cretaceous to Recent *Calantica (Scillaelepas)* (see Fig. 115,*9*).

The margins of the plates are named according to the plates which they adjoin. Details of the scutum and tergum are given in Figure 92,*1a-e, 2a,b,* and of the carina in Figure 92,*3*. A number of smaller plates arranged in whorls below the latera are seen in *Zeugmatolepas* (see Fig. 115,*5*), and *Pollicipes (=Mitella)* (see Fig. 115,*7*). These plates are collectively termed **lower latera.**

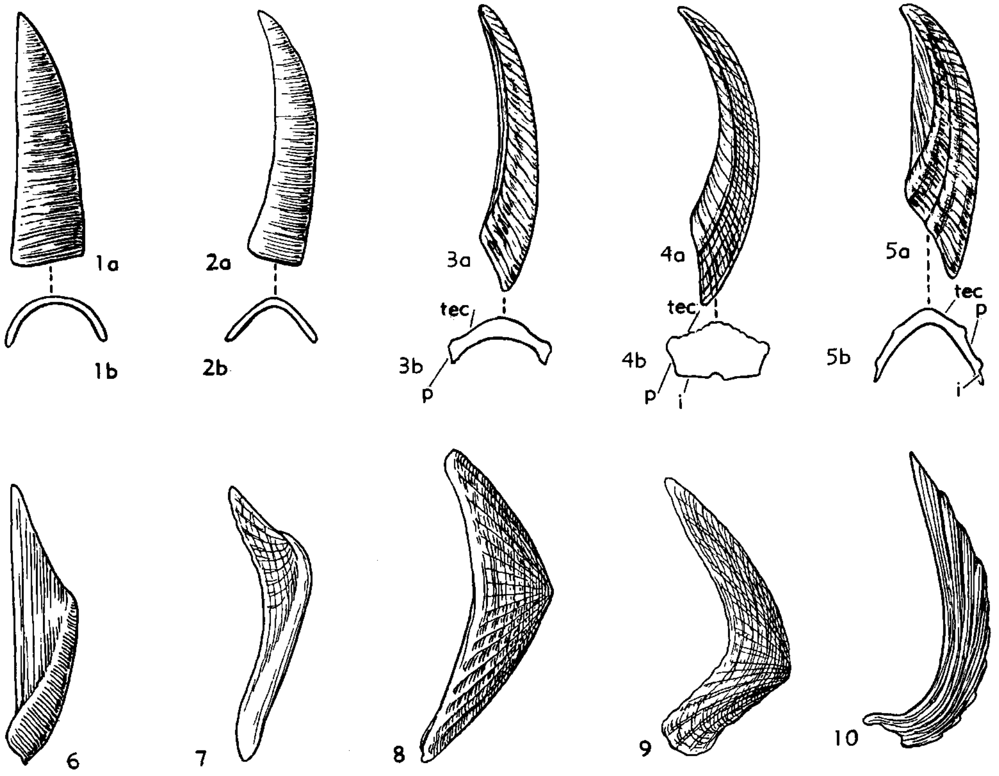


FIG. 91. Morphology of cirriped plates: carinae (not to scale) (after Withers).

1. *Eolepas quenstedti* (VON AMMON); *1a,b,* lat., transv. sec.
2. *Archaeolepas suprajurensis* (DE LORIOL); *2a,b,* lat., transv. sec.
3. *Arcoscalpellum simplex* (DARWIN); *3a,b,* lat., transv. sec.
4. *Arcoscalpellum arcuatum* (DARWIN); *4a,b,* lat., transv. sec.
5. *Arcoscalpellum maximum sulcatum* (J. DE C. SOWERBY); *5a,b,* lat., transv. sec.
6. *?Smilium parvulum* (WITHERS); lat. view.
7. *Virgiscalpellum hagenowianum* (BOSQUET); lat. view.
8. *V. darwinianum* (BOSQUET); lat. view.
9. *Oxynaspis celata* DARWIN; lat. view.
10. *Lepas (Lepas) anatifera* LINNÉ; lat. view.

[Explanation: *i,* intraparietes; *p,* parietes; *tec,* tectum.]

In some forms the inner surface of the carina, rostrum, and tergum is marked by ridges or lines of growth at the apical end. This feature is best developed in forms with massive plates. These growth ridges are caused by the recession of the hypodermis during periodic growth of the plates. In forms where this occurs, the ends of the plates come to project freely beyond the capitulum. This is a feature of great phylogenetic significance, as will be discussed shortly.

The carina in the Triassic (Rhaetic) and Jurassic Scalpellidae and the Middle Carboniferous Praelepadidae has an apical (posterior) umbo and is simple in structure (Fig. 91,*1-5*). The carina of *Eolepas* (Fig. 91,*1*) is almost straight, transversely convex, with a straight or concave basal margin, and not inwardly bowed. *Archaeolepas* (Fig. 91,*2*) shows further development, the carina being somewhat bowed inwardly, and the basal margin is rounded. The carina of other Jurassic genera such as *Calantica,* has a rounded or angular basal margin, which reflects the development of basal latera. In Cretaceous species of *Arcoscalpellum* (e.g., *A. simplex,* Aptian, Fig. 91,*3*), a roof or

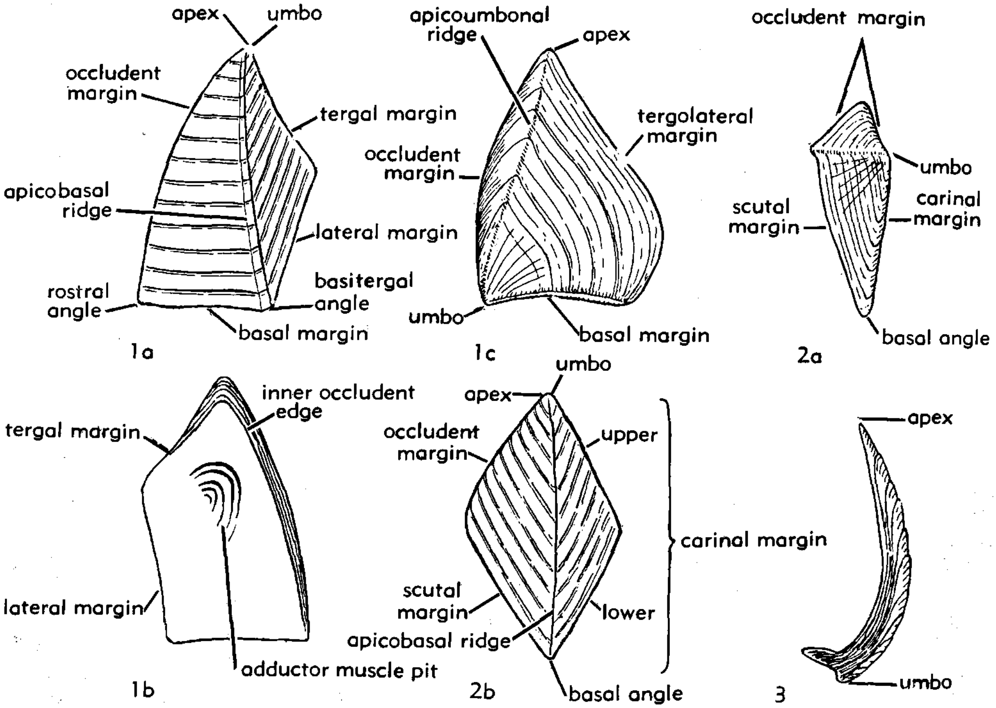


FIG. 92. Morphology of cirripeds, showing lepadomorph plates (not to scale) (after Withers).

1. Scutum.——*1a,b.* Scalpellid, exterior and interior.——*1c.* Lepadid, outer side.

2. Tergum.——*2a.* Lepadid, exterior.——*2b.* Scalpellid, exterior.

3. Carina; lepadid, lat. view.

tectum of the carina becomes demarcated from the sides, by an angle or ridge. The sides in such a carina are termed **parietes.** This term is unfortunate because of the confusion it may cause. It does not apply to the same part of the plate in the Lepadomorpha as in the Balanomorpha.

On the inner edge of the parietes in species such as the Aptian *A. accumulatum* and the Albian *A. arcuatum* (Fig. 91,*4*), a further development has taken place. The interior of the upper part of the carina is thickened by successive laminae, and the portions formed by the edges of these laminae are termed **intraparietes.** The intraparietes are marked off from the parietes by an angle or ridge. In later forms (e.g., *Arcoscalpellum maximum sulcatum*, Senonian, Fig. 91,*5*) the intraparietes are not rectangularly bent inward as in *A. arcuatum*, but form a thin wall on each side of the plate. The intraparietes always have growth lines turned obliquely upward, and these parts bridge the interval between the carina and tergum. The intraparietes extend a little beyond the umbo in the Cenomanian *A. lineatum*, and in the upper Senonian *Virgiscalpellum darwinianum* (Fig. 91,*8*) the umbo of the carina is almost equal above and below the umbo. In the Recent *Oxynaspis* (Oxynaspididae) (Fig. 91,*9*) the umbo is well below center, and in *Lepas* (Lepadidae) (Fig. 91,*10*) the umbo is basal. What is called the carina in *Stramentum* (Stramentidae) (see Fig. 116, *6*) is split longitudinally into two parts.

The scutum (Fig. 92,*1a-c*) is triangular or rhomboidal with the ventral border being termed the **occludent margin,** and the basal border simply termed the basal margin. In forms with a straight lateral border such as *Eolepas* (Fig. 93,*1*) this border is

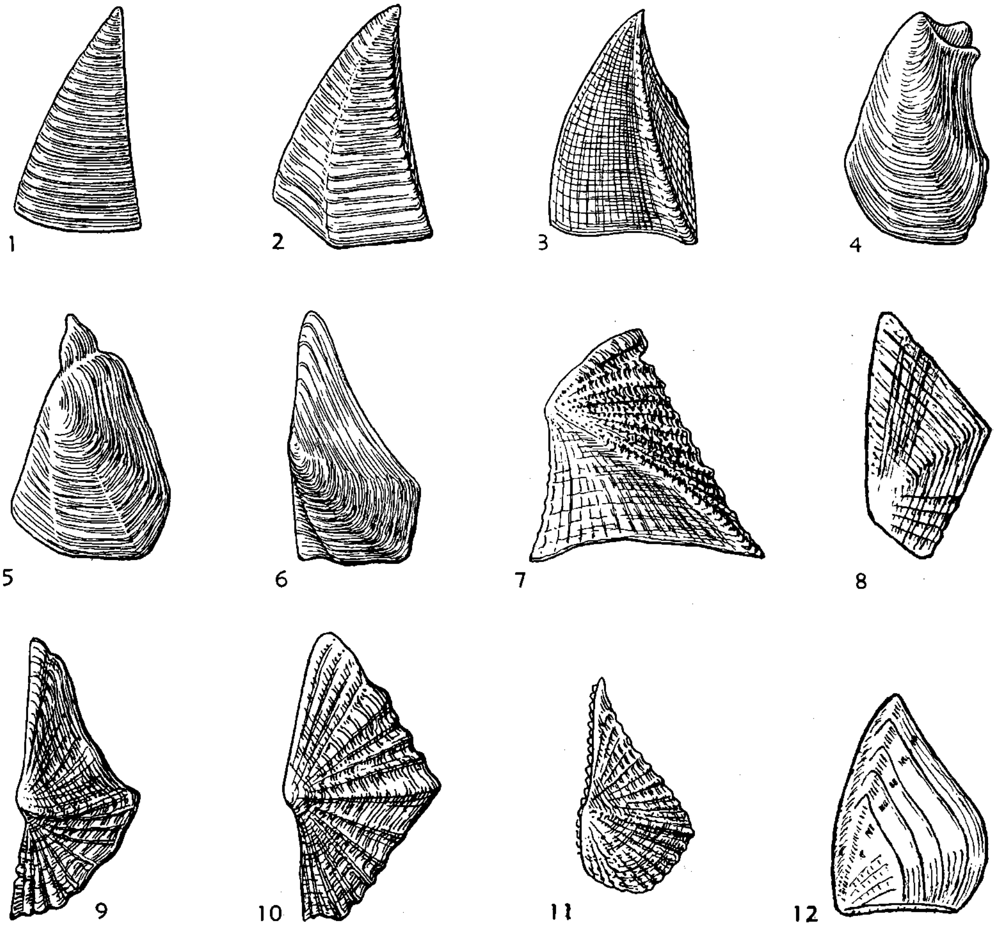


FIG. 93. Morphology of cirriped plates; scuta (all lat. views, not to scale) (after Withers).

1. Eolepas quenstedti (VON AMMON).
2. Archaeolepas suprajurensis (DE LORIOL).
3. Arcoscalpellum arcuatum (DARWIN).
4,5. Zeugmatolepas mockleri WITHERS.
6. Z. cretae (STEENSTRUP).
7. Calantica (Titanolepas) tuberculata (DARWIN).
8. Virgiscalpellum darwinianum (BOSQUET).
9. V. hagenowianum (BOSQUET).
10. V. beisseli (BOSQUET).
11. Oxynaspis celata DARWIN.
12. Lepas (Lepas) anatifera LINNÉ.

termed the **tergal margin**. In forms with an angulate lateral border, such as *Cretiscalpellum* (see Fig. 115,*4*) and *Arcoscalpellum* (Fig. 93,*3*), the posterior part is termed the tergal margin, and the anterior part is termed the **lateral margin**. Along the tergal margin the growth lines of the scutum may turn abruptly, forming an area known as the **tergal slip** which may be demarcated from the bulk of the scutum by a longitudinal ridge. The basal angle adjacent to the rostrum is termed the **rostral angle**, and the opposite angle the **basitergal angle**. The angle between the tergal and lateral margins, when present, is termed the **tergolateral** angle. That formed by the occludent and scutal margins is termed the **apical angle**. In the earliest Jurassic form *Eolepas* (Fig. 93,*1*) the scutum is triangular, without a tergal slip, and the tergal and basal margins are straight. *Archaeloepas* (Fig. 93,*2*) has a narrow tergal slip, and this fea-

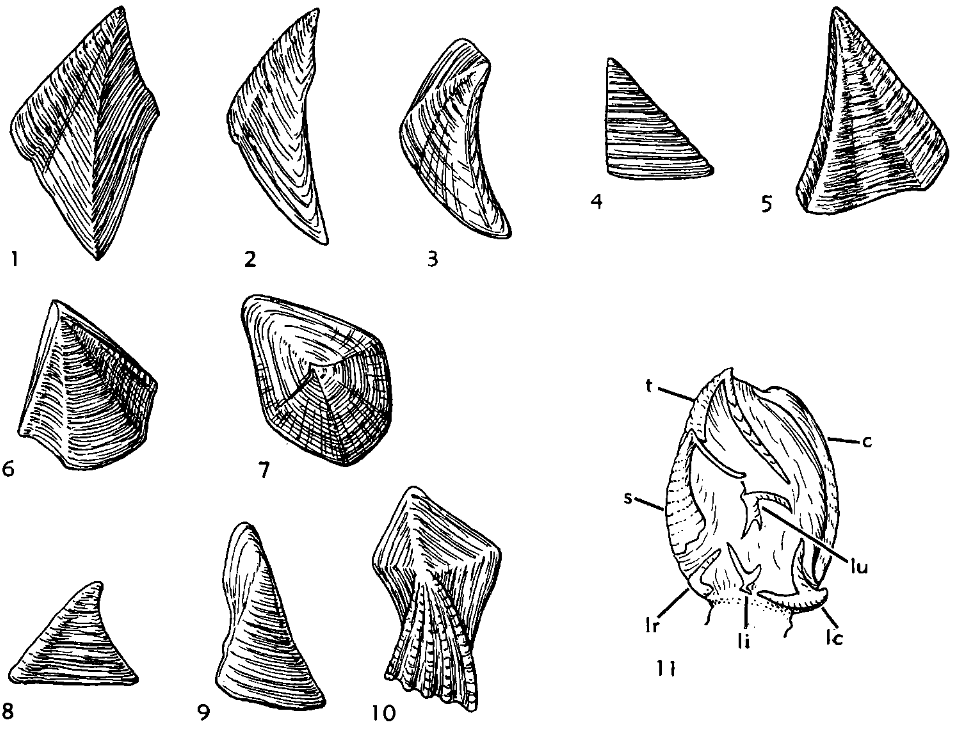


FIG. 94. Morphology of cirriped plates (all lat. views, not to scale) (*1-10,* after Withers; *11,* after Pilsbry).

1-3. Terga.——*1. Cretiscalpellum glabrum* (F. A. Roemer).——*2. Scalpellum magnum* Darwin. *3. S. burdigalense* des Moulins.

4-7. Upper latera.——*4. Cretiscalpellum glabrum* (F. A. Roemer).——*5. Arcoscalpellum fossula* (Darwin).——*6. A. quadratum* (Dixon).——*7. Scalpellum magnum* Darwin.

8-10. Inframedian latera.——*8. Arcoscalpellum fossula* (Darwin).——*9. A. maximum* (J. de C. Sowerby).——*10. Virgiscalpellum darwinianum* (Bosquet).

11. Capitulum of *Mesoscalpellum dicheloplax* (Pilsbry).

[Explanation: *c,* carina; *lc,* latus (carinal); *li,* latus (inframedian); *lr,* latus (rostral); *lu,* latus (upper); *s,* scutum; *t,* tergum.]

ture is further developed in forms such as the Albian *Arcoscalpellum arcuatum* (Fig. 93,*3*).

The scutal umbo in early Scalpellidae is apical. Young individuals of the Cenomanian *Zeugmatolepas mockleri* (Figs. 93,*4-5*) have an apical umbo, but in older individuals the upper tergal part of the plate extends beyond the umbo. Development of the upper tergal part in the higher upper Senonian species *Z. cretae* (Fig. 93,*6*) is more pronounced, bringing the umbo to a more central position. In Scalpellidae such as the Cenomanian *Calantica (Titanolepas) tuberculata* (Fig. 93,*7*), the Maastrichtian *Virgiscalpellum darwinianum* (Fig. 93,*8*), and *V. hagenowianum,* and the Senonian *V. beisseli* (Fig. 93,*10*) the umbo is subcentral. The umbo is also subcentral in the Recent *Oxynaspis* (Oxynaspididae) (Fig. 93,*11*), but is basal in the unmodified Lepadidae (*Lepas,* Fig. 93,*12*) and most Poecilasmatidae.

The tergum (Fig. 92,*2a-b*) is commonly diamond-shaped. The ventral border is termed the **occludent margin**; that adjoining the scutum, the **scutal margin**; and that adjoining the carina, the **carinal margin,** the last usually being divided into upper and lower parts. A submedial ridge or furrow usually divides this plate. The tergum of Mesozoic forms varies little, but in the Tertiary upward-directed growth from the occludent margin is observed (e.g., *Scalpellum burdigalense,* Mio., Fig. 94,*3*; *S. magnum,* Plio., Fig. 94,*2*).

The rostrum is a single plate situated at the rostral angles of the scuta. In forms where it approaches the carina in size, such as *Eolepas* (see Fig. 115,*1*) and the Recent *Pollicipes mitella,* the extent of the rostrum that projects freely is greater than in the carina. The rostral latera, when present, adjoin or may overlap the rostrum, as in *Calantica (Scillaelepas), Arcoscalpellum,* and *Scalpellum.*

The simplest form of the upper latus, as seen in *Cretiscalpellum* (Aptian-U.Senon., Fig. 94,*4*), is triangular, with a straight basal margin and an apical umbo. In certain species of *Arcoscalpellum,* such as *A. fossula* (Fig. 94,*5*), the growth lines are upturned at the sides and the basal angles consequently truncate. In other species (e.g., *A. quadratum,* Eoc., Fig. 94,*6*) the edges of the laminae forming the plate extend slightly beyond the umbo, a condition much emphasized in the Pliocene *Scalpellum magnum* (Fig. 94,*7*). Similar changes in the position of the umbo are found in the inframedian latus of some Cretaceous species of *Arcoscalpellum* (Fig. 85,*5*), and in one *Virgiscalpellum* (Fig. 85,91). The rostral and carinal latera exhibit comparable changes in umbonal position.

In certain stocks, the plates have unusual shapes which are the result of incomplete calcification, a condition usually associated with a special mode of life. This condition, for example, is seen in Recent species of *Mesoscalpellum* (Fig. 85,94) (Scalpellidae), *Octolasmis* (Poecilasmatidae), *Conchoderma* (Lepadidae), and *Oxynaspis* (Oxynaspididae).

VERRUCOMORPHA

These are sessile thoracicans with pronounced asymmetry of the shell. Of the three genera, *Proverruca, Eoverruca* and *Verruca* appearing in the Upper Cretaceous, only *Verruca* is surviving today.

The entire shell of the adult *Verruca* consists of but six plates; the paired terga and scuta, the carina and rostrum. The carina and rostrum, and the tergum and scutum of either the right or left side, form the box-like wall. The remaining tergum and scutum are movable and form a lid or operculum to the box. The basis is membranous except in one modern species (Withers, 1935).

The ontogeny of these peculiar forms was analyzed by Darwin (1854) and the gross features are briefly illustrated here (Fig. 89,*1-4*). Some asymmetry is seen in the arrangement of the primordial plates when they first appear beneath the cyprid shell, and it becomes more pronounced with development. This is particularly true of the terga and scuta, fixed and movable members of which bear little resemblance to each other in the adult. Once metamorphosis has been completed, the carina, rostrum, and fixed tergum and scutum rest directly on the substratum. The movable tergum and scutum are articulated with one another and form a rigid lid or operculum having an essentially straight hinge line along the upper margins of the carina and rostrum (see Fig. 117,*4a,b*).

The six-plated condition and asymmetry no doubt has been derived from a symmetrical ancestral stock as pointed out by Darwin (1854). Both he and Withers (1935) called attention to similarity of the unmodified tergum and scutum with the same plates in forms presently assigned to the Brachylepadomorpha. The asymmetry found in fossil verrucomorphs is somewhat less pronounced, and two lateral plates not found in modern forms, contributed to the structure of the wall. These, the rostrolateral and carinolateral plates, lie between the carina and rostrum on the side opposite the fixed tregum and scutum, as seen in *Proverruca* and *Eoverruca* (see Fig. 117,*1b, 3b*).

In *Eoverruca,* the fixed tergum and scutum stand in a relatively vertical position and resemble their movable counterparts in having surfaces divided into two regions by a central ridge or rib, and in the manner in which they articulate with one another. The central ribs have been interpreted by Pilsbry (1916) and Withers (1935) as forming a primitive articulation between the two plates in Brachylepadomorpha. Their persistence on the fixed plates in *Eoverruca* would therefore be as vestigial structures. The rostrum and carina, on the other hand, are also more normal in not extending laterally any more on one side than on the other, the lateral space on the side opposite the fixed tergum and scutum being filled by two lateral plates not found in *Verruca.* Thus the general form is higher and more laterally flattened, and as pointed out by WITHERS (1935), when viewed from the side of the movable opercular parts, there is a marked resemblance to the Brachylepadomorpha.

BRACHYLEPADOMORPHA

These are extinct symmetrical sessile thoracicans that have eight primary plates forming the shell, the basal margin of which was surrounded by several whorls of small imbricate plates. In most cases, the basis was membranous. Although sessile, the general form of these barnacles resembles the capitulum of a pedunculate barnacle, in that it is not divided functionally into wall and operculum as in the Verrucomorpha and Balanomorpha. In fact, some of the first described species were placed in the scalpellid genus *Pollicipes,* and the resemblance between *Pycnolepas* and the capitulum of *Pollicipes mitella* is remarkable (cf. Fig. 115,*7* and 117,*5*). The more primitive of the two recognized genera, *Pycnolepas,* is known probably as early as the Upper Jurassic. *Brachylepas* appears in the Upper Cretaceous.

The principal components of the shell, as in the Verrucomorpha, are the paired terga and scuta, and the carina and rostrum. The tergum and scutum of each side appear to be loosely articulated with each other, perhaps showing some advance over the condition seen in the Lepadomorpha. However, the articulation is overlain by a narrow upper latus which indicates that the articulation was no better developed than in *Pollicipes.* These six plates form the bulk of the shell and are contained between the large rostrum and the carina. Around the base small imbricate plates are arranged in several whorls.

Although these were sessile barnacles, they differed from other sessile forms in not having developed a functional separation between the plates forming the aperture and those primarily involved in forming the wall. The development of such a functional separation took two courses in other sessile forms; one seen in the Verrucomorpha, the other in the Balanomorpha, and until the separation was achieved, a truly rigid wall could not be formed.

BALANOMORPHA

The shell (Fig. 95,*1*) in balanomorph barnacles consists of a circular wall composed of a number of more or less rigidly articulated compartmental plates (Fig. 95, *4-6*) with or without a calcareous basal disc (**basis,** Fig. 95,*1*). An uncalcified basis is simply membranous. The **orifice** (Fig. 95,*1*) is occupied by four **opercular valves (or plates)**: the paired **terga** (Fig. 95,*2a-b*) and **scuta** (Fig. 95,*3*), which together form an **operculum.** The tergum and scutum of each side are more or less intricately articulated, an aperture to the exterior being retained between the opposing pairs, through which the animal can protrude the feeding appendages or cirri.

The opercular valves and compartmental plates of Balanomorpha are considered homologous to specific plates in Lepadomorpha. The accepted homologies are depicted in Fig. 90. It will be noted that whereas in the Lepadomorpha *all* hard parts are termed plates, in the Balanomorpha the opercular parts, although they are homologous with certain lepadomorph plates, are termed valves.

Each compartmental plate is usually divided into three parts (Fig. 95,*4-6*): a large, central, triangular area (**paries,** pl. **parietes**) and narrower, linear areas on either side of the paries, overlapping or being overlapped by corresponding parts of adjacent compartmental plates. When the overlapping portions differ in structure from the paries, they are termed **radii** (sing., **radius**); those which are overlapped are termed **alae** (sing., **ala**). In Chthamalidae and most Balanidae, the parieties and radii are solid. In some balanids the parietes and radii are composed of an **outer** and an **inner lamina** or lamella. The lamellae are separated by **longitudinal septa** forming **longitudinal tubes** (pores) and in some species these are crossed by secondary **transverse septa,** or are secondarily filled with calcium carbonate (see Fig. 105,106). In a few balanids, more than one row of tubes are formed (see Fig. 119,*2b,4b,9a,c,e*).

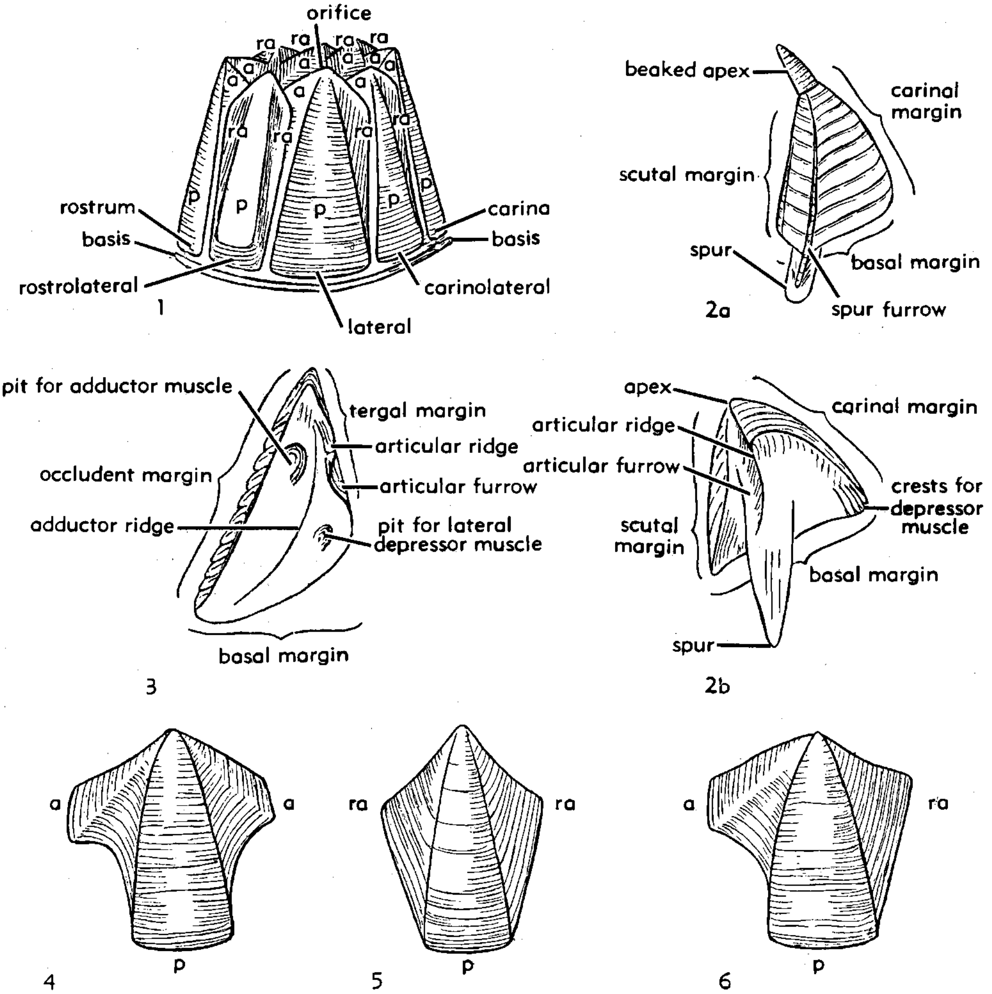


FIG. 95. Morphology of balanomorph plates and valves (not to scale) (*1,4-6,* after Darwin; *2,3,* after Withers).

1. Entire shell of eight plates, showing part of sheath in orifice; rostrum and rostrolateral compartment, usually unfused in chthamalids and fused in all balanids.
2. Tergum.——*2a,b.* Exterior and interior.
3. Scutum, interior.
4. Compartment with alae on sides as in carina or true rostrum.
5. Compartment with radii on sides, as in rostrolateral or compound rostrum.
6. Compartment with ala on one side and radius on other, as in lateral or carinolateral.
[Explanation: *a,* ala; *ra,* radius; *p,* paries.]

The balanomorph shell wall includes, at most, eight primary plates: a rostrum, paired rostrolaterals, paired laterals, paired carinolaterals, and a carina (Fig. 96,*1-2*). Some species possess one or more whorls of small supplementary plates at the base of the shell wall (Figs. 96,*1*).

A true rostrum has alae on both sides (Fig. 95,*4*). In some genera, the rostrum may be fused with the adjacent rostrolaterals to form a compound **rostral plate** in which case it overlaps rather than underlaps the adjacent lateral plates (Fig. 96,*5-7*).

The laterals and carinolaterals have alae on their carinal margins (Fig. 95,*6*). The carina has alae on both margins (Fig. 95,*4*), as does the true rostrum.

Catophragmus (Fig. 96,*1*) and *Octomeris*

(Fig. 96,*2*) have the full complement of eight plates. *Catophragmus* has several basal whorls of supplementary plates, in addition. *Chionelasmus* has a single whorl of supplementary plates. The wall is made up of six plates rather than eight, and the rostrum, having alae, is simple. In this case, the reduction to six plates has been through the loss of carinolaterals rather than by fusion of rostrolaterals to the rostrum. In *Chamaesipho* (Fig. 96,*4*), a simple rostrum is present, the carinolaterals are lacking, the laterals are apparently fused with the rostrolaterals and the carina is present. This arrangement results in a wall of four plates.

The chthamalid genera *Pachylasma, Hexelasma* (Fig. 96,*5*), and *Tessarelasma,* and all Balanidae superficially appear to have walls of six plates. In the chthamalid *Pachylasma* and the balanid *Chelonibia* (Fig. 96,*7*), eight plates can be discerned, for the rostrum is incompletely fused with the rostrolaterals. That the middle element is the rostrum in *Chelonibia* is demonstrated in a Miocene specimen of *C. caretta* (see Fig. 119,*8*) in which the middle element is not only separated from the lateral elements by deep sutures toward the apex (much deeper than in Recent specimens), but it has slightly developed alae over which the adjacent rostrolaterals distinctly overlap. In *Balanus,* on the other hand (Fig. 96,*8*), the rostral plate is considered to be formed of the fused rostrolaterals only, the true rostrum having been eliminated, and retention of the carinolaterals provides six compartmental plates. Thus, certain of the wall elements, although six in each genus, differ between *Balanus* and *Chthamalus.* In the latter, the arrangement is the same as in *Chionelasmus* excepting that the supplementary whorl is lacking. The balanids *Tetraclita* (Fig. 96,*9*) and *Creusia* (see Fig. 118A, *15a*) have lost the carinolaterals, leaving four plates, and in *Pyrgoma* (Fig. 96,*10*), these four plates are fused into a single shell, although traces of a pair of sutures in the sheath can sometimes be seen at the carinal end on the interior in some species (see Fig. 118A, *16*).

GROWTH

Both determinate and indeterminate growth occurs in the Balanomorpha. In many species of *Balanus,* full size may be attained within the first year after settlement with only small growth increments occurring during the next year or so of life. Some species (e.g., *B. (B.) nubilis*) presumably have a much longer life span, apparently within the neighborhood of 15 years. Growth of the shell wall and basis of this species appears to continue through much of the life of the individual. The remarkable growth form of the basis in the California Miocene and Pliocene species *B. (B.) gregarius* (the so-called *"Tamiosoma"*) has often been cited. Elongation of the basis into a cup-shaped or tubular form is not unusual in balanids, and is characteristic of such taxa as *Creusia, Pyrgoma, B. (B.) laevis,* and *B. (Megabalanus) tintinnabulum.* However, the filling of this cavity in *B. (B.) gregarius* with numerous thin irregular horizontal partitions results in a peculiar cellular structure which resembles that of rudistid pelecypods. In *Chthamalus hembeli* and *C. intertextus,* growth is determinate, ceasing with the advent of secondary calcification within the interior of the shell.

Growth of the shell occurs along the basal and lateral margins of the compartmental plates, and around the circumference of the basis. As the general form of the balanomorph shell is conic, increase in height and diameter, and, therefore, volume, can be attained entirely through growth at the basal margins of the shell. However, without marginal growth, the diameter of the orifice at the top (or oldest part) of the cone would remain constant and communication with the external environment as growth progressed would become proportionately reduced. In most balanomorphs, the orificial opening is enlarged by lateral growth at the sutural edges of the plates. In some taxa (e.g., *Tetraclita, Pyrgoma*) in which partial or complete concrescence of the compartmental plates has occurred, expansion of the orifice is apparently achieved by the wearing away of the upper portions of the wall by external erosion and activities of the animal.

Color and, more specifically, color pattern has proven useful in the classification of species-group taxa in the Balanidae. Various shades of red and red-brown are the prevalent colors exhibited, although blues and purples are also found (e.g., *Balanus (Austrobalanus) imperator*). Coloration appears to be confined mainly to the exterior of the parieties and to the surface of the opercular valves. In some cases, the entire surface of the parieties is of a uniform shade, but in most taxa, the coloration consists of radial color stripes on a background of a different color or shade (e.g., *B. (Megabalanus) tintinnabulum, B. (Balanus) venustus niveus, B. (B.) amphitrite amphitrite*). The pattern of these stripes has proved useful in distinguishing between various so-called subspecies of the *B. (M.) tintinnabulum* and *B. (B.) amphitrite* complexes. Radial bands are also common in such taxa as *B. (M.) tintinnabulum,* and have been employed as diagnostic characters. The origin and purpose of these colors and color markings, however, are not understood.

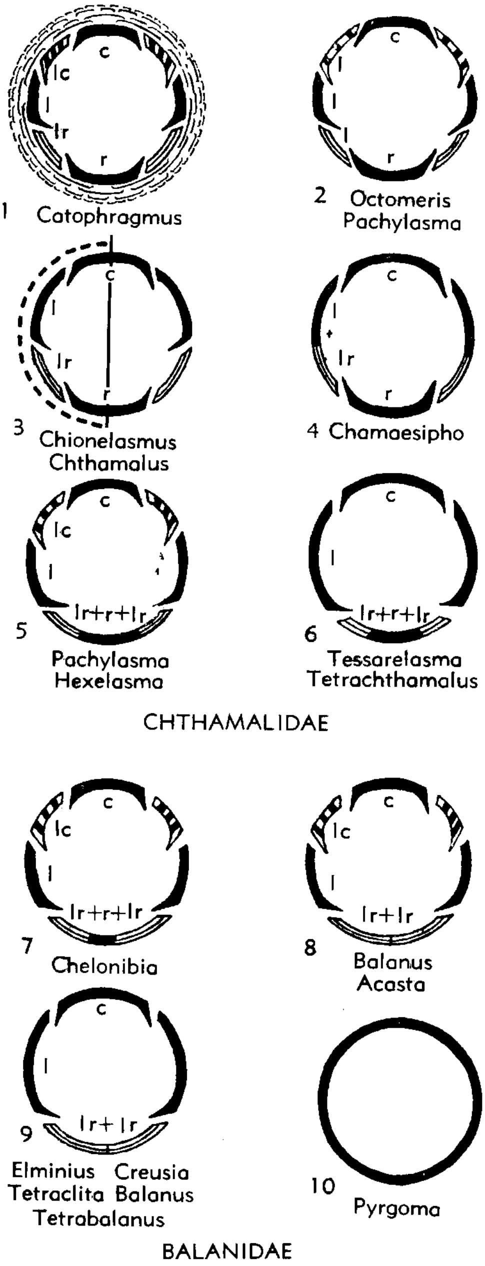


FIG. 96. Cirriped morphology. Diagrams showing modes of imbrication and homologies of compartments in the Chthamalidae *(1-6)* and Balanidae *(7-10)* (after Darwin and Pilsbry). [Explanation: *c,* carina; *lc,* latus (carinal); *l,* lateral; *lr,* latus (rostral); *r,* rostrum.]

ARTHROPODAL STRUCTURES

The Cirripedia have the fundamental body plan of the Maxillopoda (DAHL, 1956), that is, five appendage-bearing head somites, six appendage-bearing thoracic somites and five abdominal somites. Basically the abdomen is appendageless, except for the first and the last somites which bear male reproductive structures and a furca respectively (Table 1). Only a few of the least specialized Ascothoracica have an entire complement of somites and appendages in the adult stage, although it is not certain that the so-called second antenna of *Baccalaureus* (PYFINCH, 1939) is actually the homologue of this structure. In adults of all other orders, the second antennae and abdomen are lost, although a vestige of the latter may be represented by the so-called **basidorsal point** seen in certain Balanomorpha. Most of the Acrothoracica, the Verrucomorpha, most of the Lepadomorpha, and a few of the primitive Chthamalidae among

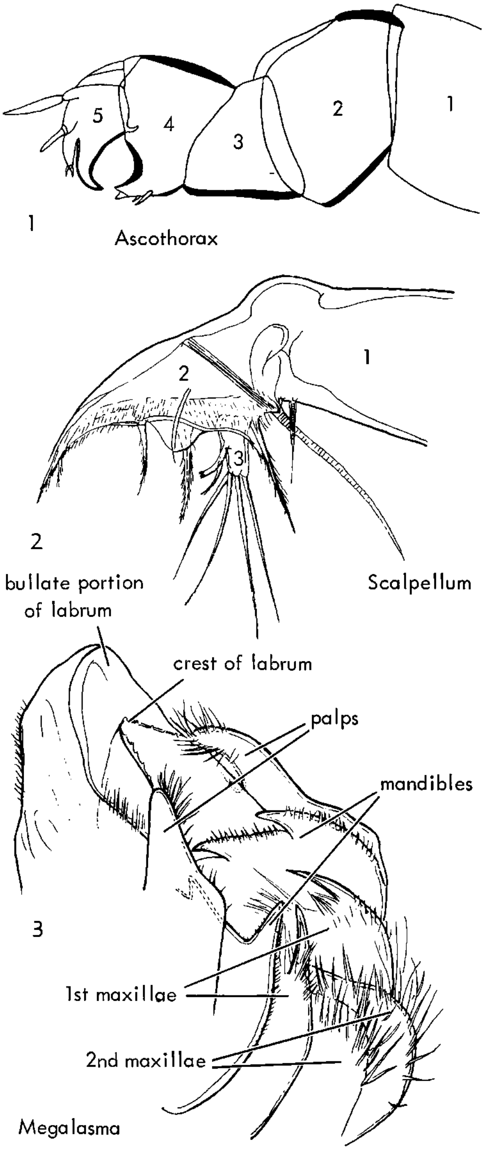


Fig. 97. Cirriped morphology. Antennae and trophi. ——*1*. First antenna, male *Ascothorax ophioctenis* Djakonov, ×35 (after *111*).——*2*. First antenna, cyprid stage, of *Scalpellum gibberum* Aurivillius, ×290 (after *77*).——*3*. Trophi, *Megalasma striatum* Hoek, ×63 (after *53*).

the Balanomorpha have terminal or caudal appendages, probably representing the caudal furca (Calman, 1909) (see Fig. 104, *1c,2a,3,4*).

In the Cirripedia, the antennules or first antennae are uniramous, and always prehensile at some stage of development. In the cyprid and adult of the Ascothoracica, they are four- or five-jointed, subchelate, and serve as devices for temporary attachment in most species. In the other orders, they are four-segmented, provided with a suction disc on the second segment used for temporary attachment in the cyprid, and with cement-producing glands, opening on the second segment used for permanent attachment prior to metamorphosis into the adult (Fig. 82; 97,*2*).

The next pair of head appendages, the second antennae, are biramous during the naupliar stages, but are lost in the cyprid and adult (Fig. 81; 82,*3*). A vestige may be found in some cyprids (Batham, 1945) or may be represented as a much modified filament-like process extending into the dorsal brood chamber of the female or hermaphroditic Ascothoracica where they probably function in care of eggs (Utinomi, 1962).

The third head appendages are also basically biramous, as in all Crustacea, and where present in the adult, the gnathobases of the protopods form the mandibles. In the Ascothoracica, the mandibles and other mouth parts are modified for piercing and sucking, but in the Acrothoracica and Thoracica, they function in grasping, manipulating, and in some forms triturating the food before delivering it to the mouth. In the Acrothoracica, the mandibles are each provided with a one-segmented palp, also present in the Thoracica. In the latter, however, the position has shifted from the outer margin of the mandibles to the outer margins of the labrum or upper lip. In either position, the palps serve to control food particles in the area over the exposed margins of the labrum, mandibles, and following mouth appendages (cf. Fig. 80, 97, 98).

Although the general form of the mandible in Acrothoracica and Thoracica is quite similar, the number, arrangement, and development of teeth, spines, and setae differs considerably among genera, particularly in the Lepadomorpha, suggesting differences in food habits (Fig. 98). These differences in structure are of considerable systematic value.

Immediately behind the mandibles, and acting in essentially the same plane, are the

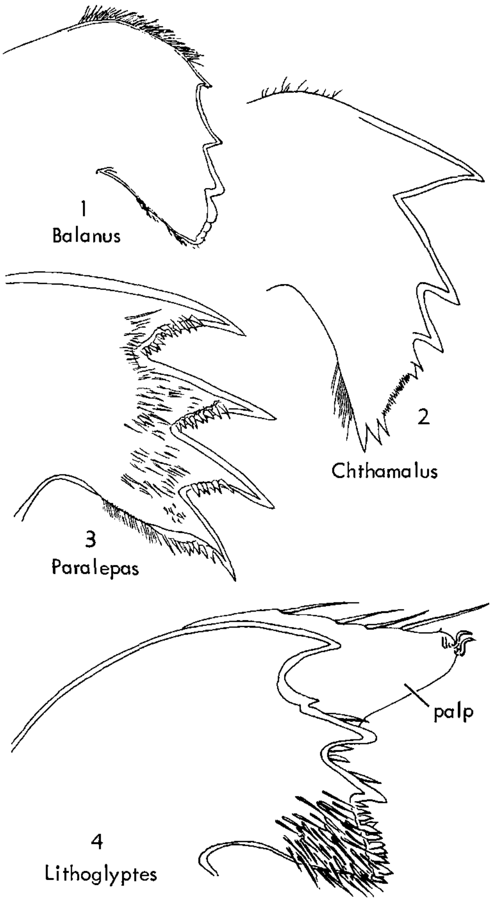


FIG. 98. Mandibles of cirripeds.——*1. Balanus (Balanus) hystrix* HOEK, ×96 (after *55*).——*2. Chthamalus challengeri* HOEK, ×147 (est.) (after *83*).——*3. Paralepas palinuri* BARNARD, ×33 (after Newman, 1960).——*4. Lithoglyptes spinatus* TOMLINSON & NEWMAN, mandible and palp, ×267 (after *103*).

first maxillae. They are somewhat similar in form to the mandibles, and, on theoretical grounds, were inferred to represent modified gnathobases of a biramous limb. Evidence that this is the case was only recently forthcoming, where the biramous rudiment was observed in a late nauplius stage (CRISP, 1962). The first maxillae are as diverse in form and armament as the mandibles, and some features, such as the presence or absence of a notch or a stepwise or protuberant portion of the cutting edge, appear to be of systematic value (Fig. 99,*1-4*).

The fifth pair of head appendages, the second maxillae, are comparable in general form to the preceding two pairs, but are more delicate and less jawlike, being provided with relatively soft setae and thin cuticle (Fig. 99,*1b,4*). They appear to act in the manner of a lower lip or labium and indeed, as in the labiate arthropods, they may be fused together, basically serving to close the back of the mouth field. Openings at or near their bases are the apertures of the maxillary glands.

In the Ascothoracica, the trophi or mouth parts are cutting, piercing, and sucking, and are surrounded by the labrum, forming a protuberant oval cone apparently adapted to dealing directly with the matter of obtaining food (Fig. 80,*1*). The trophi of the Acrothoracica and Thoracica on the other hand, are manipulating and triturating structures, having the food passed to them by the following appendages, rather than being applied directly to the matter of gathering food. The trophi nontheless are surrounded anteriorly and laterally by the labrum which extends nearly vertical from the body. This entire complex surrounds the mouth and protrudes as a unit below the ventral surface of the body. According to DARWIN, the entire trophic complex can be moved about to a considerable extent (Fig. 97,*3*).

Primitively, the labrum is bullate, with a broad, straight, or somewhat concave ventral margin or cutting edge, with or without soft setae or small sharp toothlike spines (Fig. 97,*3;* Fig. 100,*2*). This condition is seen in the Acrothoracica, Verrucomorpha, and Lepadomorpha, and in the Chthamalidae among the Balanomorpha. In the Balanidae, however, a median notch has developed as a specialization along with the loss of the bullate appearance of the labrum as a whole.

The six pairs of appendages following the second maxillae are thoracic and basically biramous. Except in the Ascothoracica, where they are straight and natatory as they are in the cyprid, they have a characteristic curled form and are called cirri. A cirrus consists of a two-segment protopod or pedicle, supporting a multiarticulate exopod and endopod. The rami are usually designated as outer and inner, but in many

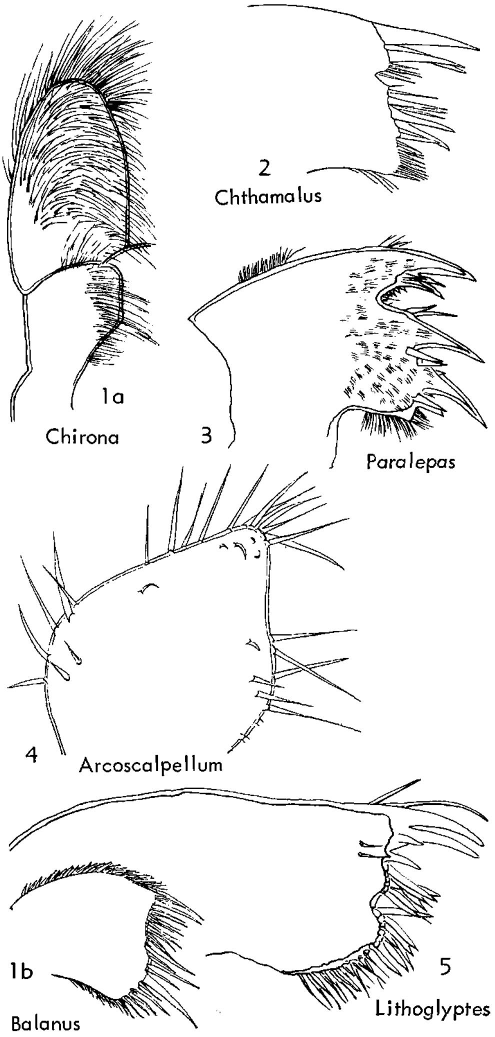


FIG. 99. Maxillae of cirripeds.——*1. Balanus; 1a, B. (Chirona) amaryllis* Darwin, second maxilla, ×20; *1b, B. (Balanus) hystrix* Hoek, first maxilla, ×96 (after *55*).——*2. Chthamalus challengeri* Hoek, first maxilla, ×147 (est.) (after *83*).——*3. Paralepas palinuri* Barnard, first maxilla, ×33 (Newman, 1960).——*4. Arcoscalpellum ventricosum* (Hoek), second maxilla, ×110 (after *77*).——*5. Lithoglyptes spinatus* Tomlinson & Newman, first maxilla, ×267 *(103)*.

forms, it is necessary to refer to them as anterior and posterior, when they appear so arranged. In the Ascothoracica, the homologues of the cirri are natatory (Wagin, 1946) (Fig. 101,*1*), while in the Acrothoracica and Thoracica the cirri serve to capture food (Fig. 101; 102,*1-3*).

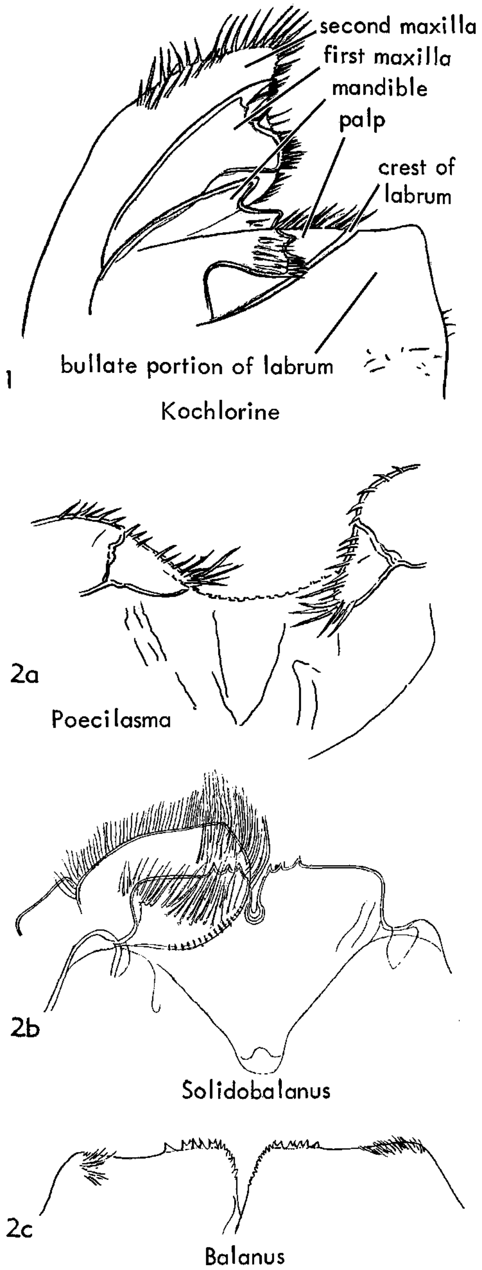


FIG. 100. Trophi and labra of cirripeds.——*1.* Trophi, *Kochlorine floridana* (Wells & Tomlinson), ×230 (Tomlinson, n).——*2.* Labrum and palps, *2a, Trilasmis (Poecilasma) gracile* (Hoek), ×72 (after *53*); *2b, Balanus (Solidobalanus) ciliatus* (Hoek), right palp removed, ×34 (after *55*); *2c, Balanus (Balanus) eburneus* Gould, both palps removed, ×16 (after *83*).

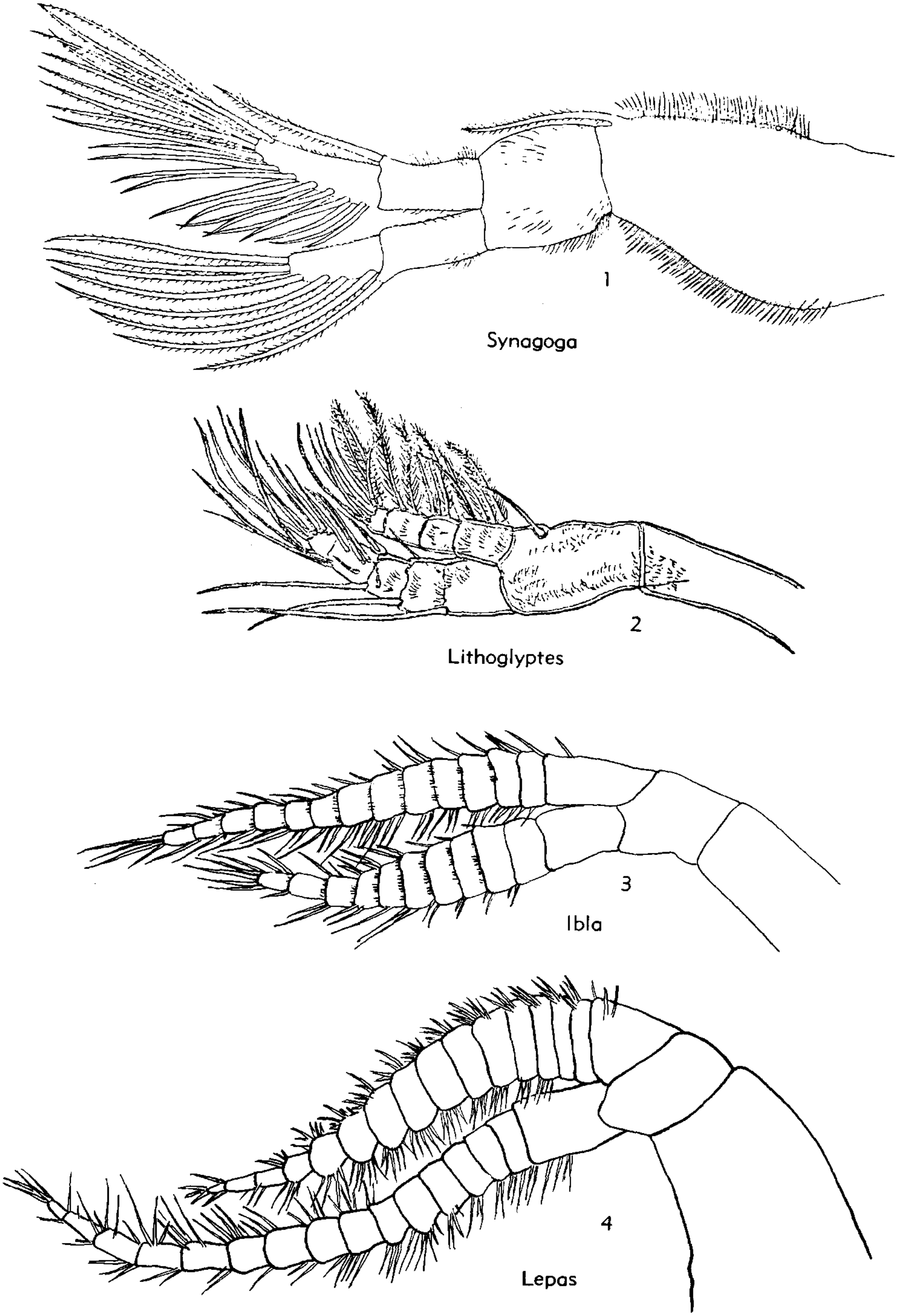


FIG. 101. First cirri of cirripeds.

1. *Synagoga metacrinicola* OKADA, ×100 (est.) (after Okada, 1939).
2. *Lithoglyptes spinatus* TOMLINSON & NEWMAN, ×150 (after *103*).
3. *Ibla cumingi* DARWIN, ×44 (Newman, n).
4. *Lepas (L.) hillii* LEACH, ×44 (Newman, n).

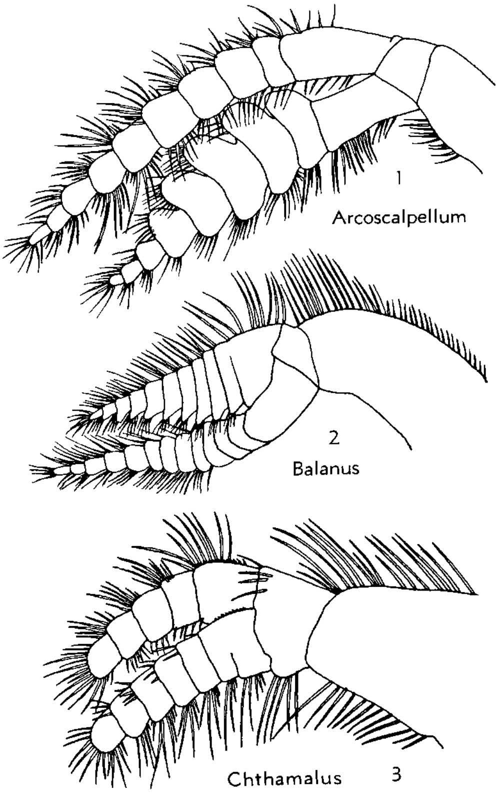


Fig. 102. First cirri of cirripeds (Newman, n).——*1. Arcoscalpellum osseum* (Pilsbry), ×16.——*2. Balanus (Balanus) amphitrite* Darwin, ×18.——*3. Chthamalus panamensis* Pilsbry, ×40.

The first pair of cirri usually differ somewhat in structure from the others, functioning as accessory mouth parts, and they can legitimately be called maxillipeds in all but the most primitive forms. Additional cirri may also be modified as maxillipeds in higher forms. Clearly they have become so modified independently of the development of this condition in other Maxillopoda and in the Malacostraca.

The first pair of cirri, when modified to form maxillipeds, have been drawn into close association with the trophi in transferring food from the cirri to the mouth. This separation from the following cirri is especially marked in the Acrothoracica, where all cirri behind the single pair of maxillipeds (formerly mouth cirri) are separated by the entire length of the thorax (Fig. 80,2). The Thoracica have up

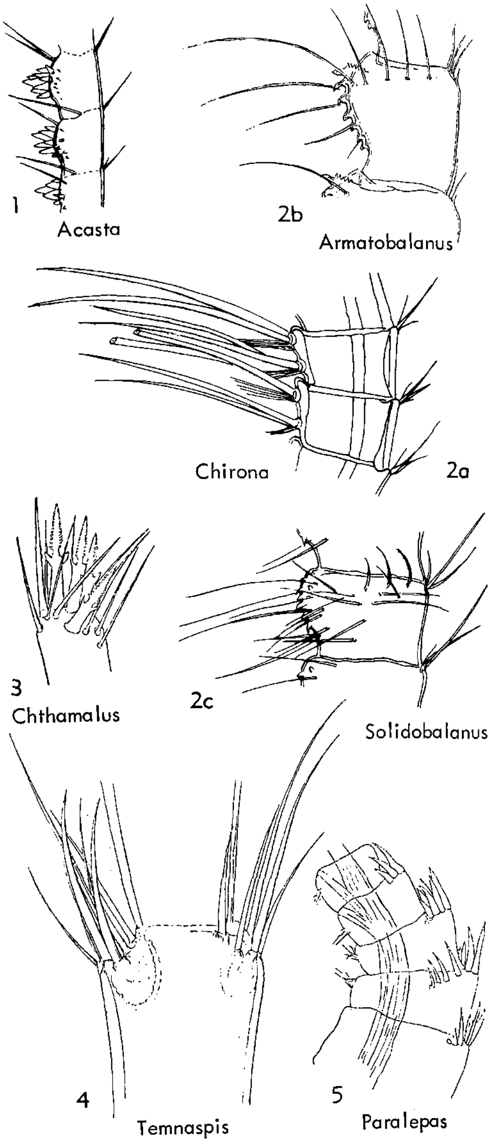


Fig. 103. Cirral armament of cirripeds.——*1. Acasta conica* Hoek, intermediate segments, fourth cirrus, ×96 (after *55*).——*2. Balanus; 2a, B. (Chirona) amaryllis* Darwin, intermediate segments of sixth cirrus, ×30; *2b, B. (Armatobalanus) arcuatus* Hoek, intermediate segments, third cirrus, ×137 (ctenopod type); *2c, B. (Solidobalanus) ciliatus* Hoek, intermediate segments, third cirrus, ×96 (after *55*).——*3. Chthamalus fragilis* Darwin, terminal spines, second cirrus, enl. (after *83*).——*4. Trilasmis (Temnaspis) fissus* Darwin, intermediate segments, sixth cirrus (lasiopod type), ×169 (after *54*).——*5. Paralepas palinuri* Barnard, intermediate segments, fifth cirrus (acanthopod type), ×33 (Newman, 1960).

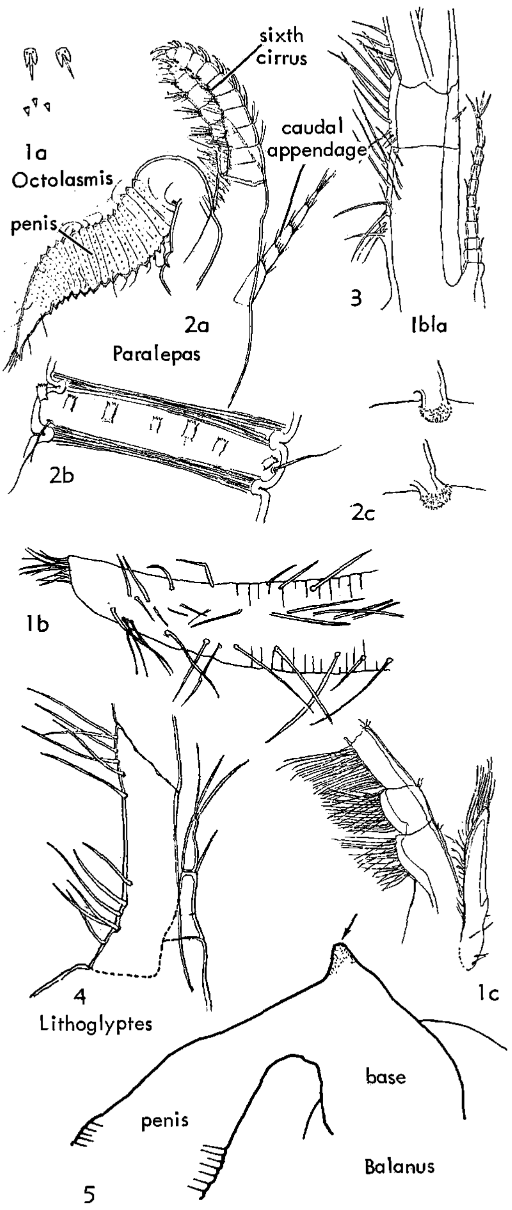


FIG. 104. Terminal appendages and penes of cirripeds.——*1. Octolasmis; 1a, O. (O.) cor* (AURIVILLIUS), two types of barbs clothing the penis, ×147; *1b, O. (O.) californiana* NEWMAN, terminal portion of penis, ×134; *1c, O. (O.) cor,* caudal appendage and pedicle of sixth cirrus, ×40 (Newman, 1960).——*2. Paralepas; 2a, P. lithotryae* HOEK, penis, sixth cirrus and caudal appendage, ×35 (after *54*); *2b, P. lithotryae* HOEK, rivet-like barbed structures clothing penis, ×169 (after *54*); *2c, P. palinuri* BARNARD, rivet-like barbed structures clothing penis, ×334 (Newman, 1960).——*3. Ibla cumingi* DARWIN, caudal appendage and pedicle of sixth cirrus, ×14 (Newman, 1960).——*4. Lithoglyptes spinatus* TOMLINSON & NEWMAN, caudal appendage and pedicle of terminal cirrus, ×100 *(103).*——*5. Balanus (Balanus) amphitrite* DARWIN, basal portion of penis, arrow indicating basidorsal point, ×22 (Newman, n).

to three pairs of maxillipeds assisting in the transfer of food, and, in general, their addition, pair by pair, follows phylogenetic lines. In the primitive Lepadomorpha (i.e., *Lepas*), only the first pair differs from the following, and then only slightly. In more advanced forms, the first pair differs considerably from the following, while the second pair has been modified slightly. In the Balanomorpha, the Chthamalidae have the first and second cirri serving as maxillipeds, while in the Balanidae, the first, second, and third pairs form a graded series on their degree of modification, differing conspicuously from the posterior three cirriform pairs.

The cirri are generally flattened laterally and curled anteriorly. The anterior margin of each ramus can be designated as the lesser curvature; the posterior margin as the greater curvature. The lesser curvature of the articles usually supports long setae arranged in a number of pairs along the length of each article, and it was suggested by PILSBRY (1911) that cirri with this arrangement be designated as **ctenopod cirri** (Fig. 103,*2a*). In ctenopod cirri, the setae of each pair spread laterally away from each other, crossing the spaces between rami, forming the cirral net when the cirri are extended. These setae can be simple or slightly plumose. Ctenopod cirri usually have a few setae at the distal edge of each article, along the greater curvature. Another type of cirrus was noticed by DARWIN (1851) in a small pedunculate barnacle, where the setae at each articulation tended to be arranged in a transverse row, and PILSBRY suggested this type be designated as **lasiopod cirri** (Fig. 103,*4*). In some species, the row of the greater curvature is composed of stout, sharp spines while there were few or no setae along the lesser curvature. This arrangement is quite distinct from the previous two types and has been designated as **acanthopod cirri** (Fig. 103,*5*).

In certain species of *Chthamalus,* a few of the terminal setae of the second cirrus are

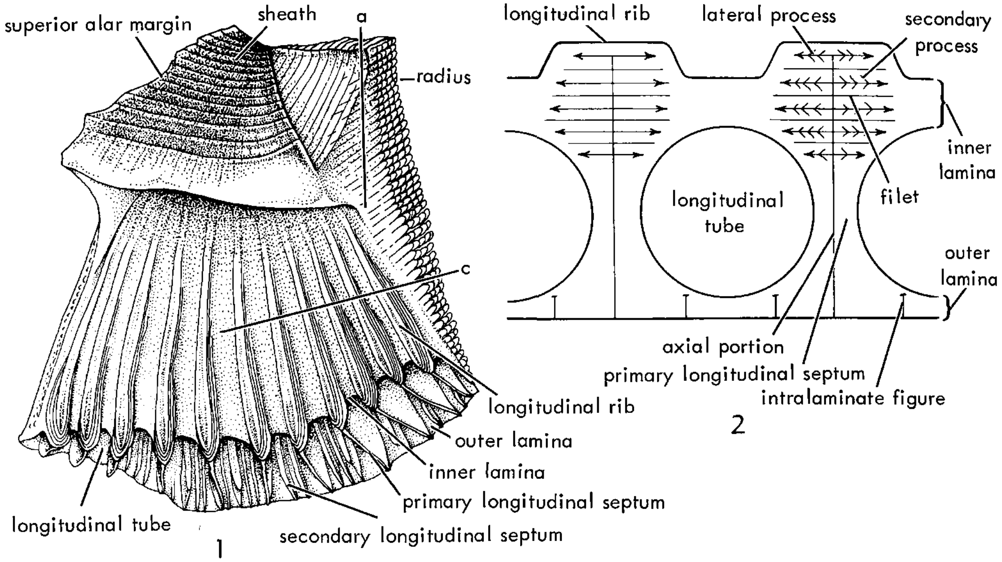


Fig. 105. Morphology of cirripeds; interlaminate figures in balanomorph shell wall (after *76*, mod.).

1. *Balanus (Balanus) amphitrite* Darwin, left lateral plate viewed from interior, enl.

2. Schematic cross section of *Balanus (Balanus)* shell wall at level *c* indicated in *1*, illustrating parts of wall and characteristics of figures; axial portion+filet+lateral process+secondary process (all or in part) belong to interlaminate figure.

[Explanation: *a*, area of transverse section in radius (see Fig. 106,*2*); *c*, area of transverse section in parietes (see Fig. 106,*3*).]

lanceolate, with serrate and barbed edges (Fig. 103,*3*). In the balanids, in addition to supporting setae, the articles are frequently armed with denticles and true spines (Fig. 103,*1,2b,2c*), especially those of the third and fourth cirri.

The number of articles of the cirri, their relative lengths, the relative lengths of the rami, and the arrangement of setae, spines, and hooks, differ considerably between many genera and species of Thoracica, indicating differences in feeding, and these characteristics are of obvious systematic value.

All female or hermaphroditic Thoracica have six pairs of cirri, but in males of this order and in female Acrothoracica the number is usually reduced. In the Acrothoracica, the full complement seen in the primitive genus *Weltneria* is present, but there are as few as two uniramous pairs in *Trypetesa.* The rami of cirri have retractor muscles but no protractors. Their extension is accomplished by hydrostatic pressure of the hemolymph (Cannon, 1947). They are therefore well provided with blood channels and under certain conditions of activity probably function as respiratory, as well as feeding organs.

On the pedicles of the cirri, particularly the first, in genera of Lepadomorpha (e.g., *Pollicipes, Heteralepas s.l., Lepas, Conchoderma, Megalasma*) filament-like extensions of the body wall are found (Fig. 83,*1*). These have been thought to be respiratory structures, but it seems likely that they are at least also concerned with the incubation of eggs within the mantle cavity. In this regard, the present authors suggest that they are analogous with the so-called branchiae or much elaborated extensions of the mantle lining found in most Balanomorpha (e.g., *Balanus, Chelonibia, Chthamalus*). It has been noted that the female genital apertures open at the bases of the first cirri, and this is the most anterior position known among the Crustacea. When cirral filamentary appendages occur in reduced numbers, they are usually found on the first cirrus or near its base and not uncommonly in close association with the genital aperture.

Sexes are separate in many of the Ascothoracica, some Thoracica, and all of the Acrothoracica, but the method of fertilization is unknown. Ascothoracica and some of the reduced males among the Acrothoracica and Thoracica have a so-called penis or intromittent organ. In the former (Fig. 82,*2*), this is located on the first abdominal somite, and in the latter, within the sac constituting the reduced male (Fig. 80,*2a*). In the Thoracica, the abdomen has been lost and in hermaphroditic species, that is, the majority of Lepadomorpha, all known Verrucomorpha, and the Balanomorpha, the intromittent organ arises from between the base of the last or sixth pair of cirri (Fig. 104,*2a*). It is prosbosciform, greatly distensible, and in many species capable of transferring sperm to neighboring individuals some distance away. In hermaphrodites, fertilization at a given mating is not known to be reciprocal, but rather one individual acts as the female and the other as the male. Presumably the roles are reversed at another time. Although sperm is actually transferred from one individual to another, where well investigated the act is not strictly copulation, for the sperm are deposited in the mantle cavity, outside the body, where fertilization occurs. The intromittent organ is generally annulated, in some cases strongly so, and DARWIN (1851-54) was inclined to consider the annulations as somites of the reduced abdomen, an interpretation accepted by KRÜGER (1940). However, the fact that no other metameric structures are associated with the annulations, that the presumably homologous intromittent organ of the Ascothoracica arises on the first abdominal somite, and that no other crustacean is known to be opisthogoneate, precludes this interpretation.

The intromittent organ is usually provided with soft setae, particularly at the apex (Fig. 104,*1b*). Setae in some forms are arranged in particular patterns, and bristles, knobs or complex spiny knobs directed basally (e.g., *Heteralepas, Octolasmis*) may be present (Fig. 104,*1a,b;2a,b*). Where such specially developed and arranged structures occur, they are regarded to be of considerable systematic value.

STUDY TECHNIQUES

PALEONTOLOGICAL METHODS

COLLECTION

Fossil taxa of lepadomorphs, brachylepadomorphs, and verrucomorphs are often based on isolated plates, as the shell of the animal usually becomes disarticulated soon after death. The shell of most balanomorph barnacles is more rigidly articulated, and complete specimens are often recovered. However, the opercular valves, which are important in identification, rarely remain fixed in their position in the orifice after death, and they may be lost.

In collecting from rocks where fossil barnacles are known to occur, a bulk sample should be taken from each barnacle-bearing stratum, washed, and screened (if possible), and sorted for all barnacle plates or fragments. In the case of loosely articulated forms such as the lepadomorphs, the complete individual can often be reconstructed. Opercular valves can usually be recovered in this manner also, although examination of the interior of shells will often reveal the full complement of valves preserved where they have fallen to the bottom of the body chamber.

INTERLAMINATE FIGURES AND THIN SECTIONS

Interlaminate figures, discovered by DE ALESSANDRI (1895) are found in balanomorphs having a wall permeated by longitudinal tubes. CORNWALL (1962 and earlier) and DAVADIE (1963) have used interlaminate figures in the shell for determination of balanomorph species from fragmentary remains. Interlaminate (and shorter intralaminate) figures are observed in the transverse section of the parietes and represent crystalline organization about an organic matrix developed during the formation of the complex articulation between the parie-

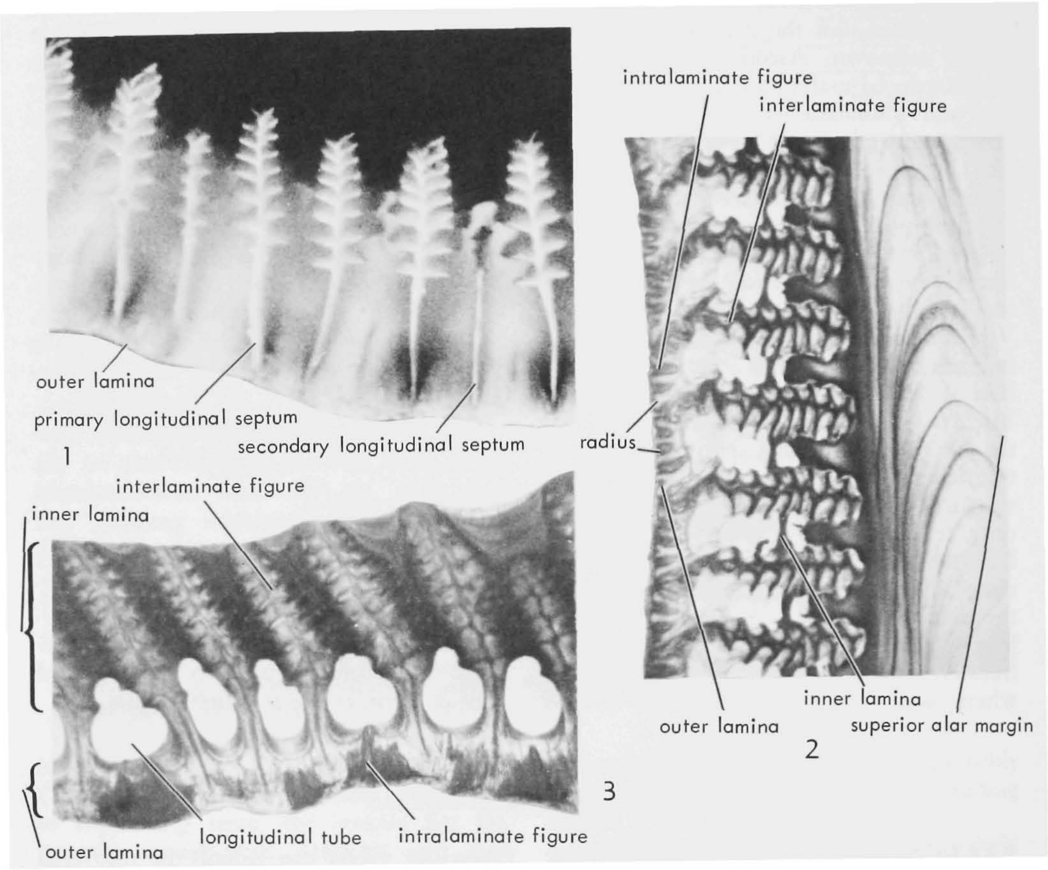


FIG. 106. Morphology of cirripeds; interlaminate figures in balanomorph shell wall *(Balanus (Megabalanus) tintinnabulum californicus* (PILSBRY), enl.

1. Basal margin of wall viewed from below, showing septa and teeth which lock between radial septa of basis (from *76*).
2. Interlaminate figures seen in radius where radial teeth interlock with ala of adjacent plate; section cut at level *a* shown in Fig. 105,*1* (Newman, n).
3. Interlaminate figures seen in transverse section of wall plate cut at level *c* in Fig. 105,*1* (Newman, n).

tes and the basis (Fig. 105,*1-2;* Fig. 106,*2*) (NEWMAN, ZULLO, & WAINWRIGHT, 1967). A similar pattern may be seen in a longitudinal section of the radii, reflecting the development of articulating sutural edges. The pattern related to these articular structures is observed as darker "figures" against the light background of the shell (Fig. 106,*1*).

Interlaminate figures appear to be characteristic of some species and are potentially of value in the determination of taxa from fragmentary material. Studies of the interlaminate figures of some Recent and Tertiary Californian barnacles indicate that some species may display more than one type of figure, and that several species may share a particular figure type. A thorough study of extant and fossil species from various localities throughout their geographic range will be required before the taxonomic value of this method can be established.

A variety of techniques and equipment are available for cutting thin sections of cirriped hard parts. The simplest procedure is to mount a piece of shell to be sectioned on a glass microscope slide and hand grind the exposed surface with a circular motion flat to about 1 mm. thickness. The specimen is then removed, turned over and reaffixed, with the freshly ground flat side toward the slide. The newly exposed surface is then ground in the same manner until, ideally, it is flat and 20-30μ thick.

The piece being sectioned can be affixed to the slide with any petrographic thermoplastic cement. The cement is melted on the slide, over an alcohol lamp, hot plate, or other heat source, with the specimen in place. Pressure is applied to the specimen before cooling, so that it comes into even contact with the slide surface. The melted cement is hot (145°F. or more) so that a piece of sponge is useful in applying the needed pressure. A piece of thin aluminum foil, foil-coated wrapping paper being ideal, is placed between the sponge and the specimen to prevent sticking.

Rough cutting and rapid removal of material requires abrasives of 100- to 200-grit, while finishing cuts and polishing utilize 400- to 600-grit. A few intermediate grades between these two extremes are useful during the grinding process. Grinding can be done by sprinkling an appropriate abrasive, or by using so-called wet and dry sand papers, on a sheet of plate glass flooded with water. Surfaces should be carefully cleaned when changing from one grit to another.

This method will yield satisfactory sections if the operator is particularly skilled, but it is difficult to get hand-held sections perfectly flat and uniformly thick. Performance can readily be improved by using guides or shims of various thicknesses. Two strips of steel shim stock placed on the glass or paper form tracks on either side of the specimen, separating the slide an appropriate distance from the cutting surface. Shims 0.001 inch thick will allow the specimen to come to within approximately 25μ of the cutting surface, and would be used for the final cut. When the section is finished, optical interference from scratches and other surface irregularities can be minimized by applying a drop of balsam and a cover slip.

For the worker cutting a section or two at infrequent intervals, the procedure outlined above is probably sufficient. If large quantities and sustained production are anticipated, one had best consult petrographic hand books on the subject, or professionals in the field, for a considerable amount of mechanization would be required. In between these two requirements are those who wish to carry out repetitive sectioning of perhaps ten samples ten times a year, and here a few accessories to the bare essentials outlined above would be reasonable. We have found the following improvements useful and they require only a modest outlay in funds.

Aside from the difficulties of getting good sections, one of the problems in hand-sectioning is holding the slide without acquiring numerous small cuts and abrading away significant amounts of skin. Also, the shim stock, although it can be held in line with tape, tends to skid about and get abrasive between it and the grinding surface and the slide, or both. To overcome these difficulties, increase the rate of production and improve the quality of the sections, a slide holder is desirable and some are commercially available. A slide holder consists of two accurately ground metal blocks, held in alignment by rods running through them, and grooved to hold a standard slide by tightening a thumb screw, which draws the blocks together. The outer surface of the slide is held slightly below the surface of the blocks so that a specimen on the slide will be ground to a thickness equaling this distance, when the surface of the block comes into complete contact with the grinding plate at the end of the cut. A specimen so ground can be dead flat and of uniform thickness. To prevent the block itself from being slowly ground away with each operation, and thus gradually decreasing the distance between the surface of the slide and the surface of the block, surfaces of the block coming in contact with the grinding surface are faced with precision ground boron carbide runners. This material is much harder than abrasives such as silicon carbide, and therefore undergoes little wear and loss of accuracy.

Slide holders presently cost less than one hundred dollars. They are designed to hold petrographic slides, which, after having been ground to a standard thickness in another specially designed holder, will clear the grinding surface of approximately 50μ, thereby yielding sections too thick for our purposes. This can be overcome by placing a piece of shim stock 0.001 inch thick between the slide and the holder, which advances the slide approximately 25μ and yields a section of comparable thickness.

We have found it convenient to use ordinary microscope, rather than petrographic slides. However, slides from any given lot, although parallel-sided, usually vary in thickness from one end to another and from side to side, some to a marked degree. A box can be checked over quickly by measuring the thickness of individual slides at each end, and at each side near the middle. Those varying only a few microns, especially from side to side, can be used for grinding thin sections. A micrometer, calibrated in 100ths of a millimeter (10μ) and readable to within a few microns by interpolation, is satisfactory for this purpose, and for estimating the thickness of the section.

Ordinary microscope slides are considerably thinner than petrographic slides, so that when used without backing shims, the first surface grinding results in a section more than 100μ thick. Such a section is strong enough to be turned over and pressed flat against the slide, in order to cut the second surface. The thickness of the section can be estimated by subtracting the thickness of the slide adjacent to the specimen from thickness of the slide and the specimen, as measured with a micrometer before beginning the second cut. The amount of material to be removed is then estimated and an appropriate number of shims placed between the slide and backing face of the holder. When the last polishing cut is to be made, it is a good policy not to rely on estimates made with the micrometer of the number of shims necessary to bring the section to final thinness, but rather to use a 0.001-inch shim as a feeler gauge inserted between the surface of the slide and a straight edge (the long edge of another slide), held across the two boron carbide runners. Sections will occasionally be lost without taking this precaution.

A sheet of plate glass, about 9x12 in. or larger, is a convenient grinding surface. The surface should be wet and, when using sand paper, running water is desirable. If a sink is available, a simple way to achieve this is to mount the glass on a pair of wooden supports arranged so as to bridge the sink. The relatively new silicon rubber cements for glass and ceramics are excellent for bonding the glass to the supports. A rubber tube from the cold water faucet can then be used to provide a slow stream of water, the runoff spilling into the sink.

Ordinary water-proof sand paper, especially in the coarser grits, has proved satisfactory. The relatively new abrasive coated *Mylar* films sold under the trade name *Flex-i-grit,* are more durable, especially in the finer grits, but are not generally available locally.

Preparation of blanks of the material to be sectioned can be accomplished by breaking, filing, sawing, and power grinding. Small, relatively inexpensive, diamond-impregnated discs or wheels available through dental supply houses, driven and manipulated by hand-held motors such as those available under the trade name *Mototool,* are highly recommended. With them, relatively thin, flat-sided portions of a specimen can be removed, often leaving the bulk of the specimen intact. Although manufacturers recommend that these wheels be run wet, satisfactory cutting or microslabbing can be accomplished dry.

NEONTOLOGICAL METHODS

The diversity of habitats in which cirripeds occur may even be surprising to the marine biologist with considerable field experience. This would be especially true in the tropics where, although not usually occurring in great numbers in any one place, the variety of niches occupied is remarkable.

The Acrothoracica are burrowing forms, able to penetrate any calcareous substratum, particularly mollusk shells and skeletons of living and dead scleractinian corals. They are less often found in echinoid and balanoid shells, but are frequently encountered in limestone. All described species are from shallow water, although an undescribed species is known from approximately 1,000 meters of depth on the Bermuda slope in the western Atlantic.

Usually the only visible sign of an acrothoracican's presence in a piece of calcareous substratum is the small slitlike opening to the burrow, generally a millimeter or so in length and shaped like a straight or slightly curved apostrophe. This small aperture opens into a commodious oval chamber excavated and inhabited by the female which usually is accompanied by one or more dwarf males. The chamber may extend straight or somewhat obliquely down from the surface and can be studied by making casts with materials not attacked by acid and then dissolving away the substratum, or by successively grinding the substratum, gradually exposing the outline of the burrow. X rays are useful in exploring certain kinds of materials, especially gastropod shells inhabited by hermit crabs, where the burrows open on the interior surface.

The aperture of the burrow is guarded by the chitinous lips formed at the mantle opening of the barnacle. Shortly after placing an object bearing living acrothoracicans back in sea water, the operculum formed by these lips will be drawn back and the cirri thrust forth forming the cirral net. The appearance of cirri is useful in confirming the presence of living specimens and is especially useful in locating them in materials encrusted with sponges, bryozoans, and algae. Females can be removed by chipping the substratum away, but usually not without some obvious damage, especially if cemented to the burrow. Another method involves treatment with acid after the material has been properly fixed in Bouin's fluid, 70 percent alcohol, or another appropriate fixative. A specimen can be studied externally and dissected in much the same manner as the relatively unarmored Lepadomorpha described below. Or it can be treated with dilute sodium hydroxide in the manner described by TOMLINSON (1960), until most of the soft tissues have been digested away, but care must be taken in making observations on specimens so treated, because frequently the new cuticle developing beneath the old will have separated, giving a multiple or otherwise inaccurate appearance of structures. After this treatment and a thorough washing, the specimens may be stained or simply mounted directly in an appropriate medium on a microscope slide. Glycerin as a mounting medium is useful in allowing specimens to be manipulated, although, to avoid distortion of delicate structures, it is best to infiltrate the specimen gradually by placing it in a glycerin and alcohol solution and allowing the latter to evaporate. This procedure is equally desirable before mounting a specimen in glycerin jelly. Whole mounts need the support of a glass or plastic ring. The whole preparation should be sealed with an appropriate ringing medium, and clear "finger-nail polish" is convenient.

The acrothoracicans occur in calcareous substrates and therefore are relatively limited in the diversity of habitats they can occupy. The thoracicans on the other hand, are rarely obligated to any one particular substratum or association, are basically not dependent on support or armament provided by the environment, and consequently, exploit a great diversity of habitats. Some members of each of the suborders are found intertidally, on rocks and other intertidal organisms, and most are in a size range readily detected with the unaided eye. Of the Lepadomorpha, only a few genera occur intertidally. In particular, there are *Pollicipes* and *Lithotrya* among the Scalpellidae and *Ibla* of the Iblidae. The Verrucomorpha are primarily subtidal, but there are a few intertidal species, some being very small. The Balanomorpha contain a large number of species in both subtidal and intertidal situations. Although there are probably no rules for general collecting, it is desirable to obtain all of a particular specimen. The ease with which this can be accomplished will depend on where and how the animal is attached and, it is probably best to bring materials to the laboratory where they can be observed alive and carefully removed from their attachment place. As far as collecting is concerned, every conceivable habitat washed by sea water should be explored, specifically the surfaces of rocks to the highest reaches of the tides, the surfaces of living animals including mollusks, crustaceans, large jellyfish, sea urchins, other barnacles, sea snakes, turtles, cetaceans and so forth. The interiors of other animals should also be explored, especially the gill chambers of large decapod crustaceans, sponges, turtle gullets, and corals, and alcyonarians. At least one genus is known from within living clams and another between the pedal disc of sea anemones growing on gastropod shells inhabited by hermit crabs. Some species are also found on plant materials, including mangrove roots and leaves, seaweeds and flotsam in the sea.

Observations on living barnacles are interesting and instructive. Adult shore barnacles, especially estuarine or harbor forms, can often be maintained on young brine shrimp *(Artemia)* for extended periods of time, and frequently individuals will reattach to the walls of the container in which they are kept. Growth, molting, feeding, reactions to currents and shadowing, and mating can be observed. The mantle forms lips around the aperture that can adequately be observed only in living material. These are expanded when the animal is relaxed or feeding and have more or less striking color patterns. The function of these colors has not been determined, but they are of some systematic value (SOUTHWARD & CRISP, 1963).

Larvae can also be obtained in the laboratory, either spawned directly from the adults or from ovigerous lamellae removed from sacrificed animals and suspended in sea water (COSTLOW & BOOKHOUT, 1957). Culture techniques have become considerably refined, and differences in dietary requirements are being analyzed (MOYSE, 1963). Through the rearing of larvae, much has been learned of the morphology of different species, and methods of description are still in the process of development. Setation formulae have been used for descriptive purposes and appear to be an important aspect in comparative studies. However, considerably more work is needed before an understanding of larval relationships and affinities contribute to our knowledge of the systematics of the cirripeds *(75)*.

The larvae or their molts are readily prepared for microscopical study. Molts are usually obtained from individuals reared singly. Living nauplii, on the other hand, are generally handled in relatively large numbers. They are usually photo-positive and can be pipetted from a container illuminated on one side. These can be concentrated in a small glass tube opened at one end, and with a fine mesh of silk bolting cloth stretched and secured over one end. In this, the larvae are washed, fixed, and stained if desired, before transferring to a drop of glycerin on a microscopic slide. In glycerin, individuals can be manipulated or dissected so that the appendages can be observed, drawn, and setation counts made. If dissection proves difficult, preparations can be lightly squashed under a coverslip.

Preparation of adult barnacles for examination is relatively simple once the anatomical relationships are understood. Removing the body from the mantle or shell requires certain tools, the sizes of which will depend on the size and type of barnacle. In general, ordinary dissecting needles and forceps are useful. For small specimens, finer instruments are necessary. Small dissecting needles can be constructed from small sewing needles or insect pins mounted in appropriate holders. Fine jeweler's forceps are indispensible and not infrequently the finest available can be ground a little finer.

Acrothoracicans and small unarmored lepadomorphs can be removed from the mantle by plucking a hole in the side, withdrawing the body and then freeing it completely by teasing away the attachments of the adductor muscles. The body of armored lepadomorphs usually can be removed through the aperture by grasping the attachment area at the adductor muscle lying between the scuta, and gently withdrawing the body. Some teasing of the membranes between the scuta may be necessary in order to enlarge the aperture sufficiently, but this is usually unnecessary. In the Balanomorpha, the body is too large, relative to size of the aperture, to be removed in this manner, but it can be removed through the base, leaving the shell wall intact. The body is attached almost entirely to the scutal valves, which are in turn articulated with the terga. Therefore, in removing the opercular parts, the body is removed at the same time. The ease with which these parts are removed will depend on the structure and condition of the barnacle. Usually, inward pressure applied to the operculum, and teasing or cutting of the arthrodial membrane connecting it to the sheath of the wall, will allow the entire mass to be forced out through the base. Once removed, the body is easily dissected free of the opercular parts, under water in a small dish such as a Syracuse dish. The mantle cavity may contain ovigerous lamellae of eggs, developing embryos or larvae, and these should be saved for study. Frequently, the first larval stage can be obtained in this way. It can be either the first naupliar stage or the cyprid larva, depending on the life history of the species.

The opercular parts, as well as the wall plates, can be cleaned and disarticulated by soaking in sodium hypochlorite (commercial bleach such as Clorox). Methods of handling these parts will vary with the nature of the material and the interests of the investigator. Small vials, gelatin capsules, boxes, Curtin and Riker mounts are useful.

Once the body is removed, it can be studied under water, note being taken of the attachment and arrangement of cirri, the presence or absence of filamentary appendages (Lepadomorpha) or branchiae (Balanomorpha), and so forth. After these observations, the specimen can be dissected. The appendages and parts will usually mount satisfactorily on one or two slides, although large specimens may require special handling. Before dissection begins, some estimate of these requirements should be made. The actual dissection will vary with the worker, as will the selection of the mounting medium. Permanent synthetic resins and media such as Turtox CMC and Euparal, have certain advantages, but glycerin jelly has been satisfactory for us.

A clean microscope slide is warmed over an alcohol lamp and a few square millimeters of glycerin jelly are placed on it. The jelly should be spread so as to form a film covering the area to be occupied by the cover slip. Spreading can be aided with a warm dissecting needle and bubbles can be removed by pricking with the tip of a hot needle. The slide is then placed conveniently near the microscope and allowed to cool. The body of the barnacle in a dish of water will usually lie on one side or the other. For right-handed workers, it is usually convenient to place the animal on its left side and to dissect away the right cirri one by one, starting with the first. Special care must be taken if caudal appendages are present, as it is preferable that each remain attached to the base of the pedicle of each sixth cirrus. Then usually the cirri of the left side are removed, working from posterior to anterior.

As each cirrus of the right side is removed, it is generally placed in glycerin jelly on the slide outside surface up, in order from left to right. A little water is carried with the appendage and the tips of the forceps, and this aids in slowing the infiltration of jelly and rapid osmotic removal of water. The cirri of the left side are placed in a like manner so that their inner surfaces are up. Due to the osmotic situation, the penis with its delicate cuticle will generally shrivel if placed directly in the glycerin jelly and should be first infiltrated with glycerin.

At this point one is left with the appendageless thorax, and the prosoma supporting the buccal mass. These can be separated, and the former discarded, provided it does not support filamentary appendages. Some experience is helpful in dissecting out the mouth parts. Generally the first maxillae and mandibles are removed before attempting to remove the second maxillae. This is because the second maxillae are rather delicate and are fused together basally. They are best taken off as a pair and then teased apart, before mounting. The numerous muscles and adhering shreds of cuticle are removed from the labrum. It may be desirable to detach one of the palps and mount it separately, so that the crest of the labrum can be viewed. Although the mouth parts are readily distinguishable and there is little likelihood of getting them confused, it is best to mount them in a meaningful way, as was done with the cirri. This completes the dissection and the mount should be inspected and adjustments in the positions of parts made with the tip of a warm needle. The slide is then warmed gently to soften but not completely liquify the jelly, and a warmed coverslip is lowered into place, allowing one edge to touch first so that air can escape without forming bubbles. The finished slide should be cleaned and sealed and given an identifying mark or label.

A certain amount of flattening is unavoidable in a preparation of this sort, and structures such as the penis and labrum may best be studied in glycerin alone, without a coverslip, before being transferred to glycerin jelly.

It has long been customary to store barnacles dry and many collections are presently so maintained. Dried materials that have not been damaged by insects can be "reconstituted" to a considerable extent by soaking for several days in alcohol and glycerin. If the preparation does not soften sufficiently for dissection, it should be treated with a dilute solution (0.5 to 1 percent) of trisodium phosphate for one to several days. Specimens that have been dried for more than one hundred years have been successfully dissected after having been treated in this way.

ONTOGENY

EMBRYONIC AND LARVAL LIFE

Eggs are laid in the mantle cavity of the female or hermaphrodite where they are fertilized (Fig. 107). A substance secreted during laying forms a matrix holding the eggs in a mass of a more or less definite form. When formed in sheets, the masses are termed **ovigerous lamellae** (Darwin, 1851). In many species, the egg masses lie free within the mantle cavity, conforming closely to the space occupied, or, in *Lepas*

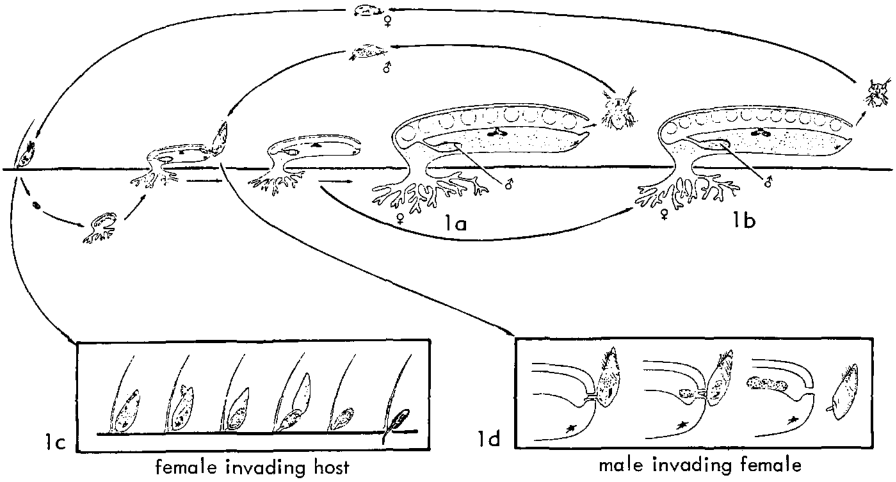


FIG. 107. Life cycle of *Peltogasterella gracilis* (BOSCHMA) (Rhizocephala); *1a,* female producing large eggs, nauplii and male cyprid larvae; *1b,* female producing small eggs, nauplii and female cyprid larvae; *1c,* female cyprid kentrogon invading hermit crab host; *1d,* male cyprid cells being injected into mantle cavity of young female and migrating toward male cell receptacles (Newman, simplified, after Yanagimachi, 1961).

and its allies, a pair of ovigerous lamellae are held in position by special structures called **ovigerous frenae.** Although the eggs are relatively yolky, cleavage is characteristic of the Spiralia, being total, unequal and presumably determinant in genera such as *Lepas* (BIGELOW, 1902). After a period of incubation, the eggs usually hatch as **nauplii** which are subsequently released by the adult (GROOM, 1894). The free-swimming nauplius generally molts five times, thus passing through six stages, each of increasing complexity (BASSINDALE, 1936). The nauplius has a pair of **frontolateral horns**—distinguishing the nauplii of Thoracica, Acrothoracica, and Rhizocephala from all other Crustacea; a nauplius eye, uniramous first antennae and natatory biramous second antennae and mandibles (Fig. 81). Gnathobases on the last two pairs of appendages serve to capture food and tuck it beneath a large labrum covering the mouth. By the last naupliar stage, compound eyes, first maxillae, the incipient six thoracic somites have appeared beneath the cuticle, and the setation of the naupliar appendages has gained considerable complexity. The sixth naupliar molt involves a complicated metamorphosis into a **cyprid larva** (GROOM, 1895; BATHAM, 1945) (Fig. 81, 84). The broad dorsal shield of the nauplius becomes the bivalved carapace of the cyprid, the first antennae become prehensile (Fig. 91, 2), the second antennae disappear, the mouth parts persist as rudiments, and the six thoracic limbs appear as natatory appendages.

The cypríd larva is not known to feed. It settles out of the plankton and selects the site where it will attach. Attachment is effected initially by the first antennae and once cemented in place, the cyprid undergoes a complex metamorphosis and reorganizaton in attaining a juvenile form (RUNNSTRÖM, 1925; BERNARD & LANE, 1962) (Fig. 108).

The nauplius stage is passed through in the egg in a number of thoracic cirriped species (Fig. 109,*A*), the larvae being liberated as fully developed cyprids (BARNARD, 1924; BROCH, 1924; HOEK, 1883; NILSSON-CANTELL, 1921) (Fig. 109,*B*). The deletion of the nauplius as a free-swimming stage is seen in the other orders of cirripeds: Ascothoracica (WAGIN, 1946; BRATTSTRÖM, 1948), Acrothoracica (NILSSON-CANTELL, 1921; TOMLINSON & NEWMAN, 1960; BATHAM & TOMLINSON, 1965), and Rhizocephala (NILSSON-CANTELL, 1921; BOCQUET-VÉDRINE, 1961). Yet the nauplius is a fundamental part of the basic cirriped life cycle, its elimination being a secondary development that appeared independently in the various orders.

EARLY DEVELOPMENT OF LEPADOMORPHA

Lepas has a nauplius larva which passes through six stages (Moyse, 1963). The last stage metamorphoses into a cyprid, which is weakly free-swimming. The cyprid swims about for an unknown, but presumably short, period of time, and then settles on virtually any floating or suspended object. Shortly after settling, five uncalcified primordial plates (carina and paired scuta and terga) appear beneath the bivalved cyprid shell. Then the cyprid shell becomes loosened, opens along the ventral margin, and is worked off, usually before the calcified plates appear (Fig. 87,*2-3*). The calcified plates are formed under, and extend beyond, the primordial plates and in later stages may be seen on the umbo of the calcified plates unless worn away (Fig. 87,*5-6*).

Development of plates in the Scapellidae is well shown in a series of *Pollicipes polymerus typica* described by Broch (1922), whose figures are reproduced here (Fig. 88,*1-7*). This barnacle exhibits a similar ontogeny to that of *Lepas,* including the appearance of five primordial plates as primary centers of calcification. At this point, a number of additional calcified plates appear which are not associated with primordial plates. Thus, although the basic number of primordia seems to be five, primordia are not required for a calcified plate to develop. In fact, the functional relationship between the primordial plates and calcification is unknown.

In the ontogenetic development of *Pollicipes* and *Lepas*, it was seen that a stage occurs where the animal is enclosed by the primordial plates and connecting membrane. It is only later that the calcareous plates are formed, and as they develop, the primordial plates are displaced farther and farther from each other, remaining on the umbo of the calcified plates. In Lepadomorpha, the five primordial plates are present, as they also are in the sessile asymmetrical forms included in the Verrucomorpha (Fig. 89,*1-4*).

Primordial plates, however, have not been found in Balanomorpha.

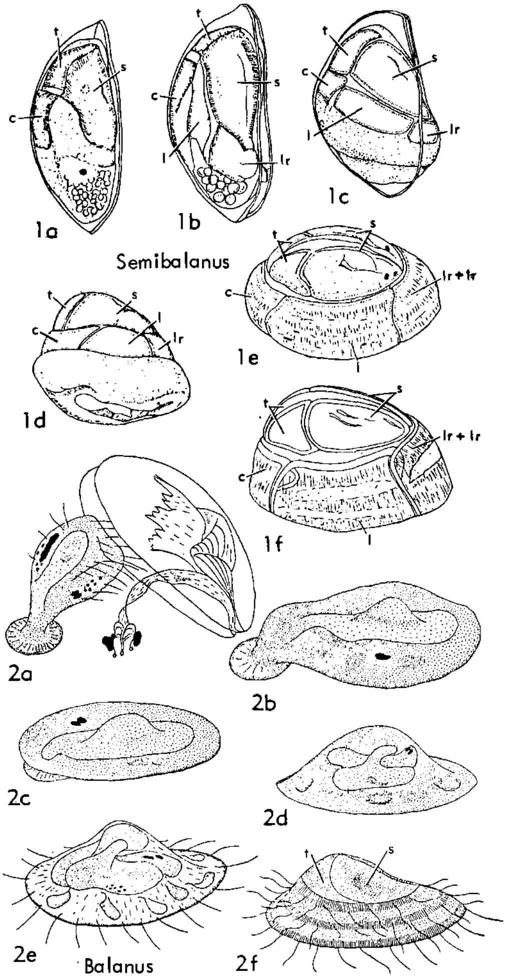


Fig. 108. Morphology of cirripeds. Metamorphosis in *Balanus.*——*1. Balanus (Semibalanus) balanoides* (Linné), enl.; *1a,* freshly settled cyprid larva with presumptive tergum, scutum and carina beginning to appear; *1b,* further differentiation of presumptive plates and appearance of two pairs of lateral plates; *1c,* cyprid shell about to be cast, terga and scuta becoming organized to form the opercular valves; carina, lateral and rostrolateral plates becoming organized into wall; *1d,* further differentiation and development of opercular and wall parts, rostrolaterals still separate; *1e,* rostrolaterals fusing, forming compound rostrum; *1f,* four-plated stage of *Semibalanus* (after Runnström, 1925, from *61*).——*2. Balanus (Balanus) amphitrite* Darwin; *2a,* settled larva shedding cyprid shell and compound eyes, devoid of presumptive plates, ×53; *2b-e,* successive metamorphic stages with changes in external morphology toward the juvenile form, ×93; *2f,* differentiation of opercular valves (terga and scuta) and wall, ×93 (after *10*). [Explanation: *c,* carina; *l,* latus; *lr,* latus (rostral); *r,* rostrum; *s,* scutum; *t,* tergum.]

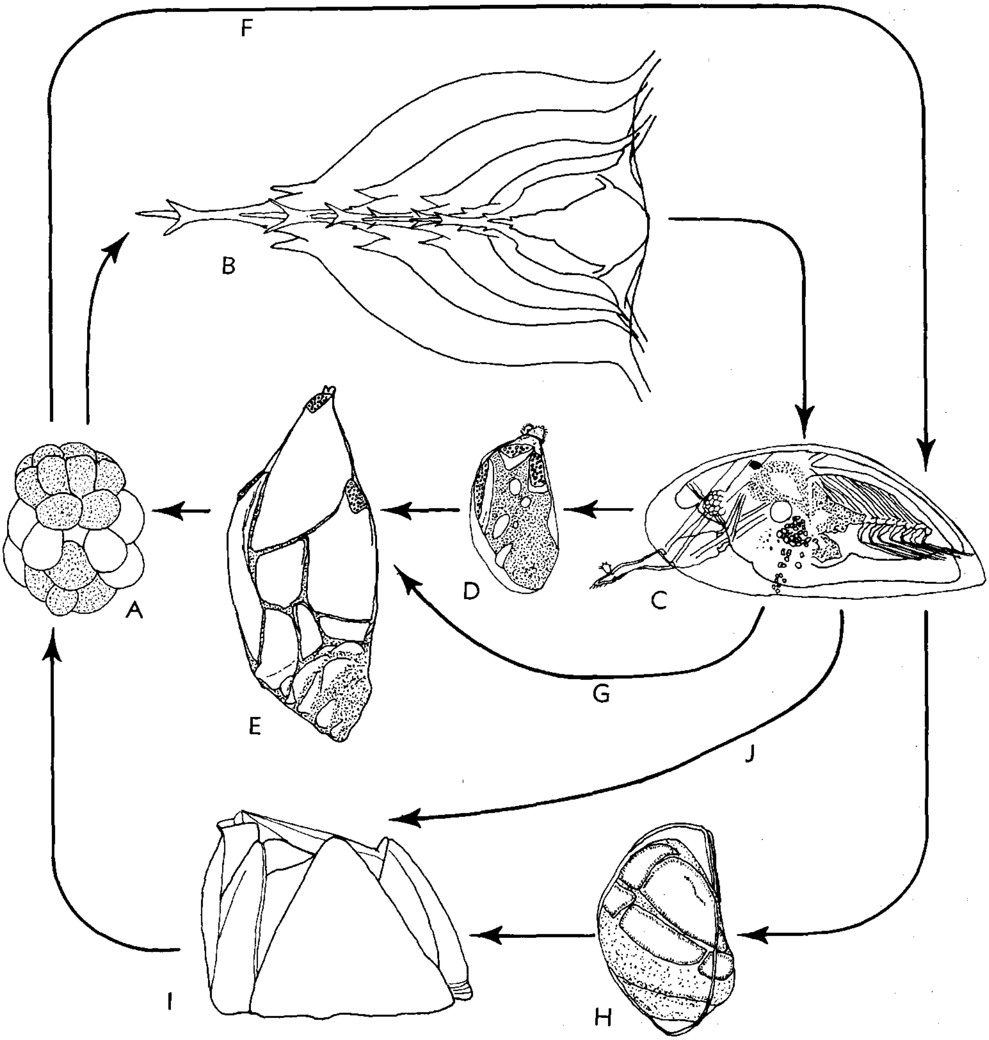


FIG. 109. Life cycles of thoracican cirripeds (Newman, n).

The generalized life cycle includes spirally cleaving egg brooded in mantle cavity *(A)*, naupliar stages, usually six *(B)*, nonfeeding cyprid larva *(C)*, pupal or metamorphic stage *(D* or *H)*, and adult, usually pure hermaphrodite, less commonly hermaphrodite accompanied by complemental males or female accompanied by dwarf males *(E* or *I)*. In some species, naupliar stages are passed through in egg, and cyprid emerges as first larval stage *(A,* through *F,* to *C)*. In some species with males, certain cyprids metamorphose into minute degenerate male attached to hermaphrodite or female *(C,* through *G* or *J,* to *E* or *I)*, within mantle cavity (Iblidae, Fig. 86,*2a*); along scutal margin of aperture (Scalpellidae, Fig. 86,*3b*); at rostral end of aperture (Koleolepadidae, Fig. 114,9), or on inner surface of rostrum and rostral ends of scuta (Balanidae, Fig. 118,*3a-b*) *(A,* after *12; B,* after *7; C,* mod. from Kühnert, 1935; *D, E,* after *20; H,* after *91; I,* after *55)*.

EARLY DEVELOPMENT OF BALANOMORPHA

The balanomorph larva also passes through six naupliar stages and one cyprid stage (BASSINDALE, 1936; COSTLOW & BOOKHOUT, 1957; BARNES & COSTLOW, 1961). Upon settlement, the cyprid body has been observed to undergo a metamorphosis similar to that seen in the Lepadomorpha (RUNNSTRÖM, 1925), or to enter a stage in which no structure can be discerned

(Doochin, 1951; Bernard & Lane, 1962). These two types of metamorphosis have been described for species belonging to different subgenera of *Balanus* so that it is possible the apparent differences are real rather than mistaken observations. The two processes are illustrated here (Fig. 108,*1a-f, 2a-f*). In the latter, the cyprid carapace is discarded and the barnacle appears as a small, dome-shaped, amorphous lump attached to the substrate. The compartmental plates and the opercular valves begin to take form after the carapace is discarded, and presumably at this time the adult body also forms.

Runnström (1925) and Broch (1927) have described the ontogeny of the shell wall in *Balanus (Semibalanus) balanoides* in which five wall plates (two rostrolaterals, two laterals, and carina; rostrum being absent), are first discernible. The rostrolaterals fuse to form a single plate, leaving four in the shell wall. This is followed by the appearance of the carinolaterals, on either side of the carina, to form the full complement of six compartmental plates. The observations on the formation of the rostral plate are, for a good part, the basis for concluding that it is made up of the fused rostrolaterals and that actually the true rostrum is lacking in *Balanus* and derived genera (Fig. 96,*8*). However, Costlow's (1956) observations on *B. (B.) improvisus* do not confirm this finding. Two plates first appear, one of which is the rostrum. The other subsequently divides to form the carina and paired laterals, yielding the four-plated stage. The carinolaterals then appear between the carina and the laterals, in the same manner as described for *B. (S.) balanoides.* From this description, the rostral plate would be homologous with the rostrum of other Thoracica. Whether one or the other, or both, of these methods of formation of the rostral plate is actually the case is not known.

Costlow (1956) has also described the early ontogeny of the wall in *Balanus (Balanus) improvisus,* and identifying certain cells in the basal margin of the mantle responsible for the secretion of the cuticle and the organic matrix that subsequently becomes calcified. His description includes details of the inception of complex wall elements such as parietal tubes, septa, and the inner lamina composing the wall of higher balanomorphs.

CLASSIFICATION

An outline of the taxonomic divisions of the Cirripedia, which seems most acceptable in light of published knowledge of these crustaceans accumulated to the present, follows.

Order ACROTHORACICA Gruvel, 1905

In his first volume on the living cirripeds, Darwin (1851), considered *Alcippe* Hancock (=*Trypetesa*), and an undescribed form *(Cryptophialus),* were sufficiently distinct from the ordinary cirripeds (Thoracica) to constitute a distinct order. However, when the time came to erect the order (Abdominalia), he described and placed *Cryptophialus* but not *Alcippe* in it (1854). This decision was in good part due to difficulties in the homologies of segmentation in the cirripeds that had grown out of the prevalent tendency to compare entomostracan segmentation patterns to that of the Malacostraca, to difficulties in reconciling the apparently aberrant segmentation of *Alcippe* with that of *Cryptophialus,* and in the similarities he noted between the plan of *Alcippe* and that found in other lepadomorphs, especially the reduced males of some species. Noll (1872) recognized the underlying bases for certain of these difficulties and placed *Alcippe* in the Abdominalia, and Gruvel (1905) cognizant of the thoracic rather than abdominal situation of the posterior cirri, changed the name of the order to Acrothoracica.

Since Darwin, more than 30 Recent and fossil species have been described. The classification of living species generally reflects the degree of reduction of the appendages. The most generalized genus, *Weltneria,* has a complete complement of cirri, and caudal appendages are present. Other genera are primarily characterized by the loss of one or more pairs of cirri, the presence or absence of caudal appendages, the condition of the mouth parts and to some degree, the musculature. All those having a well-developed posterior end and complete gut, BERNDT (1907) considered to form a suborder, the Pygophora. In contrast, *Trypetesa,* with the posterior end quite rudimentary and hind gut closed, he set aside as a separate suborder, the Apygophora. Classification in the *Treatise* follows that of BERNDT (1907) as suggested by TOMLINSON (1967, personal communication) (p. *R*251).

Order RHIZOCEPHALA F. Müller, 1862

The Rhizocephala were first recognized as crustaceous organisms by CAVOLINI (1787), through the discovery of nauplius larvae in *Sacculina.* It was 50 years later, without knowledge of CAVOLINI'S work, that J. V. THOMPSON (1836) correctly referred these highly modified parasites of crustaceans to the Cirripedia. MÜLLER (1862-63) advanced knowledge of their life history and adult anatomy, and confirmed LILLJEBORG'S (1861) observations and interpretations on the existence of males, found as cyprids attached to the parasite. The males were considered complemental in function because the parasites were presumed to be hermaphroditic, a sexual relationship comparable to that discovered by DARWIN (1851-54) in certain thoracican cirripeds. DELAGE (1884) made important studies on anatomy, further confirmed the presence of males, and discovered the manner in which the cyprid stage of the parasite infects and establishes the internal parasitic phase, by way of the so-called kentrogon stage. GIARD (1891) recognized that infection resulted in parasitic castration of the host.

Much controversy has surrounded sexuality in the rhizocephalans. The consensus primarily fostered by SMITH (1906) and POTTS (1912) was that when so-called testes were found along with ovaries in the same parasite, the individual was a hermaphrodite. In such cases, the males would be complemental and were construed as functionless. This concept persisted until REINHARD (1942) demonstrated in *Peltogaster* that the so-called complemental male was functional. That the so-called testes were in fact males that had left their cyprid integument attached outside the mantle opening, and had migrated into special pockets formed for them within the mantle cavity of the female and many other important details in the life cycle were uncovered by ICHIKAWA & YANAGIMACHI (1958) in *Peltogasterella.* Comparable processes have been recently described in other rhizocephalans (VEILLET, 1962; YANAGIMACHI & FUJIMAKI, 1967).

Whereas the Rhizocephala were generally considered more closely related to ordinary cirripeds than to other crustaceans, DELAGE (1884) inferred that they were sufficiently distinct to form a coordinate group, and proposed the name Kentrogonida for them. Such separation was not generally accepted, however. KOSSMANN (1872) considered them best regarded as a subfamily of the Lepadidae. Morphological intergradations between pedunculate barnacles and rhizocephalans have been observed and the nauplii of Rhizocephala, Acrothoracica, and Thoracica have frontolateral horns, structures found in no other Crustacea. The Rhizocephala are simply cirripeds highly modified for parasitism. Furthermore, it is likely that the Rhizocephala are polyphyletic, lines having arisen from different thoracican stocks.

The studies of COUTIÈRE (1902) suggested that, unlike *Sacculina, Thylacoplethus* (=*Thompsonia*) probably did not pass through an internal phase, and therefore lacked a kentrogon stage. On this basis, HÄFELE (1911) divided the Rhizocephala into two groups, the Kentrogonida and Akentrogonida. This division was not adopted by CALMAN (1909) or KRÜGER (1940).

It had been thought that each reproductive sac of *Thompsonia* was supported by an individual set of nutritive processes that had become established in the host without loss of communication with the exterior. This level of organization, on theoretical grounds, would have to have preceded the evolution of the kentrogon. However, POTTS (1915) demonstrated that the individual reproductive bodies in *Thompsonia* were actually interconnected by nutritive processes and were undoubtedly developed from a single individual, rather than by multiple infection. Yet it has not been determined whether *Thompsonia* passes through a kentrogon stage. Consequently, the retention of the genus in the Akentrogonida is tentative. *Duplorbis* and *Mycetomorpha,* especially the former, are suspected of being at the akentrogonid level of organization, but their life histories, too, are incompletely known. *Chthamalophilus,* on the other hand, has been critically examined and is defintiely assignable to the Akentrogonida (Bocquet-Védrine, 1961), so that the suborder, provisionally including *Thompsonia, Duplorbis, Microgaster,* and *Mycetomorpha,* is adopted here, outlined on p. *R*251.

Order ASCOTHORACICA Lacaze-Duthiers, 1880

When Lacaze-Duthiers (1880) described *Laura,* he recognized its affinities with the Cirripedia. The prehensile first antennae, bivalved carapace and natatory thoracic limbs provide a strong facies similarity with cyprid larvae, and the female genital ducts opening on the first thoracic somite, as in the ordinary cirripeds but in no other crustaceans, further indicated this. In consideration of the uniqueness of organization, and adaptations made to parasitism, he proposed a separate category for *Laura,* the Ascothoracida or Rhizothoracida, to be included as the fourth suborder of otherwise peculiar or parasitic forms, or both, the *Cirripedia abortiva* of Gerstaecker (1866). Thus he recognized suborders designated as 1) Suctoria or Rhizocephala, 2) Apoda, 3) Abdominalia, and 4) Ascothoracida or Rhizothoracida.

The inclusion of these suborders under an order distinguishing them from the Cirripedia genuina (Thoracica), proved highly artificial in terms of natural affinities, and in his revisionary work, Gruvel (1905) arranged them simply as separate orders under the subclass Cirripedia: 1) Thoracica, 2) Acrothoracica (=Abdominalia), 3) Ascothoracica (=Ascothoracida or Rhizothoracida), 4) Apoda, and 5) Rhizocephala.

In subsequent studies, Wagin (1937, 1946) concluded that the Ascothoracica were sufficiently distinct from the cirripeds to be considered as separate and of equal rank. This view was accepted by Krüger (1940). Yet, the comparative analyses were made with respect to the thoracican barnacles rather than with the cirripeds in general, and as Wagin (1946) pointed out, there were difficulties in separating specialized from fundamental features. Upon reexamination, the only fundamental difference between the two groups seems to be the absence of frontolateral horns in ascothoracican naupliar stages. Otherwise the closer affinities of the ascothoracicans with the cirripeds than with any other group of crustaceans is admitted by all. There is no compelling reason, then, to place the Ascothoracica equal in rank with other maxillopodan subclasses, and the category is retained here as the most generalized order of Cirripedia (p. *R*251).

Order THORACICA Darwin, 1854

Linné (1758) did not distinguish genera among the cirripeds, but included all known species in *Lepas.* Da Costa (1778) was the first binomial author to distinguish between the "sessile" barnacles, which he placed in the genus *Balanus,* and the stalked or pedunculate barnacles for which he retained the name *Lepas.*

Leach (1817, 1818, 1825) and Gray (1825) were among the first to classify barnacles in a more modern manner. Leach (1825, p. 208-209) proposed orders designated as 1) Campylosomata (="Pedunculata" of later authors), including families Clytiadae, Pollicipedidae, Iblidae, and 2) Acamptosomata (="Operculata" of later authors), including families Coronuladae, Balanidae, Clisiadae.

In the same year Gray (1825) proposed division of the Thoracica into families named Anatiferidae, Pollicipedidae, Pyrgomatidae, Balanidae, and Coronulidae.

Darwin (1851, 1854) not only revised the classifications of Leach and Gray, but established the genera on firm morphological bases, defined species which at that time were in a chaotic state, and established a definite terminology. He demonstrated relationships between supraspecific taxa, his more important contributions being definition of the families Lepadidae, Verrucidae, and Balanidae as groups of equal rank, separation of the Chthamalinae and Balaninae as subfamilies of the Balanidae, and determination of important differences in the morphology of the "turtle" *(Chelonibia)* and "whale" *(Coronula)* barnacles.

Gruvel's (1905) classification represents a radical departure from that proposed by Darwin, being based, especially in the Balanomorpha, on number of plates in the shell wall. The inadequacies of this classification, discussed by Pilsbry (1916, p. 13), Withers (1928, p. 62) and Krüger (1940, p. 26-27), result from the fact that the compartmental plates are not always homologous in taxa having a like number of plates in the shell wall. Continued usage of this classification is not recommended.

Pilsbry (1907) divided the Lepadidae into five subfamilies: Lepadinae, Scalpellinae, Oxynaspidinae, Alepadinae, Iblinae.

Hoek (October, 1907) and Pilsbry (November, 1907) independently proposed to group members of *Scalpellum* into a number of subgenera. These studies later led Pilsbry (1908) to divide *Scalpellum* into four genera: *Calantica* (with subgenera *Calantica s.s.,* and *Scillaelepas*), *Smilium, Euscalpellum,* and *Scalpellum* (with subgenera *Scalpellum s.s.* and *Arcoscalpellum* (=*Holoscalpellum*), the latter including the "sections" *Mesoscalpellum* and *Neoscalpellum*). *Arcoscalpellum* and *Mesoscalpellum* (=*Neoscalpellum*) have subsequently been recognized as genera. These six genera are based on the armature of the females or hermaphrodites and to some extent that of the males.

Pilsbry (1916) confirmed revision of the Thoracica, and expanded and modernized the classification of Darwin's Balanidae. His major contributions include separation of the Chelonibiinae ("turtle" barnacles) and the Coronulinae ("whale" barnacles) as distinct subfamilies apart from the Balaninae; the creation of a number of subgenera in the genus *Balanus* following the basic work of Hoek (1913); the designation of type species for genera and subgenera; and the recognition of two distinct morphological groups in the genus *Chthamalus.* Pilsbry's (1916) classification of the Thoracica recognized 1) suborder Turrilepadomorpha (=Machaeridia, Withers, 1926), Lepidocoleidae, Turrilepadidae; 2) suborder Lepadomorpha, Loriculidae (=Stramentidae), Brachylepadidae, Scalpellidae, Lepadidae; 3) suborder Verrucomorpha, Verrucidae; 4) suborder Balanomorpha, Balanidae, (Balaninae, Chelonibiinae, Coronulinae), Chthamalidae.

The suborder Turrilepadomorpha was renamed Machaeridia by Withers (1926) and removed by him from the Cirripedia. Withers concluded from crystal structure of the plates that the machaeridians were probably allied to the echinoderms. This conclusion was in part substantiated by Pope (1962) who recognized that the Lepidocoleidae represent cover plates of the brachial spines in echinoderm "Carpoidea." It can be assumed reasonably that the Turrilepadidae are of similar origin. Withers (1923) also removed the family Brachylepadidae from the Lepadomorpha and created a separate suborder Brachylepadomorpha for this group.

The diversity of opinion regarding classification of the Lepadomorpha is exhibited in the following two examples. In 1909 Annandale divided what is now recognized as the Lepadomorpha into three families: Pollicipedidae, including *Pollicipes, Scalpellum,* and *Lithotrya;* Iblidae, with the genus *Ibla;* and Lepadidae. The Lepadidae were divided into four subfamilies: Oxynaspidinae, with *Oxynaspis;* Lepadinae, including *Lepas, Conchoderma,* and *Heteralepas;* Poecilasmatinae including *Poecilasma, Dichelaspis* (=*Octolasmis*), and *Megalasma;* and Alepadinae, including *Alepas s.s., Chaetolepas* (=*Ibla*), *Microlepas, Anelasma,* and *Koleolepas.* Later Annandale (1910, 1916) distinguished two subgenera in *Scalpellum: Smilium* and *Scalpellum s.s.*

Nilsson-Cantell (1921) divided the Lepadomorpha into the families Scalpellidae, including *Pollicipes, Scalpellum* (with groups *Calantica, Smilium, Euscalpellum, Scalpellum*), and *Lithotrya;* Iblidae containing only *Ibla;* Oxynaspididae with *Oxynaspis;* Lepadidae, including *Lepas, Conchoderma,* and *Alepas;* Heteralepadidae, containing *Heteralepas* (with the subgenera *Heteralepas s.s.,* and *Paralepas*); and Poecilasmatidae, including *Poecilasma* (with the subgenera *Poecilasma s.s., Glyptelasma,* and *Temnaspis*), and *Octolasmis.*

The generally acceptable features of this classification were incorporated by WITHERS (1953), and with some additions and emendations, his classification has been adopted for the *Treatise,* as given in the following outline.

Order APODA Darwin, 1854

Proteolepas bivincta, a curious parasitic crustacean, was found in the mantle cavity of a pedunculate barnacle, *Heteralepas cornuta* (DARWIN) from the West Indies. On the basis of a single specimen, DARWIN (1854) developed an analysis that led him to believe the form was a member of the Cirripedia, for which he established the order Apoda. No specimens attributed to *Proteolepas* have been found subsequently.

The interpretation, that *Proteolepas* is a cirriped, was based primarily on the marked similarity between the pair of appendages by which it attached to the host and the first antennae of ordinary cirripeds. However, in order to consider these appendages homologous with the first antennae of cirripeds requires that they should have migrated backward on the body as many as five segments. Peculiarities in the pair of biting mouth parts, as compared to the cirriped mandible, led DARWIN to speculate on their formation. He concluded that the relatively complex structure had resulted from fusion of the mandibles with the first and possibly the second maxillae, and had rotated through 180°. At the present level of our knowledge, both of these interpretations seem highly unlikely. The appendages of attachment could be first or second maxillae, rather than first antennae, and thus the parasite could be interpreted as a copepod. On the other hand, if the mouth parts were interpreted as malacostracan mandibles, as they appear, then the parasite might be an epicaridean. Therefore, until new material is discovered, the affinities of *Proteolepas* remain conjectural.

Certain larvae were attributed to the Apoda by HANSEN (1899). Termed Y-larvae by him, they were subsequently found by other workers (STEUER, 1904; MCMURRICH, 1917). The assignment of Y-larvae to the Apoda was by process of elimination, since they resembled the larvae of no cirriped known at the time. On the basis of present knowledge, it seems equally possible that Y-larvae, provided they are cirripeds, belong to ascothoracicans, because of the absence of frontolateral horns. However, some of them have compound eyes, which, while found in late naupliar and cyprid stages of other cirripeds and in the Branchiura, are unknown in larvae of Ascothoracica. Therefore the affinities of the Y-larvae with the Apoda, with other cirriped groups, or with other crustaceans remain doubtful.

Classification of Class Cirripedia

Order Acrothoracica
  Suborder Pygophora: Lithoglyptidae, Cryptophialidae (Rodgerellidae, Zapfellidae provisional).
  Suborder Apygophora: Trypetesidae
Order Rhizocephala
  Suborder Kentrogonida: Peltogastridae, Sacculinidae, Lernaeodiscidae, Clistosaccidae, Sylonidae.
  Suborder Akentrogonida
Order Ascothoracica: Synagogidae, Lauridae, Petrarcidae, Dendrogastridae
Order Thoracica
  Suborder Lepadomorpha: Cyprilepadidae, Praelepadidae, Scalpellidae, Heteralepadidae, Iblidae, Koleolepadidae, Lepadidae, Malacolepadidae, Oxynaspididae, Poecilasmatidae, Stramentidae, Family uncertain
  Suborder Verrucomorpha: Verrucidae
  Suborder Brachylepadomorpha: Brachylepadidae
  Suborder Balanomorpha: Chthamalidae, Balanidae (Balaninae, Tetraclitinae, Chelonibiinae, Coronulinae, Emersoniinae)
Order Apoda

FOSSIL TRACES

Of the four orders of Cirripedia, only the Thoracica is represented by actual fossil remains. No fossil evidence has been found for the purely parasitic Rhizocephala. The remaining two orders (Acrothoracica, Ascothoracica) have been identified by the traces left in the substrates they inhabited.

The characteristics of fossil acrothoracican burrows were summarized by TOMLINSON (1963) from whose table the following list of species was obtained.

Acrothoracican Fossil Burrows

Family ZAPFELLIDAE

Zapfella pattei SAINT-SEINE, 1954, Mio.-Plio., in large gastropods, few pelecypods, calcareous marls.

Simonizapfes elongata CODEZ, 1957, Trias.-Jur., in belemnites, pelecypods, crinoids, gastropods, etc.

Brachyzapfes elliptica CODEZ, in belemnites, pelecypods. TAYLOR (1965) has described burrows identified as *B. elliptica gigantea* (new), from Antarctic (Aptian) belemnite rostra.

Family RODGERELLIDAE

Rodgerella lecointrei SAINT-SEINE, 1951, Cret., in echinoids.

Rodgerella mathieui SAINT-SEINE, 1955, M.Jur.-Cret., L.Mio.-Plio., in echinoids, pelecypods, belemnites, corals.

Rodgerella cragini SCHLAUDT & YOUNG, 1960, Cret.(Alb.), in *Ceritella proctori* (gastropod).

Family TRYPETESIDAE

Trypetesa caveata TOMLINSON, 1963, Penn.-L. Perm., in myalinid pelecypods. Unnamed species, in JOYSEY, 1959, Cret., in *Echinocorys* (echinoid).

Unidentified acrothoracican burrows were also described by SCHLAUDT and YOUNG (1960) and later by RODDA and FISHER (1962) from the Pennsylvanian and Permian of Texas in myalinid pelecypods, brachiopods, crinoids, rugose corals, and bryozoans, and by ROSS (1965) from the Miocene of Florida in the bryozoan *Holoporella.*

The Ascothoracica were apparently represented in the Cretaceous. Fossil traces, in the form of cysts in the octocoral *Moltkia minuta,* from the Maastrichtian, have been identified and named *Endosacculus moltkiae,* by VOIGT (1959). Furthermore, holes comparable to those made by the ascothoracican *Ulophysema* in the test of certain extant sea urchins, have been discovered in the Upper Cretaceous (Turon.-Maastricht.) in an extinct irregular urchin, *Echinocorys* by MADSEN & WOLFF (1965). Therefore, not only does it appear that Ascothoracica were present in the Cretaceous, but some members were already highly specialized endoparasites before the close of the Mesozoic.

STRATIGRAPHIC DISTRIBUTION

Fossil cirripeds have a total known range from Upper Silurian to Recent, Paleozoic forms being represented by thoracicans, except for a genus of acrothoracicans *(Trypetesa)* identified from borings in bivalve shells (Penn.-Perm. myalinids). Also, discovered Mesozoic and Cenozoic cirripeds belong almost entirely to the Thoracica.

The stratigraphic distribution of Cirripedia found preserved as fossils is indicated graphically in the accompanying Tables 2 and 3.

PHYLOGENY

ORIGIN OF CIRRIPEDS

Within the Crustacea, the Cirripedia have their closest affinities with the Maxillopoda. The Maxillopoda are typified by a fundamental five-six-five body plan, in contrast, for example, to the Malacostraca with a fundamental five-eight-seven plan. The divisions include a head with five pairs of appendages, a thorax of six appendage bearing segments, and a five-segmented abdomen which includes a telson with furca (Table 1). The abdominal somites are without appendages, except for the furca and the male reproductive structure on the first somite which may represent modified limbs. The Maxillopoda include, either by definition or by inference, the Copepoda, Branchiura, and Mystacocarida, as well as the Cirripedia. The Ostracoda, although highly reduced segmentally, could have been derived from a basic five-six-five plan, and are generally considered closer to the Maxillopoda than to other groups.

Among the Cirripedia, only the Ascothoracica have a complete five-six-five plan (Fig. 82,*2*). The abdomen is absent in adult Acrothoracica and Thoracica, but is represented by at least three segments in the cyprid larvae of these orders (Fig. 82,*3*). The Cirripedia seem to have their closest affinities with the Copepoda and Branchiura. Before the life cycle of the harpacticoid copepod *Longipedia* was known, its nauplius larvae were thought to be those of a cirriped. The carapace and cirrus-like thoracic appendages of Branchiura are comparable to those of cirripeds, and detailed similarities between larval cirriped and branchiuran compound eyes further indicate a relationship between the two groups. Thus it can be inferred that the stemline of the Cirripedia is closer to the copepod-branchiuran line of the Maxillopoda than to any other crustacean group (Tables 1, 3).

The ascothoracican grade of construction is the most generalized body plan found in cirripeds, despite the secondary parasitic nature of the group. This body plan is not readily detected in other cirriped groups, but is clearly defined in their cyprid larvae. Therefore, it appears that cirripeds stem from free-living Maxillipoda that had a bivalved carapace, compound eyes, prehensile first antennae, generalized copepod-like mouth parts, natatory thoracic appendages, and an abdomen with telson and furca. Such a form would differ from other Maxillopoda in having female genital apertures on the first thoracic somite, and male genital apertures on the first abdominal somite. The majority of cirripeds are hermaphroditic. However, it may be possible that some species among the Thoracica, having either separate sexes or hermaphrodites accompanied by complemental males, have arrived at this condition through reversion from a purely hermaphroditic condition. It can be inferred that fundamentally the sexes were separate, as separate sexes are found in all cirriped orders, as in the Maxillopoda in general.

The hypothetical ancestral cirriped stock would have resembled extant Ascothoracica in many details, including a basic nonsetose omnivorous feeding mechanism in which only the mouth parts were involved. Such an organism would be suited to an epibenthic existence, but the prehensile first antennae, so fundamental to cirripeds, suggest an epizootic habit, probably on arborescent forms of life (Fig. 110,*A*).

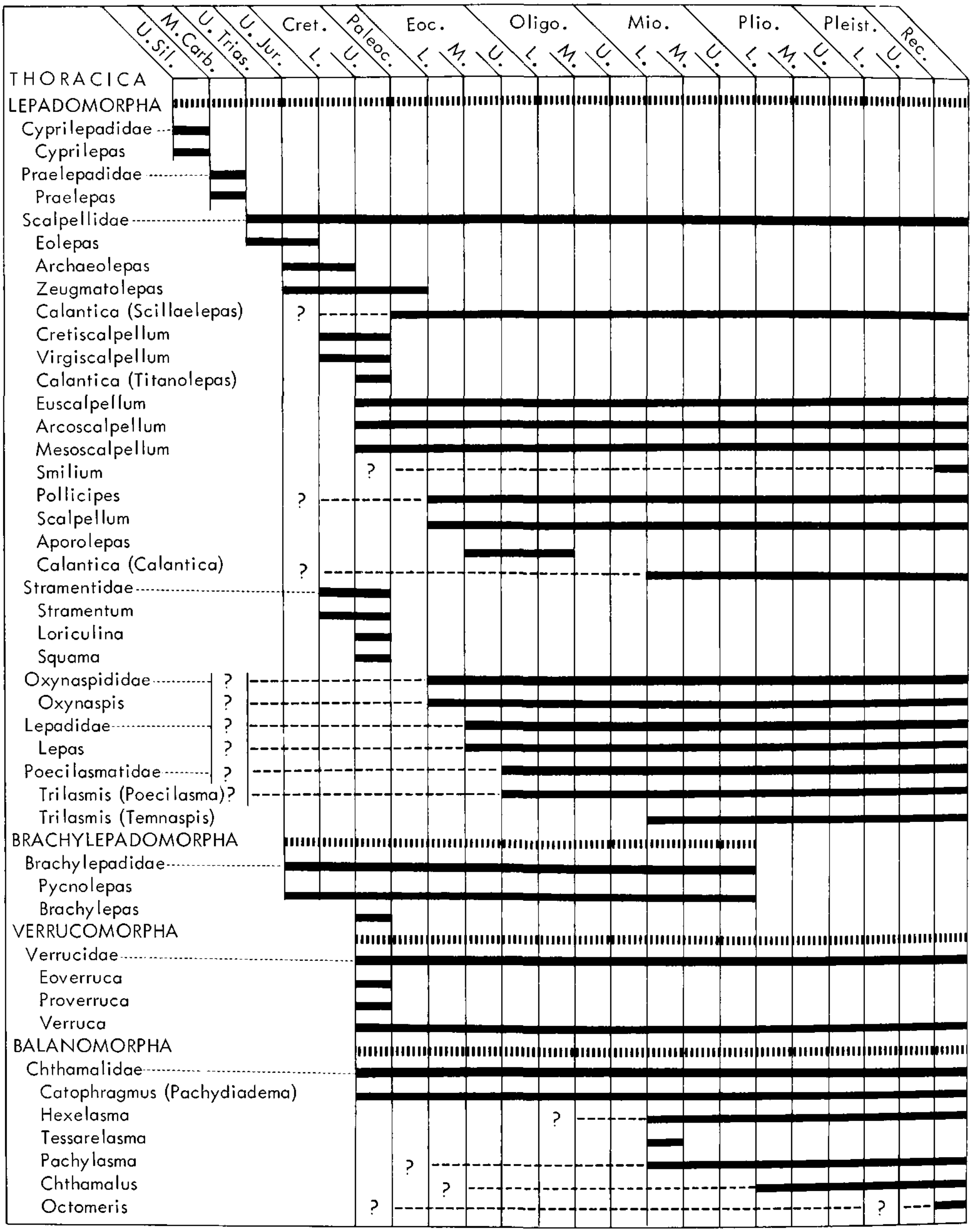
ORIGIN OF CIRRIPED ORDERS

The ancestral cirriped would have given rise directly to the Ascothoracica with little modification. The early separation of Ascothoracica from other Cirripedia is exemplified by the generalized form, lack of setose feeding mechanism, complete loss of compound eyes in all stages of the life cycle, and the absence of frontolateral horns in the nauplii.

Two fundamental developments are necessary for transition from the hypothetical cirriped to the level of organization seen in Thoracica and Acrothoracica. The first is acquisition of a setose feeding mechanism, and the second is development of cement glands in connection with the prehensile first antennae. Beyond these basic advances relatively few and simple modifications are necessary to arrive at the highest forms among the cirripeds. Acquisition of a setose feeding mechanism by a generalized omnivore probably developed through modification of a grooming or cleaning behavior, in which the natatory appendages were drawn over the mouth parts to remove particles of detritus adhering to the setae. Sufficient nutrients must have been obtained in this way to place a selective advantage on forms having thoracic appendages with setae that required frequent cleaning. The more food was collected in this manner, the less the necessity of foraging, thus allowing for a more sedentary existence. Once freed of foraging, it is possible for an organism to become cemented in place, if ecological factors such as substratum and predation permit.

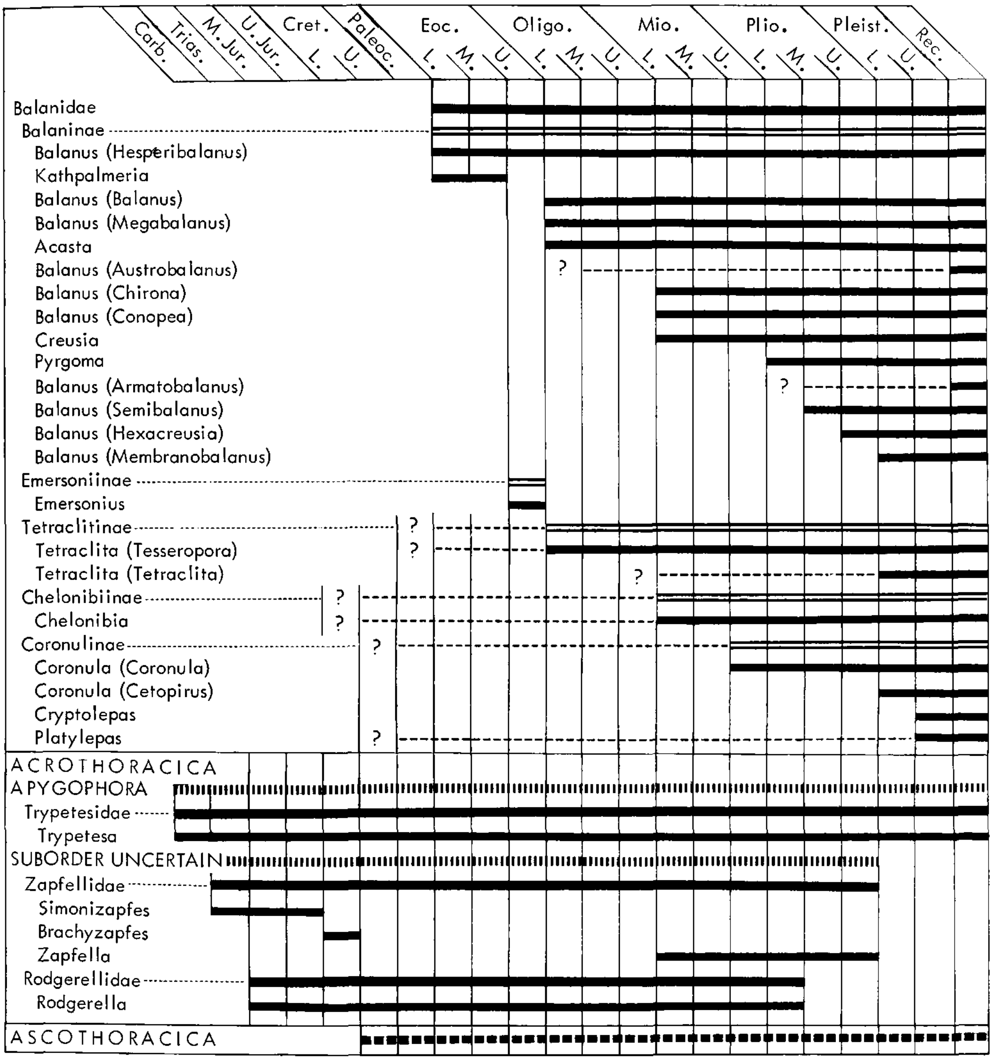
It follows, therefore, that the Thoracica and Acrothoracica could have evolved from a stock at the ascothoracican grade of construction (Fig. 110, Table 3). The inferences utilized, however, rest entirely on knowledge of extant cirripeds. Nothing has been recognized in the fossil record that sheds light on the subject. This is not surprising, because most Maxillopoda are small and lack a heavily calcified exoskeleton. Therefore, the probability of being preserved is low, and of being detected, even lower. It is not until the cirripeds gained a well-calcified exoskeleton that their fossil history becomes well documented.

TABLE 2. *Stratigraphic Distribution of Genus-group Taxa with Fossil Records.*



The earliest and perhaps most remarkable fossil attributed to the Cirripedia is *Cyprilepas* WILLS, found attached to the appendages of Upper Silurian eurypterids (Fig. 111,*1*). *Cyprilepas* is clearly divided into peduncle and capitulum, and, therefore, is already a thoracican at the lepadomorph grade of construction. With one exception it differs from all known Lepadomorpha in having a bivalved carapace. The extant *Trilasmis eburneum* HINDS also has a bivalved shell, but as shown by DARWIN

TABLE 2. *(Continued).*



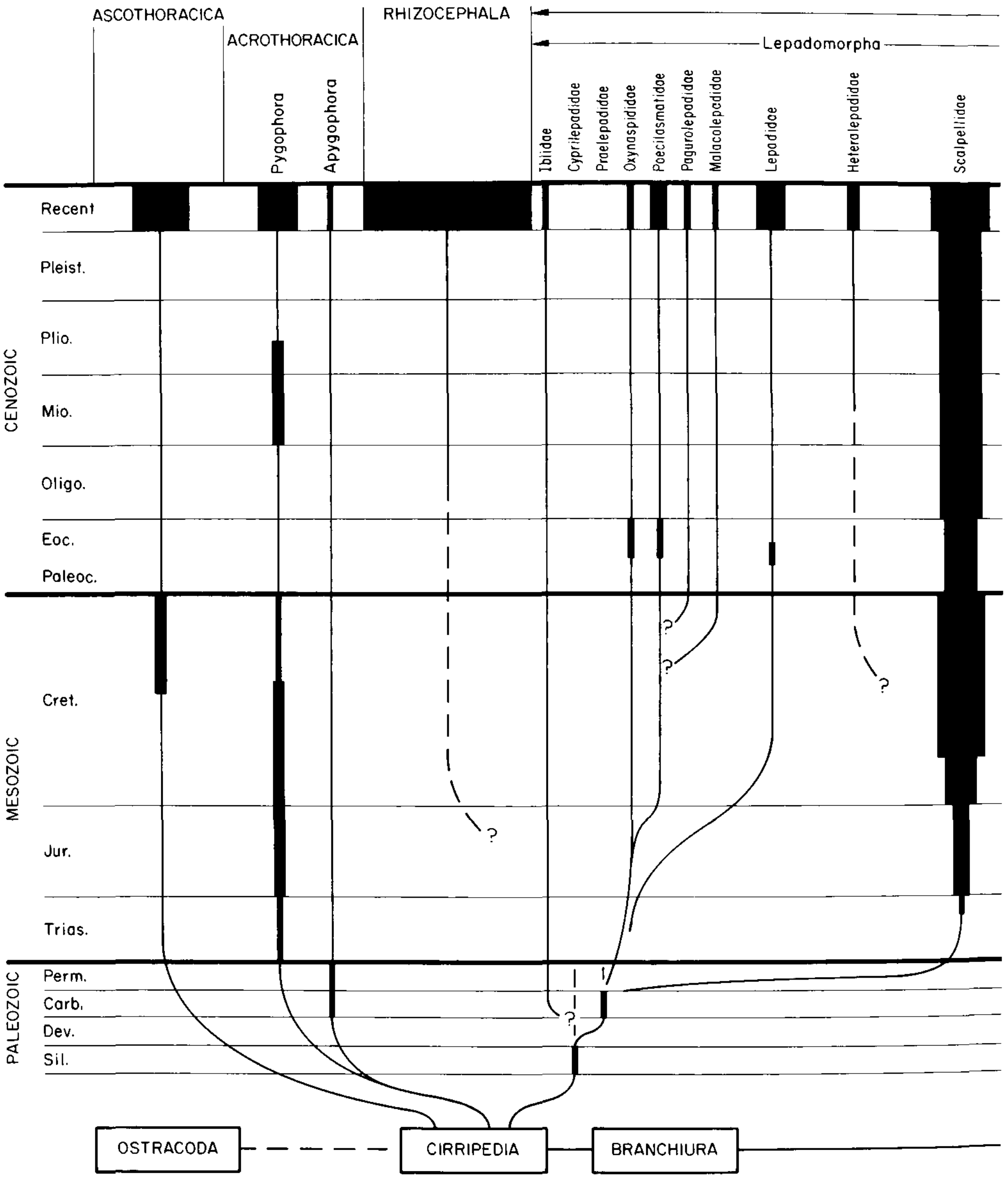
Explanation: Known ranges, solid bar; inferred ranges, broken bar (Zullo, n).

(1851), this condition is the result of secondary reduction (see Fig. 116,9). On the other hand, the bivalved condition seen in *Cyprilepas* probably represents the level of organization attained by cirripeds in the early Paleozoic, and is homologous with the bivalved carapace of Ascothoracica and cyprid larvae of other orders.

Cyprilepas may differ from known Lepadomorpha in an even more fundamental way. The absence of growth lines on the carapace suggests that the entire exoskeleton was shed at each molt, rather than only the exoskeleton lining the mantle cavity and clothing the body and appendages. This is the manner of growth in Acrothoracica, Ascothoracica, and most crustaceans, and could be expected in the stock leading to Thoracica.

In size and grosser form, *Cyprilepas* fits the concept of the ancestral thoracican. However, nothing is known of the body

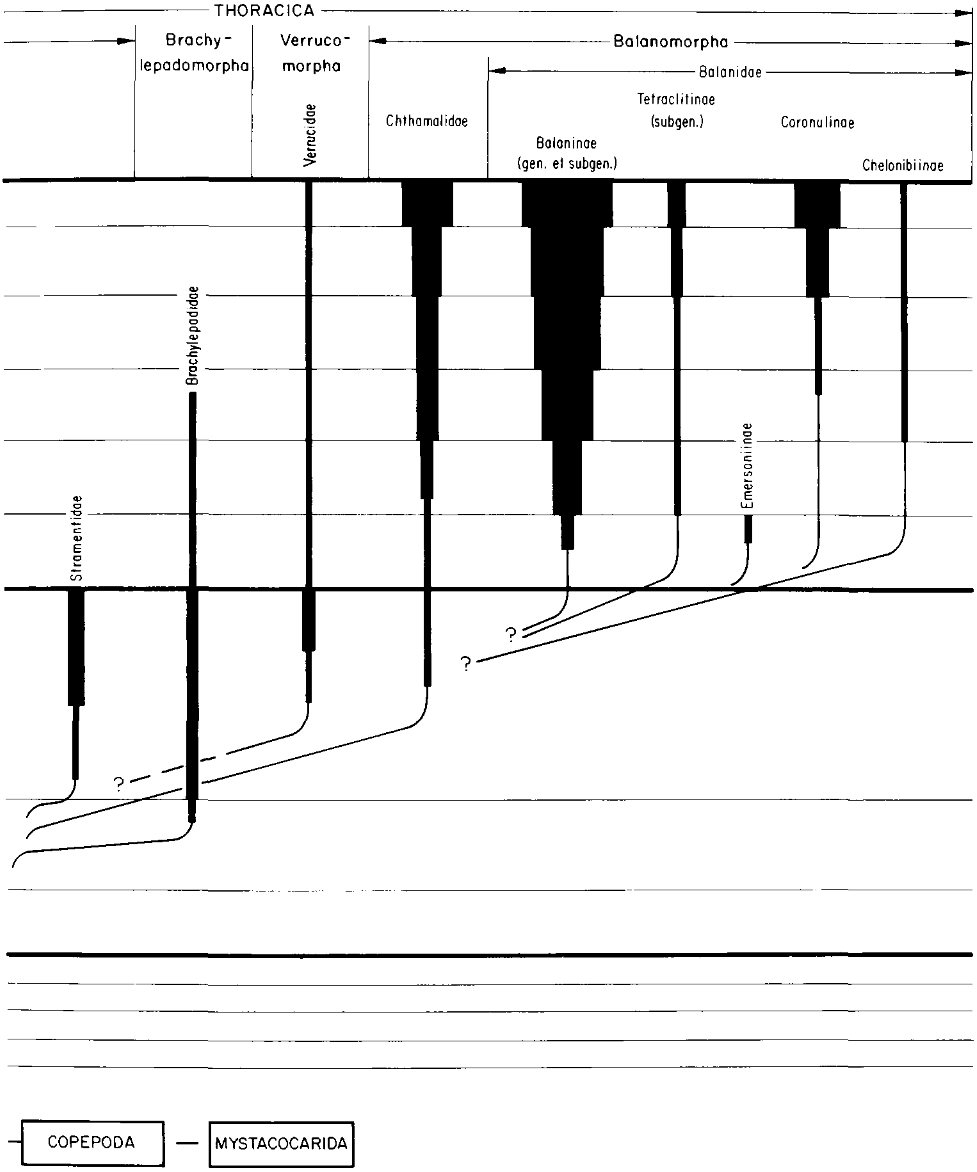
TABLE 3. *Stratigraphic Distribution and Inferred Phylogeny of Cirriped Orders and Families (Newman, n).*



and appendages, and such information would be desirable in assessing its significance in cirriped evolution. From present knowledge, the *Cyprilepas* grade of construction can be considered the basis from which the array of forms seen in the Lepadomorpha, Verrucomorpha, Brachylepadomorpha, and Balanomorpha have evolved.

It has not been resolved whether the Acrothoracica are descended from the ancestral stock of the Thoracica, or from Thoracica themselves. No fossil acrothoracicans are known, although their characteristic burrows have been recognized in carbonate substrata from as early as Late Carboniferous. The ability to burrow is a specialization acquired after the develop-

TABLE 3. *(Continued).*



ment of a setose feeding mechanism and attached mode of life. Unlike Thoracica, with the possible exception of *Cyprilepas,* Acrothoracica molt the exterior as well as the interior lining of the carapace, along with the lining of the body and appendages. Burrowing is accomplished, at least initially, by chitinous hooks and spines covering the exterior of the carapace, and these, too, are replaced at each molt. The cyprid larva attaches itself by the first antennae, with the ventral surface of the shell applied to the substratum. The metamorphosing barnacle, covered by the cyprid shell, begins

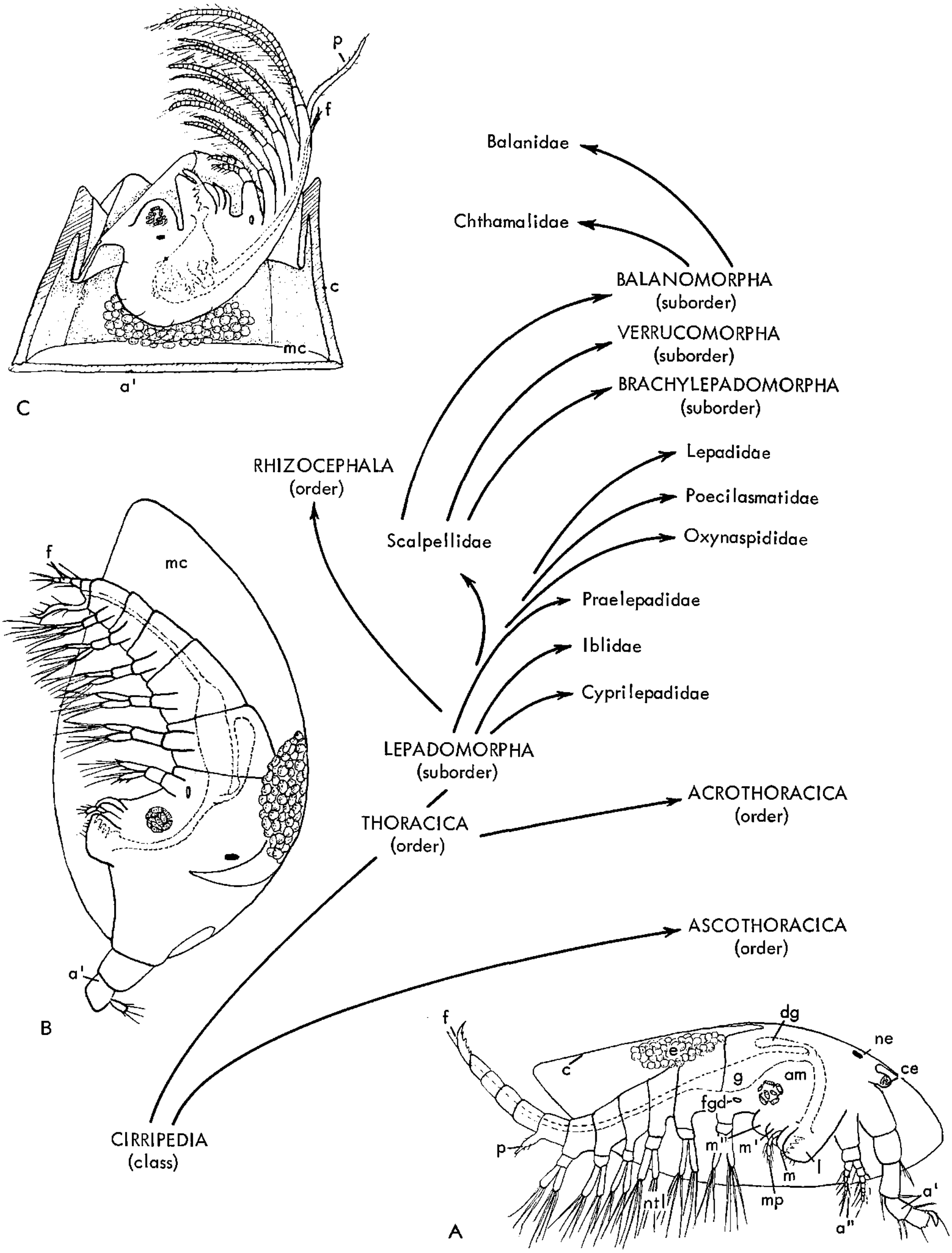


FIG. 110. Evolution of Cirripedia (Newman, n).

A. The ascothoracicans share a 5-6-5 body plan with the Maxillopoda. A generalized ancestral stock having prehensile first antennae and bivalved carapace and differing from Acosthoracica only in having compound eyes and generalized rather than piercing mouth parts, is hypothesized. Such a stock, sharing characters of the Copepoda, Branchiura and Ascothoracica, woud be typified by the form illustrated at the lower right.

B. Transition from the ascothoracican to thoracican level of organization would include acquisition of setose feeding, concomitant with more or less permanent attachment by means of first antennae.

C. From this level remaining cirripeds evolved, the to burrow mechanically into the substratum by chipping away flakes of carbonate with the carapace spines (BATHAM & TOMLINSON, 1965). If these barnacles did not burrow, but merely remained attached to the substratum, they probably would be included in Thoracica, rather than in a separate order. Since burrowing is a secondary adaptation in the cirriped facies, and in consideration of the geological record of the order, it seems likely that the Acrothoracica descended from lepadomorphan ancestors at a level of organization comparable to that found in *Cyprilepas*. Whereas most Lepadomorpha have developed an external calcareous armament, the Acrothoracica rely on the substratum for protection.

The origin of the Rhizocephala is presently unknown. Members of the order are exclusively parasitic. It might seem that the Rhizocephala are most closely allied to the parasitic Ascothoracica in which the feeding mechanism involves only the mouth parts. However, the rhizocephalan nauplius larva bears frontolateral horns, and although the functional significance of these horns is unknown, their presence demonstrates a closer affinity of the Rhizocephala with Thoracica and Acrothoracica than with Ascothoracica. Furthermore, while the cyprid larva of these three orders cement themselves in place, the cyprid of the Ascothoracica does not.

While Acrothoracica show no tendency towards parasitism, grades of parasitic development are found in Thoracica that suggest the direction evolution must have taken in development of rhizocephalan organization. *Rhizolepas* DAY, parasitic on a polychaete annelid, and *Anelasma* DARWIN, parasitic on sharks, are lepadomorphs, which, although retaining vestigial limbs, have given up setose feeding in favor of development of a system of processes which invade and draw nutrients from the host tissues. The gut is complete in *Anelasma,* but mouth parts are vestigial (Fig. 112,*2-3*). The gut in *Rhizolepas* closes blindly at both ends and mouth parts are apparently lacking. Forms such as these give us definite clues to rhizocephalan evolution.

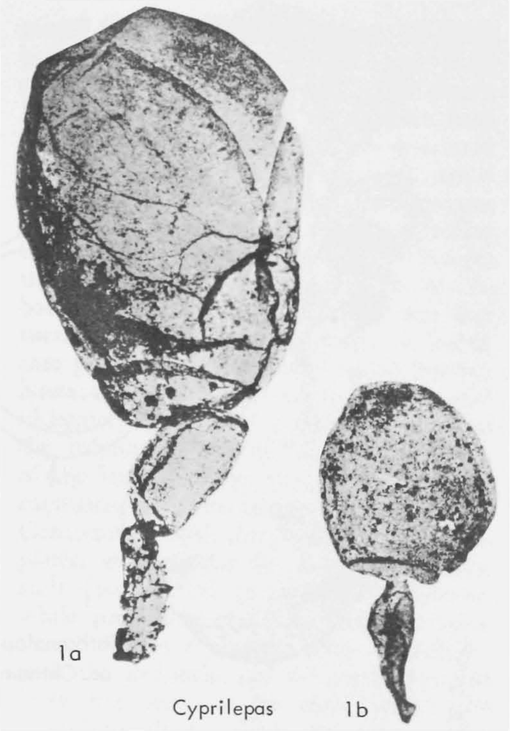


FIG. 111. Silurian cirriped, interpreted as possible and most generalized ancestral thoracican, *Cyprilepas holmi* WILLS; *1a,* large specimen, viewed from left side, peduncle somewhat wrinkled and bilateral valves of carapace forming capitulum displaced, thickening along carinal and basal margin of carapace evident; occludent margins forming aperture of carapace visible; *1b,* small, less distorted specimen, viewed from same side, revealing same characteristics, ×11 *(112).*

Rhizocephala are generally considered to pass through an endoparasitic phase before the appearance of the external reproductive structures. However, the recently discovered *Chthamalophilus* BOCQUET-VÉDRINE (1961), although a rhizocephalan by most criteria, does not develop a kentrogen, and has an entirely ectoparasitic life cycle (Fig. 112,*1*). Thus it would

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FIG. 110. *(Continued from facing page.)*

highest level of organization being attained in the Balanomorpha, as discussed in text.

[Explanation: *a'*, first antennae; *a"*, second antennae; *am,* adductor muscle; *c,* carapace; *ce,* compound eye; *dg,* digestive gland; *e,* egg mass; *f,* furca; *fgd,* female genital duct; *g,* gut; *l,* labrum; *m,* mandible; *m'*, first maxilla; *m"*, second maxilla; *mc,* mantle cavity; *mp,* mandibular palp; *ne,* naupliar eye; *ntl,* natatory thoracic limbs; *p,* penis.]

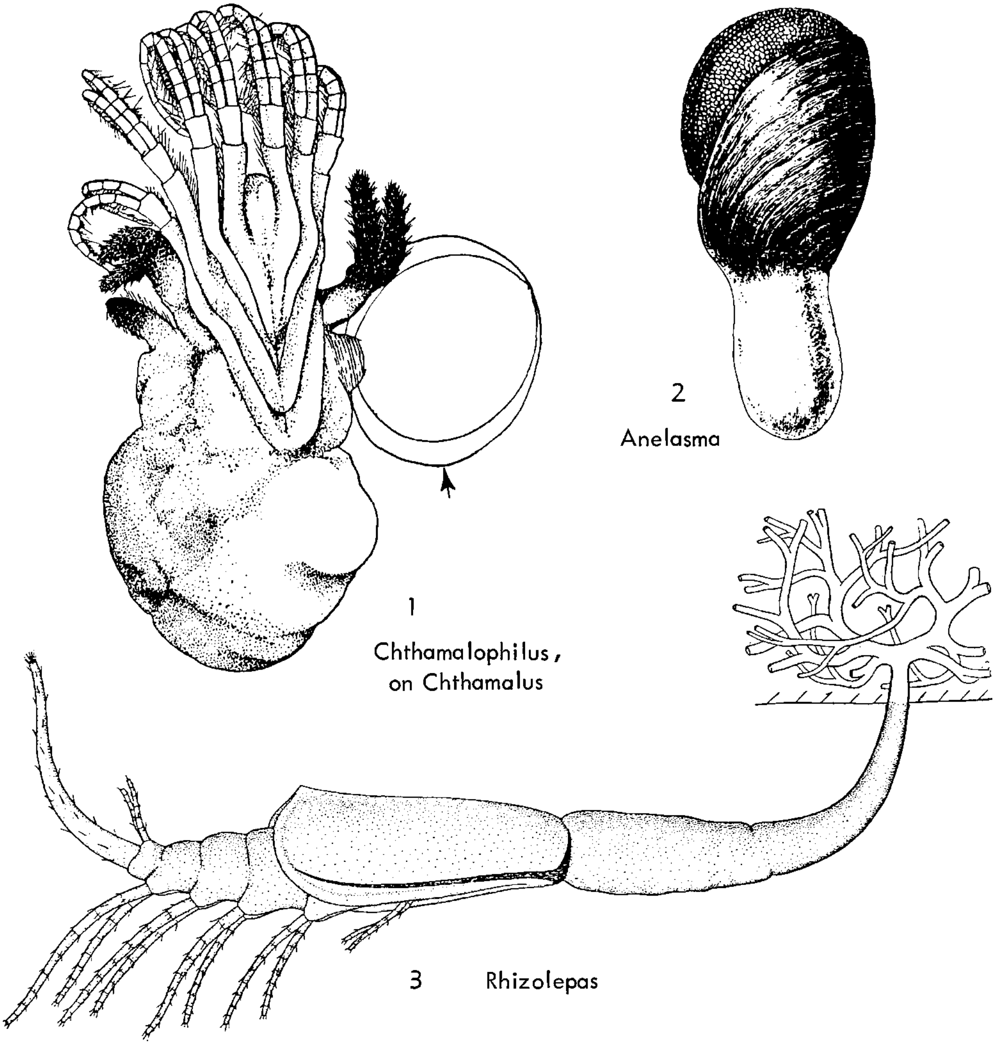

FIG. 112. Parasitic adaptations of cirripeds:——*1*. Akentrogonid rhizocephalan on a barnacle (after *13*).——*2*. Lepadid parasitic on certain sharks (peduncular nutritive processes not illustrated) (after Darwin, 1851, 37).——*3*. Lepadomorph parasitic on a polychaetous annelid (after Day, 1939).

appear that *Chthamalophilus* represents a level of organization intermediate between the rhizocephaloid lepadomorph parasite and the endoparasitic Rhizocephala.

In summary, it appears that the Cirripedia evolved along two major lines, one giving rise to the basically free-living Ascothoracica and the other to the permanently attached Acrothoracica, Thoracica, and Rhizocephala. These two lineages stemmed from a common maxillopodan ancestral stock related to the progenitors of the Copepoda and Branchiura. This stock was similar in general organization to the Ascothoracica, but differed mainly in possessing compound eyes of branchiuran type. Setose feeding and the development of cement glands in conjunction with the prehensile first antennae led to a lepadomorphan level of organization, probably comparable to that seen in the fossil *Cyprilepas*. This level of organization differs from that seen in other fossil and living Lepadomorpha in the periodic molting, rather than retention of the carapace exterior. At this point, one group, leading to Acrothoracica, gained the ability to burrow mechanically into calcareous substrata, whereas another, leading to Thoracica, developed the ability to retain exterior portions of the carapace while molting the remaining exoskeleton, thus forming a tough exterior shell that provided protection during all periods of the molt cycle. This step apparently preceded the development of the typical thoracican shell laid down in successive layers. Subsequent lines of Lepadomorpha developed sessile forms, such as the extinct Brachylepadomorpha, the Verrucomorpha, and the Balanomorpha. It appears further that the trend towards parasitism seen in certain Lepadomorpha led to the evolution of the Rhizocephala.

THORACICA

LEPADOMORPHA

The Lepadomorpha can be distinguished from other suborders by the presence of a peduncle representing a prolongation of the anterior part of the cephalic region, and a capitulum supporting two or more plates derived from the carapace. The suborder includes ten families, three of which are extinct. The oldest, Cyprilepadidae, appears only in the Silurian. There are 38 recognized lepadomorph genera, of which only two occur in the Paleozoic. One Recent genus, *Arcoscalpellum,* ranges back to the Lower Cretaceous. The two principal families are named Scalpellidae and Lepadidae and it is with these and their relationship to less well known groups that the following discussion is mostly concerned.

The origin of the Lepadomorpha has been considered in the preceding section. Within the suborder, the Scalpellidae are generally interpreted to be more primitive than the Lepadidae (Darwin, 1851; Hoek, 1883; Gruvel, 1905; Pilsbry, 1907; Annandale, 1910; Krüger, 1920; Nilsson-Cantell, 1921; Withers, 1928-53). In fact, the original scheme proposed by Darwin in 1851 has been little modified in its essentials since it was proposed. He envisaged a *Pollicipes*-like stem form giving rise to *Pollicipes, Lithotrya,* and the Balanomorpha, on one hand, and to the Lepadidae, through *Scalpellum* and *Oxynaspis,* on the other. Following this view, the ancestral stock would have been already highly derived, having a capitulum and peduncle well armored with numerous calcareous plates. For the capitulum there would have been six plates—paired terga and scuta associated with carina and rostrum—all with apical umbones, and for the peduncle, numerous unspecialized calcareous plates or scales. Subsequent evolution would then involve the addition of peduncular plates to the basal area of the capitulum. In one line these would form basal whorls of imbricate plates, some of which would become latera, as seen in *Pollicipes,* and these would ultimately be utilized in the formation of the balanomorph wall. In another, some of the latera become incorporated into the capitulum in the manner seen in *Scalpellum.* Concomitant with this, umbones of certain plates, in particular the carina and scuta, shift from apical to subcentral, because, while previously the body had been contained within a mantle cavity formed by both the peduncle and the capitulum, the body has come to lie more within the capitulum alone. With this change, the armament of the peduncle and the basal portion of the capitulum becomes reduced, and this eventually results in a five-plated *Oxynaspis*-like form, which in turn leads to the other five-plated Lepadomorpha. In this conception, the six-plated scalpellids are primitive.

Fossil Mesozoic scalpellids, particularly *Eolepas* and *Archaeolepas,* discovered after the time of Darwin, support the view that the six-plated facies was basic to the archetype thoracican, as Withers (1928-53) further advocated. However, Broch (1922), while admitting the great age of the six-plated Scalpellidae, did not concede that this meant they were necessarily archetypes. He pointed out that the really primitive thoracicans probably lacked plates impregnated with carbonate, and therefore would be unlikely subjects for fossilization. Furthermore, Broch looked to ontogenetic evidence suggesting that a five-plated condition is actually as fundamental to the Scalpellidae as to the Lepadidae, and accordingly judged that both groups must have descended from a common five-plated stock. This would place the Lepadidae as primitive as the Scalpellidae, if not more so, quite the reverse of what other authors had thought. These two fundamentally different points of view have not been reconciled, but we offer an argument here which is more in keeping with that of BROCH.

WITHERS (1928-53) assumed the primitive capitular valve complement to be six, paired terga and scuta plus carina and rostrum, as exhibited by the oldest known Triassic and Jurassic scalpellids, *Eolepas* and *Archaeolepas*. BROCH (1922), on the other hand, considered the complement of primitive capitular plates to be five, the same as in scalpellids minus the rostrum, as seen in the ontogeny of extant members of both families where five chitinous primordial plates appear before calcification begins. The development of the rostral plate has never been observed to be anticipated by a chitinous primordium. At the time, BROCH's arguments were weakened by the relative scarcity of paleontological evidence, and WITHERS' argument by giving little weight to the ontogenetic evidence. WITHERS also minimized the importance of the only Paleozoic thoracican known at the time, *Praelepas,* described by CHERNYSHEV in 1930, from the Upper Carboniferous. This genus not only had chitinous rather than calcareous capitular plates, a condition thought probable by both authors on theoretical grounds, but it also had only five plates (rostrum lacking), a fact that adds much support to BROCH's hypothesis.

WITHERS rejected *Praelepas* as an important form in thoracican evolution not only because it lacked the sixth capitular plate, but because the umbo of the scutum was central rather than apical. Since Mesozoic forms, *Eolepas* and others had apical umbones on all plates, this condition was taken as primitive and the idea rigorously adhered to. Thus he was compelled to regard the Carboniferous *Praelepas* as an early specialization ancestral to neither the Mesozoic scalpellids nor the Cenozoic lepadids.

We think, however, that *Praelepas* should not be so readily dismissed as an early specialization. BROCH (1922) has stressed the generality and uniformity of five rather than six principal primordial plates in the development of both the Scalpellidae and Lepadidae, and this cannot be lightly put aside. Even where as many as 11 primordia are known during development (*Scalpellum balanoides* HOEK, cf. BROCH, 1931), the rostrum appears without one. At the present level of our knowledge it seems inescapable that there are five fundamental capitular plates in both the Scalpellidae and Lepadidae, and that any larger number is secondarily derived. The rostrum, so fundamental to the Scalpellidae, never has a primordial plate and is therefore very much secondary. These facts must be considered as such in our thinking on the evolution of the Lepadomorpha, even though at present they do not clarify the phylogenetic history of the group.

The next problem relates to position of the umbo. In the Scalpellidae all the umbones appear to be fundamentally apical, whereas those of the carina and scuta in the Lepadidae seem to be fundamentally basal. Following WITHERS, the apical position would be primitive, whereas other conditions were derived. The apical condition seen in the earliest known scalpellid, *Eolepas* of the Triassic and Jurassic, carries through in Recent *Pollicipes* and its allies, but this line, while old as far as fossil evidence is concerned, appears well advanced. In particular, the rostrum is very large, the apical portion having grown free of the capitulum, and the plates in general overlap, a specialized condition in itself. *Eolepas* and its allies, including *Archaeolepas, Zeugmatolepas, Pycnolepas,* and others, are clearly already well separated from the stem line of the Lepadomorpha.

Apical umbones and more or less overlapping plates seem to be general features in other Mesozoic scalpellids. A notable exception, however, is seen in *Virgiscalpellum,* from the Lower and Upper Cretaceous. Not only do the plates lack overlap, but the umbones of the scuta and carina are central rather than apical, and the rostrum is minute. This is a very different facies from that presented by *Eolepas* and its allies, and one that, according to WITHERS' suggestion, anticipated the five-plated Eocene lepadid *Oxynaspis,* a form considered primitive to the Lepadidae. Although the primordium of the carina is generally subcentral or basal in adults of most oxynaspidid species, it was shown by TOTTON (1940) to move considerably during ontogeny from an apical position. This suggests that *Oxynaspis* is more primitive than the adult form had previously indicated. It should be mentioned also, that BROCH (1922) tended to dismiss the so-called primitive features seen in *Oxynaspis* because of its special way of life in association with antipatharians, and in one case a sponge. However, it seems just as reasonable that *Oxynaspis* has retained rather than evolved these features, just as *Chelonibia*, although specialized to life on turtles and large decapod crustaceans, has retained a very primitive feature (separate rostrum) seen in no other balanid. It happens that these characters, specifically the central scutal umbo and apical carinal umbo, as well as simply five plates, the characters that lead us to believe *Oxynaspis* is primitive, are the characters it shares with the oldest known five-plated thoracican, *Praelepas* from the Carboniferous. In fact, if *Praelepas* existed today, and nothing of its internal anatomy indicated otherwise, it would be classified as an oxynaspidid.

Thus it seems that evidence based on the position of umbones is not alone valid in establishing primitiveness. Comparisons that have been made assume the lineage from Scalpellidae to Lepadidae (or "migration" of the umbo from an apical to basal position) to be established, whereas this is not the case. The definitive position of the umbo is related to allometric growth of the plate and therefore is interrelated with the overall form of the capitulum and the distribution and number of plates. The great antiquity of the five-plated *Praelepas*, and its possession of chitinous rather than calcareous plates, are strong points in favor of its consideration as a primitive, unmodified lepadomorph at the level of organization of the extant Oxynaspididae. *Praelepas* and the general lack of Paleozoic thoracicans suggests that calcareous plates did not evolve until the Mesozoic.

This general hypothesis is supported by the recent discovery of *Cyprilepas* in the Silurian, found living on eurypterids (WILLS, 1963). These minute (2.2 to 4.8 mm.) lepadomorphs consist of a chitinous bivalved capitulum and cylindrical peduncle, and somewhat resemble recently settled lepadomorph cyprid larvae. Although there is no indication that the capitulum bore calcareous plates, the microstructural patterns found on the plates of some specimens are suggestive of the hexagonal pattern apparently occurring in the cyprid shell of *Lepas* and in the primordial plates of the lepadomorphs in general. The presence of a peduncle with attachment disc, and the relatively large size of the biggest individuals, rule out the possibility that *Cyprilepas* is only a cyprid stage. It appears that there are actually two size classes and these could be interpreted either as growth stages or separate male and female individuals. *Cyprilepas* is very similar in size and form to certain of the Poecilasmatidae living on large decapod crustaceans.

Cyprilepas and *Praelepas* suggest a primitive lepadid facies. The relative primitiveness of extant Lepadidae is further demonstrated by the nervous system (CORNWALL, 1953). The nerve cord of *Lepas* is the most ladder-like of the known Thoracica, with greatest separation of the ganglia. In contrast, the Scalpellidae show progressive fusion of the cords and condensation of ganglia. In the Balanomorpha, which are without question phylogenetically most highly advanced, all cirral nerves stem from one large subesophageal ganglionic mass.

The cirral arrangement is no more specialized or generalized in the Scalpellidae than in the Lepadidae. In *Lepas, Alepas,* and *Scalpellum* only cirrus *I* is modified as a maxilliped, with the anterior ramus rotated posteriorly and attenuated, the articles of both rami somewhat protuberant. In *Conchoderma*, a close relative of *Lepas*, cirrus *I* is hardly modified, with nonrotated anterior ramus, and the cirri form a simple graded series. The simplest and perhaps most primitive arrangement is found in the Iblidae, where all cirri are structurally similar (cf. Fig. 101,*3-4;* 102,*1*).

In summary, available paleontological and neontological evidence indicates that the Lepadidae are more closely related to *Cyprilepas* and *Praelepas* stocks than are the Scalpellidae. It had been assumed by DARWIN and WITHERS that shell development exhibited by Scalpellidae is the more primitive method. However, the situation seen in *Cyprilepas* and *Praelepas* suggests that the lepadid type of shell development is probably the more primitive mode. Here the scutum or its equivalent is the principal capitular plate, covering most of the animal's body, as does the single bivalved shell of the Ascothoracica and the cyprid larva of cirripeds in general.

WITHERS (1928, 1935, 1953) has described in some detail the phylogeny of Mesozoic Scalpellidae for which there is a relatively continuous although fragmentary fossil record. Much less, however, is known of other lepadomorph families. The Lepadidae (Lepadinae) are known only from the Cenozoic by a few fossil representatives included in the genus *Lepas*. WITHERS (1953) proposed *L. (Dosima) fascicularis* as the most primitive of extant species, based on the more central position of the carinal umbo. However, he pointed out that this species is highly specialized for a pelagic existence. It is very thin-shelled, the peduncle produces a gas-filled float, and the entire animal is globular in form. Of other five-plated families, the Oxynaspididae are represented in the fossil record by one species from the middle Eocene of England, and the Poecilasmatidae are known by two scuta and a tergum from the English upper Eocene.

EVOLUTION OF SCALPELLIDAE

WITHERS postulated three trends in the evolution of the Scalpellidae, in regard to the capitular plates: 1) changes in number, 2) change in position of umbones as a result of differential growth, and 3) reduction in the extent of calcification.

1) Many-plated scalpellids of the genera *Calantica* and *Zeugmatolepas* occur with six-plated *Archaeolepas* and *Eolepas* in the late Middle and Upper Jurassic, suggesting an initial trend toward multiplication of the number of capitular plates. In the Cretaceous, *Scalpellum*-like forms are first found, suggesting a reversal in trend toward fewer plates, from 17 in *Cretiscalpellum* to 15 in extinct, or 14 or ?13 in extant species of *Arcoscalpellum*, and 14 in *Virgiscalpellum*. The reduction to 13, through loss of the rostrum in many species of *Arcoscalpellum*, is in need of confirmation. Among extant scalpellids, the 11-plated *Scalpellopsis* exhibits yet further reduction from the condition seen in *Arcoscalpellum*, through the loss of the rostral latera.

On the other hand, a trend toward an increased number of capitular plates is seen in *Zeugmatolepas* and Jurassic *Calantica*, and this is apparently continued in extant *Calantica* and the related *Pollicipes*. Thus it appears that both multiplication and reduction has occurred in various scalpellid lineages.

2) The position of the umbo, which was discarded above as the definitive guide to major evolutionary trends in the Lepadomorpha, is apparently of real value in the interpretation of lineages within genera or closely related groups, as illustrated by the following examples.

Euscalpellum. This genus ranges from Upper Cretaceous to Recent, but is known in the Cretaceous only by large peduncles. *E. minutum* (BROWN) from the lower Eocene (Ypresian) of England has the umbo of each plate in an apical position, and also has an extra plate, the subrostrum, unknown in later species. The umbo is removed from the apex of the carina, scutum, and upper latus of *E. vomer* (BERTRAND) from the middle Eocene (Lutetian) of France and England. The umbones of the carina and scutum are subapical in *E. eocenense* (MEYER) from the middle Eocene (Claiborne, Lutetian) of the USA, but the upper latus still possesses an apical umbo. The greatest change in position of the umbones is found in the extant *E. rostratum* (DARWIN) from the Philippines, in which on the carina, scutum, upper latus, and all latera they are subapical. However, some Miocene and Recent species still have the umbones of all plates apical in position.

Arcoscalpellum. In *Cretiscalpellum* and the earlier Cretaceous species of *Arcoscalpellum*, the umbo of every valve is apically situated. However, the later upper Senonian species *A. fossula* (DARWIN), which is apparently derived from the Cenomanian-Turonian *A. angustatum* (GEINITZ), exhibits definite upward growth of the inframedian and upper latera, leaving the umbones slightly removed from the apex. The Eocene *A. quadratum* (DIXON) shows this development more clearly, especially in the inframedian latus.

Scalpellum. The earliest known species of *Scalpellum* is *S. fischeri* BERTRAND from the lower Eocene of France and England. It exhibits an upward growth in all the plates except the rostral latus, and this growth is greatest in the upper and inframedian latera. It is in these latter plates that upward growth is first seen in *Arcoscalpellum.* Some Eocene, Miocene, and Recent species (e.g., *S. stearnsi* PILSBRY) show progressive migration of the umbones away from the apices of the plates. In fact, *S. stearnsi* differs from *S. fischeri* only in the progressive development of the plates, for the umbones, especially of the carina and scutum, are still farther removed from the apices, and the rostral and carinal latera have become lower and wider. Instructively, the *S. fischeri* stage is ontogenetically recapitulated during development of *S. stearnsi.*

From examination of the fossil species of *Arcoscalpellum* and *Scalpellum,* and from studying the ontogeny of *S. stearnsi,* it appears that *Scalpellum* was derived from an *Arcoscalpellum* stock.

Virgiscalpellum. This genus is first found in the Lower Cretaceous (Aptian) together with *Arcoscalpellum* and *Cretiscalpellum.* The capitulum has 14 plates, including a long, thick and narrow rostrum; no subcarina has been found. *Virgiscalpellum* represents the earliest known scalpellid in which both the carinal and scutal umbones are subapical. It is peculiar among *Scalpellum*-like barnacles in that the scutum possesses a nearly central umbo, except in the Maastrichtian *V. darwinianum,* in which the umbo is in the basal third of the scutum. The placement of the carinal umbo varies widely in the several species, and in fact is nearest the base of the carina in the earliest (Aptian) species, *V. wrighti.* In other species (e.g., *V. ryckholti, V. hagenowianum*) the carinal umbo is subapical. In *V. darwinianum* the umbo is nearly central, although in some older specimens it is nearer the base. The scutal umbo varies little in position from species to species. The form of the upper, rostral, inframedian, and carinal latera suggests either that *Virgiscalpellum* represents a side lineage from *Arcoscalpellum,* or that both genera had a common ancestor. *Virgiscalpellum* reached a more advanced stage of capitular development than any other scalpellid genus, and has little in common with the *Scalpellum* stock.

3) WITHERS (1928), in concurrence with interpretations of other students of the cirripeds, in particular DARWIN (1851), has pointed out that certain species of the Lepadomorpha, having plates that do not fully cover the capitulum, are forms that have descended from fully armored stocks. Trends in reduced armament occur in very distantly related lines, as can be amply documented in the families Lepadidae, Poecilasmatidae, Oxynaspididae and Scalpellidae. Such trends were categorized by WITHERS under the heading "Decalcification" but this term is somewhat misleading because the plates are not first formed ontogenetically and then subsequently reduced by a decalcification process as it would imply. Rather, the situation is a case of allometry where calcification of the plates has lagged behind general growth, so that the plates come to occupy proportionately less and less of the area of the capitulum, during development of an individual. HOEK (1883) considered such forms among the Scalpellidae as "imperfectly calcified" and PILSBRY (1907) pointed out that ontogenetic development progressed from fully armored juveniles to adults with reduced plates.

The failure of a particular calcified plate to develop at a rate sufficient to maintain its margins approximate to those of its neighbors may occur uniformly around its perimeter, so that its fundamental shape is retained, or it may occur in specific areas while the remainder continues to grow. This type of development is clearly illustrated in *Mesoscalpellum convexum* (NILSSON-CANTELL), in which the juvenile stages are initially completely armored, but become progressively less so as maximum size is reached. In the adult of this species, the latera have come to occupy as little as a sixth of the space available to them, yet their original shape has for the most part been maintained. However, only portions of the terga have been affected, so that while the distal portions appear normal, development of the proximal portions have lagged behind, thus altering the form of the plate from simply triangular to quadrangular, with a basal spur (NILSSON-CANTELL, 1930,

p. 2445, fig. 9). A more extreme example is seen in the Recent *M. dicheloplax* (Pilsbry) where the basic form of all plates, except the carina, is modified in this manner (Fig. 94,*11*).

In the Lepadidae and Poecilasmatidae with reduced armor, an ontogenetic recapitulation of the fully armored form is not seen, and the juvenile begins virtually as fully armored as the adults. In the Poecilasmatidae, a curious reversal has come about. A typical case of reduction in calcified portions of the plates is seen in *Octolasmis (Octolasmis) neptuni* (MacDonald) where, while the full extent of the plates can be seen in the chitin of the capitulum, the calcified portions are much reduced at their inception and they retain relatively the same proportions during subsequent growth. However, certain other species of the genus, *O. (O.) cor* (Aurivillius), *O. (Dichelaspis) orthogonia* (Darwin), and *O. (O.) tridens* (Aurivillius) for example, begin their ontogenetic development in the same ways as *O. (O.) neptuni,* but as growth progresses the plates become proportionately more extensive and appreciably altered in form. This is effectively a rearmament process where adults come to have more complete plates than juveniles. In fact, the trend towards rearmament is completed in such species as *Trilasmis (Trilasmis) eburneum* Hinds and *T. (Temnaspis) fissus* (Darwin), where, although the plates cover the entire capitulum, it is evident that the scutum was once very much reduced, having been formed of two principal arms as in *O. (Octolasmis)*. However, the terga are missing in *T. (T.) eburneum,* indicating that this plate was completely lost during an earlier phylogenetic period when the plates in general were much reduced, as in present day *O. (O.) cor.* This

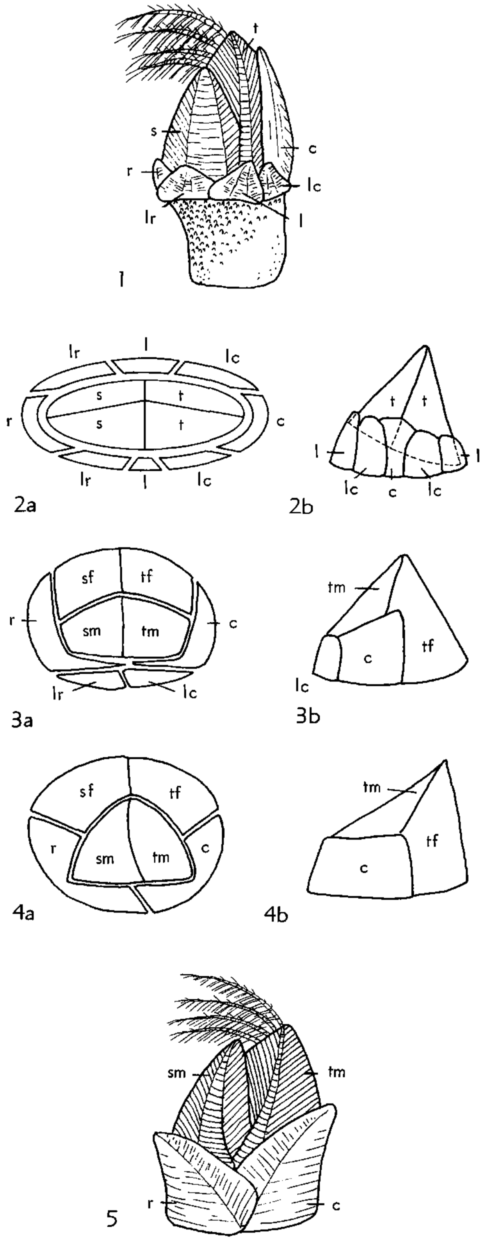

Fig. 113. Inferred origin of plate arrangement in Verrucomorpha (Newman, n).

1. Bilaterally symmetrical pedunculate ancestor comparable to living species of *Calantica,* viewed from right side.

2. Hypothetical intermediate sessile form in which tergum and scutum of one side contact the substratum basally, to become incorporated into structure of the wall, while tergum and scutum of other side act as the operculum.

3. Arrangement of plates in extinct genera *Eoverruca* and *Proverruca,* in which rostrolateral and carinolateral plates of one side are still present.

4. Arrangement of plates, as in *Altiverruca.*

5. Generalized *Verruca,* viewed from right side. [Explanation: *2a, 3a, 4a,* plan views; *2b, 3b, 4b,* carinal or dorsal views; *c,* carina; *l,* lateral plate; *lc,* carinolateral plate; *lr,* rostrolateral plate; *r,* rostrum; *s,* scutum; *sf,* scutum (fixed); *sm,* scutum (movable); *t,* tergum; *tf,* tergum (fixed); *tm,* tergum (movable).]

indicates that once a plate is lost, a homologue is not likely to be regained.

In the Scalpellidae, then, since the Mesozoic two trends can be discerned, one in reduced number and the other in reduced area occupied by plates of the capitulum. These do not necessarily go hand in hand, for many species with plates much reduced in number have remained fully armored. However, reduction in extent has led to loss in number in such forms as *Scalpellopsis.*

The lepadids have undergone similar trends, but the trend in reduction of area covered by the capitular plates has been reversed in some species. Some of these through a rearmament process, in particular in *Trilasmis (Temnaspis) fissus,* have come to appear structurally as armored as species that cannot be demonstrated to have passed through a reductional phase. Both the Lepadidae and Scalpellidae have given rise to forms in which only a trace of the scutum remains: *Alepas,* showing affinities with *Lepas* on one hand, and Heteralepadidae showing affinities with the scalpellids on the other.

VERRUCOMORPHA

The Verrucomorpha contain a single family, the Verrucidae. Three genera are known: *Proverruca* ranging from the upper Senonian (Cretaceous) to the Miocene; *Eoverruca* known only from the middle Senonian; and *Verruca* ranging from upper Senonian to Recent.

The Verrucomorpha are sessile cirripeds, differing from the Balanomorpha in the highly asymmetrical development of the shell wall and the operculum (Fig. 113). In the Lepadomorpha, two pairs of plates, the terga and scuta, border along the occludent margin of the aperture. In the scalpellids, these plates never form the operculum-like arrangement as that seen in the Balanomorpha, but they do become somewhat specialized in their role of guarding the aperture. The separation of these plates from those forming the wall develops during the transition from a pedunculate to a sessile mode of life. In the transition from pedunculate to balanomorph, a clear separation is made between the opercular and wall plates, and the basic bilateral symmetry of the plates is maintained. However, in the transition from pedunculate to verrucomorph, one of each pair of potential opercular plates becomes incorporated into the wall, rather than separating off to form one side of the operculum, so that the basic bilateral symmetry both of the shell wall and the operculum is lost (Fig. 90).

The earliest known verrucomorphs, *Proverruca* and *Eoverruca,* have a six-plated wall closed by two plates forming the opercular valves. The carina and rostrum form the ends of the boxlike shell, a carinolateral and rostrolateral form one side, and a fixed tergum and fixed scutum form the other. It is quite evident that this asymmetrical arrangement has come about through the loss of at least two latera, in conjunction with the incorporation of the tergum and scutum into that side of the wall. Thus the protoverrucomorph, before the separation of the operculum from the wall, must have had a bilaterally symmetrical wall composed of carina, rostrum, and at least two pairs of latera; effectively the same grade of construction is seen in *Calantica (Paracalantica),* although without phylogenetic implications. Like *C. (Paracalantica),* the verrucomorph presumably descended from a form with three pairs of latera, such as *Calantica (Scillaelepas)* or *C. (Titanolepas)* (Fig. 115,*9,12*).

The grade of construction seen in *Proverruca* and *Eoverruca* leads to that seen in *Verruca,* through the loss of the remaining latera, and the joining of the carina and rostrum on the carinorostral side (Fig. 113). As will be seen, this trend toward simplification and rigidity by reduction in number of parts in the verrucomorphs is paralleled in several distinct lines of balanomorphs, although the latter maintain their bilateral symmetry.

Except for the carina and rostrum, the plates of *Proverruca* (see Fig. 117,*1*) have not departed far in structure from those of the Lepadomorpha. The suppression of the two latera of *Proverruca,* and the joining of the carina and rostrum on what becomes the carinorostral side, are all the changes required to arrive at the plate arrangement seen in *Verruca.* This trend is indicated in *Proverruca,* as one of the two latera is already nearly excluded from the wall by the underlying carinal latus and the rostrum.

Eoverruca (see Fig. 117,*3*), like *Proverruca,* had at least two latera opposite the side of the fixed tergum and scutum, but the carina and rostrum are only slightly asymmetrical. In this respect *Eoverruca* is closer to the pedunculate ancestor than *Proverruca,* but on the other hand, the fixed scutum and tergum possess interlocking ribs which indicate an advanced condition. The plates of *Eoverruca* bear a marked resemblance to those of the brachylepadomorph *Pycnolepas,* and differ considerably from those of *Proverruca,* suggesting that these two verrucomorph genera are not closely related.

The shell of *Verruca* exhibits the greatest degree of asymmetry seen in the suborder, and even in Cretaceous representatives, the carina and rostrum form one side of the wall and are articulated by means of several interlocking ribs. An asymmetrical shell wall is not confined to the Verrucomorpha. In the lepadomorph *Calantica,* the rostrum and subcarina are often asymmetrical. Also, the carina and rostrum in the balanid *Chelonibia* and the chthamalid *Chthamalus* are not precisely opposing, although the animals remain effectively bilaterally symmetrical. However, a curious parallel has occurred in *Chthamalus anisopoma* PILSBRY that verges on the type of asymmetry seen in verrucomorphs. The opercular valves, although fundamentally bilateral in the genus, have been displaced on one side so that the set formed by one tergum and scutum lies horizontally across the aperture and acts as the principal part of the operculum. The other set is very much reduced in size and serves more as a rim on which the opercular set rests, than as a movable part of the opercular apparatus. The body of the animal also lies somewhat on its side, and like *Verruca,* the cirri tend to be projected laterally rather than vertically, but the functional significance of this is unknown.

BRACHYLEPADOMORPHA

The suborder Brachylepadomorpha includes a single family, the Brachylepadidae, and the two genera, *Pycnolepas* and *Brachylepas.* The shell is formed by the carina and rostrum, surrounded at the base by three or four whorls of small imbricating plates. A feature that distinguishes this suborder from all sessile cirripeds but is shared with *Pollicipes mitella* among the scalpellid Lepadomorpha is the presence of a long, narrow upper latus between the scuta and terga of each side.

Pycnolepas (see Fig. 117,5) is possibly represented in the Upper Jurassic (Tithon.) by certain carinae, but it is definitely represented in the Albian by *P. rigida* (SOWERBY); which ranges into the Cenomanian. Another species, *P. brünnichi* WITHERS, which is related to *P. rigida,* occurs in the Danian, but the evolution of this lineage in the intervening time is not known. *Pycnolepas* has a cylindrical carina and a laterally flattened shell, the plates being similar to those of lepadomorphs. Imbricating plates form whorls at the base of the carina and rostrum, and at least the two outer whorls have deep "muscle-pits" on the inner extremity of the inwardly projecting basal ledge.

Brachylepas fallax (DARWIN) (Turon.-L. Maastricht.) once assigned to *Pycnolepas,* was transferred to the genus *Brachylepas,* on the basis of the structure of the basal imbricating plates. Since it occurs in the time interval between the two above-mentioned species, the reassignment alleviated the problem of attempting to include *B. fallax* in the *Pycnolepas* lineage. *B. fallax* is like *Pycnolepas* in having a cylindrical carina and laterally flattened shell, and was probably a derivative of the *Pycnolepas* stock. *B. naissanti* (HEBERT) (see Fig. 117, 2) which is widespread in comparatively deep-water deposits of the upper Senonian (*Belemnitella mucronata* Zone), has a radially symmetrical shell, but the basis was probably membranous. The remaining species, *Brachylepas guascoi* (BOSQUET) (Maastricht.) from shallow-water deposits, also has a radially symmetrical shell, but the basis is calcareous and the scuta and terga resemble somewhat those of primitive Balanomorpha.

In the Brachylepadomorpha, the geologically earliest representative *(Pycnolepas)* is closely similar in structure to the Lepadomorpha. *Brachylepas,* which was probably derived from *Pycnolepas,* appears to be transitional between a form with laterally flattened shell and membranous basis to one with a radially symmetrical shell and a calcareous basis. The Brachylepadomorpha, in view of the reduced number of elements in the shell wall, are apparently not ancestral to the Balanomorpha, but represent an early and independently developed group which became widespread in the late Senonian and Maastrichtian. Except for the reduced number of shell plates and the retention of the upper lateral, brachylepadomorphs bear a closer resemblance to the chthamalid *Catophragmus* and to the scalpellid *Pollicipes mitella* than to other extant thoracicans. In fact, species of *Pycnolepas* and *Brachylepas* were assigned to *Pollicipes* by early workers, including both DARWIN and WITHERS. Although it seems inescapable that they represent a specialization in themselves and are not in the stem line of the balanomorphs, the evidence is equally convincing that they are closely related to the pedunculate stock that did give rise to the Balanomorpha.

Even though the Brachylepadomorpha appear to have no direct relationship to Balanomorpha, such fossils as *Brachylepas guascoi* help to elucidate the homologies of the opercular valves in balanomorphs. In *Pycnolepas* and *B. fallax* the scutum has an almost median apicobasal ridge, in *B. naissanti* the tergal side is narrower and more steeply sloping, and in *B. guascoi* the tergal side of the scutum is very narrow and reflexed at right angles to the outer surface so that the apicobasal ridge forms the tergal margin. The scutum of *B. guascoi* is similar in shape to that of *Balanus,* but lacks the articular ridge and lateral depressor muscle pit on the inner surface. The narrow basal part of the tergum of *B. guascoi* needs little modification to form the characteristic balanid spur, but lateral depressor muscle crests are absent. The upper latus of *B. guascoi* has not yet been identified, and there is some indication from the form of the scutum that it was reduced or even absent.

BALANOMORPHA

The suborder Balanomorpha includes two families, Chthamalidae and Balanidae. It is distinguished from other sessile thoracican groups by the presence of a symmetrical, basically eight-plated shell wall, with paired scuta and terga forming an operculum. The Chthamalidae are considered phylogenetically more primitive and to have been derived from a lepadomorph stock. *Catophragmus* most closely resembles the present concept of the early balanomorph. The presence of eight compartmental plates, additional whorls of smaller plates about the base of the shell wall, opercular valves which lack well-defined internal structures, caudal appendages, and an unmodified cirrus *III* are all features which link *Catophragmus* with such scalpellid lepadomorphs as *Pollicipes* (as noted by DARWIN, 1854) and *Calantica (Scillaelepas)* (as indicated by PILSBRY, 1916). It is probable that *Catophragmus* and the above mentioned scalpellids shared a common ancestry. Also, it is significant (and fortuitous) that the oldest known balanomorph, the only undoubted balanomorph from Mesozoic deposits, belongs to the genus *Catophragmus* (i.e., *C. (Pachydiadema) cretaceum*).

Chthamalids are not well represented in the fossil record. *Hexelasma* has been identified tentatively from early Oligocene rocks and is definitely recorded from Miocene deposits of New Zealand *(114)*. *Pachylasma* is known from the Miocene of Italy *(2)*. *Tessarelasma* is known only from the early Miocene of India (WITHERS, 1936), and *Chthamalus* has been recorded from Pliocene (Piacenz.) deposits in Italy (ALESSANDRI, 1906). *Chthamalus* is found rarely in late Pleistocene deposits in southern and Baja California (ZULLO, herein), and WITHERS (1932) has reported *Octomeris* from a supposed Pleistocene limestone in Australia. Therefore, many of the inferences made at the present time concerning the phylogeny of the Chthamalidae must be based on comparisons of extant taxa.

The evolutionary history of the Chthamalidae has been one of reduction in the number of elements in the shell wall and modifications in the feeding apparatus (ZULLO, 1963). Two lineages can be distinguished. In the first, leading from *Catophragmus* to *Octomeris, Chionelasmus, Chthamalus,* and *Chamaesipho,* shell wall reduction was achieved primarily through exclusion of elements, and feeding modifications were confined to changes in mandibular structure. *Octomeris* differs from *Catophragmus* principally in the absence of whorls of smaller plates about the base of the shell wall. *Chionelasmus* retains one of the basal whorls, but the carinolaterals have been lost. *Chthamalus* is closely related to *Chionelasmus,* but differs in having lost all traces of the basal whorls, and in possessing (in some species) a mandible modified from the basic lepadomorph type. *Chamaesipho* represents a further step beyond *Chthamalus* in the reduction of the number of elements in the shell wall. In this genus, the laterals and rostrolaterals have apparently fused to form a four-plate shell wall (Fig. 96).

In the second lineage, leading from *Octomeris* to *Pachylasma* to *Hexelasma,* and *Tessarelasma,* shell wall reduction was accomplished primarily through fusion of elements, and feeding adaptations involved the modification of cirrus *III* for use as a mouth appendage. Fusion of the rostrum with the adjacent rostrolaterals is exhibited in species of *Pachylasma,* and from this, the tripartite rostral plate is inferred in *Hexelasma,* and *Tessarelasma.* These last two genera also differ from *Pachylasma* in the form of the opercular valves which are more like those of the balanid barnacles than of other chthamalids. Also, in *Hexelasma,* in which the body is known, cirrus *III* has been modified somewhat for use as a mouth appendage. *Tessarelasma,* as *Chamaesipho,* has attained a four-plate shell wall, but in this case the reduction was apparently achieved through loss of the carinolaterals as in *Tetrachthamalus* (Newman, 1967).

The development of a compound rostral plate, the modification of cirrus *III,* and the change in form of the opercular valves in the *Pachylasma-Hexelasma* lineage indicates that the Balanidae were derived from a *Pachylasma*-like ancestor. The compound nature of the balanid rostral plate is demonstrated by *Chelonibia,* in which the sutures between the rostrum and rostrolaterals are still visible. It is no doubt through the highly specialized habitat of this genus that this primitive character has been retained. All other balanids bear no trace of the sutures uniting the elements of the rostral plate. RUNNSTRÖM (1925) and BROCH (1927) have concluded from a study of ontogenetic development of the shell in *Balanus (Semibalanus) balanoides,* that the rostrum is not present in the balanid rostral plate, which therefore would be formed only of the two rostrolaterals.

The ancestral balanid was probably a form similar to *Balanus (Solidobalanus)* [includes *Hesperibalanus*] in possessing a shell wall with solid parietes and moderately developed radii, a solid calcareous basis, and heavy opercular valves which lacked prominent internal structures. Some of the geologically earliest balanids from the middle and late Eocene of Europe, and southeastern and northwestern United States can be included in the subgenus *B. (Solidobalanus)* (ZULLO, 1960). More recently Ross (1965) has established a new genus *Kathpalmeria* to include other Eocene balanids. Rapid diversification apparently took place during the Oligocene. Forms with parietal tubes and tubes in the radii (e.g., *B. (Balanus), B. (Megabalanus), Tetraclita*) have been reported from Oligocene strata, as well as the solid-walled subgenus *B. (Austrobalanus). B. (Balanus)* was probably derived from a solidobalanid-like stock through a form similar to *B. (Balanus) crenatus. B. (Balanus)* gave rise to *B. (Semibalanus)* through the multiplication of rows of parietal tubes and the loss of the calcareous basis, and subsequently to *Tetraclita* (?and *Elminius*) through loss of the carinolaterals. *Tetrabalanus* also appears to be a derivative of *Balanus s.s.,* perhaps through such a species as *B. (B.) amphitrite. B. (Chirona)* was probably derived independently from a solidobalanid-like stock, with *B. (Metabalanus)* representing a relatively recent offshoot of *B. (Chirona).*

The complex *Balanus (Armatobalanus), B. (Conopea), B. (Membranobalanus),* and *Acasta* represents another independent offshoot of the hesperibalanid stock, and the differences between these taxa primarily reflect differences in habitat. The lineage *Hexacreusia - Creusia - Pyrgoma-Pyrgopsella* was derived in the Miocene from this *Armatobalanus* complex which may also have given rise to the coronuline barnacles. The proposed derivation of *Cryptolepas* from *Coronula,* and *Tubicinella* from *Cryptolepas* appears valid, but the relations between the other coronuline taxa are at present difficult to interpret.

SYSTEMATIC DESCRIPTIONS

Class CIRRIPEDIA Burmeister, 1834

Sedentary marine Crustacea having fundamental affinities with the Maxillopoda;[1] forming initial attachment by first antennae; following appendages (when present) and body contained within carapace (mantle); mantle in principal order (Thoracica) typically supporting calcareous plates persisting through molt cycles during adult life. Development usually includes six naupliar stages, and bivalved cyprid stage. Sexes separate or combined; males, when present, always reduced, occurring with females or hermaphrodites. *U.Sil.-Rec.*

Order ACROTHORACICA Gruvel, 1905

[=Abdominalia Darwin, 1854]

Cirripedia with separate sexes; females always found burrowing in calcareous substrate, accompanied by reduced males which lack feeding appendages. Females differ from thoracican cirripeds in having the cirri (except first pair) terminal rather than evenly distributed along thorax, in not developing calcareous plates, and in molting the entire exoskeleton, including exterior of carapace, rather than just the interior lining and appendages. *Carb.-Rec.*

Suborder PYGOPHORA Berndt, 1907

Gut complete, and three or more pairs of biramous terminal cirri present. *Rec.*

The following classification parallels that of Berndt (1907), as suggested by Tomlinson (1967, personal communication).

Family LITHOGLYPTIDAE Aurivillius, 1892

[=Kochlorinidae Gruvel, 1905; Berndt, 1907; Balanodytidae Utinomi, 1950 *(103a)*; Berndtiidae Utinomi, 1950 *(103b)*; Chytraeidae Utinomi, 1950 *(103b)*; Utinomiidae Tomlinson, 1963]

Pygophora without lateral bar, gastric mill or elongate labrum. *Rec.*

Lithoglyptes Aurivillius, 1892 (p. 133) [**L. indicus;* OD]. Five pairs of cirri (1 mouth, 4 terminal), and caudal appendages. *Rec.,* IndoPac.-Carib.

Balanodytes Utinomi, 1950 (p. 1) [**B. taiwanus;* OD]. Five pairs of cirri (1 mouth, 4 terminal), without caudal appendages. *Rec.,* Taiwan.

Berndtia Utinomi, 1950 (p. 7) [**B. purpurea;* OD]. Six pairs of cirri (1 mouth, 5 terminal), without caudal appendages. *Rec.,* Japan.

Kochlorine Noll, 1875 (p. 114) [**K. hamata;* OD]. Four pairs of cirri (1 mouth, 3 terminal) and caudal appendages. *Rec.,* Spain.-S.Afr.-W.Atl.

Kochlorinopsis Stubbings, 1967 (p. 306) [**K. discoporellae;* OD]. Like *Kochlorine* but lacking longitudinal retractor muscles along rostral sides of mantle. *Rec.,* W.Afr.

Weltneria Berndt, 1907 (p. 289) [**W. spinosa;* OD] [=*Utinomia* Tomlinson, 1963 (p. 264)]. Six pairs of cirri (1 mouth, 5 terminal), and caudal appendages. *Rec.,* S.Afr.-Japan-Hawaii-Bermuda.

Family CRYPTOPHIALIDAE Gerstaecker, 1866

Pygophora with lateral bar, gastric mill, and much elongated labrum. *Rec.*

Cryptophialus Darwin, 1854 (p. 566) [**C. minutus;* OD]. Five or four pairs of cirri (1 mouth, 4 or 3 terminal), no caudal appendages. *Rec.,* S. Am.-S.Afr.-W.Afr.-Antarctic-N.Z.

Suborder APYGOPHORA Berndt, 1907

Acrothoracica with incomplete gut, three pairs of uniramous terminal cirri. *Carb.-Rec.*

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[1] As previously noted, not recognized in *Treatise* classification. Dahl (1963, p. 1) grouped cirripeds with mystacocarids, copepods, and branchiurans in so-called maxillopods.—Ed.

Family TRYPETESIDAE Stebbing, 1910

[=Alcippidae HANCOCK, 1849]

Trypetesa NORMAN, 1903 (p. 369) [**Alcippe lampas* HANCOCK, 1849; SD STEBBING, 1910]. Characteristics of family. *Carb.-Perm.* (burrows in exterior of mollusk shells); *Rec.* (burrows in interior of gastropod shells inhabited by hermit crabs), cosmop., N.Hemis.

Suborder UNCERTAIN

Burrows in a variety of calcareous substrates have been identified as those of Acrothoracica. The appropriateness of applying Linnean nomenclature has been questioned by RODDA & FISHER (1962), and there is in fact good reason to voice concern when it is recognized that only *Cryptophialus* and *Trypetesa,* among extant Acrothoracica, can be recognized presently by the form of their burrows alone. *Trias.-Plio.*

Family RODGERELLIDAE Saint-Seine, 1951

Burrow depth exceeding length, with peduncular slit and marginal flange; in echinoid tests, mollusk shells, and corals. *M.Jur.-L.Plio.*

Rodgerella SAINT-SEINE, 1951 (p. 1053) [**R. lecointrei;* OD]. Characteristics of family. *M.Jur.-L.Plio.*, Eu.-N.Am.

Family ZAPFELLIDAE Saint-Seine, 1954

Burrow depth at least half length, without peduncular slit or marginal flange. *Trias.-Plio.*

Zapfella SAINT-SEINE, 1954 (p. 449) [**Z. patei;* OD]. One end of aperture greatly enlarged. [Burrows in gastropods, pelecypods, and marl.] *Mio.-Plio.*, Eu.

Brachyzapfes CODEZ, 1957 (p. 706) [**B. elliptica;* OD]. Form of aperture elliptical. [Burrows in belemnites and pelecypods.] *L.Cret.*, Eu.-Antarctica.

Simonizapfes CODEZ, 1957 (p. 704) [**S. elongata;* OD]. One end of aperture slightly enlarged. [Burrows in belemnites and other mollusk shells.] *Trias.-Jur.*, Eu.

Order RHIZOCEPHALA F. Müller, 1862

[=Suctoria LILLJEBORG, 1861; Kentrogonida DELAGE, 1884]

Parasitic crustaceans without appendages or digestive tract in adult stage; recognized as Cirripedia by characteristic nauplius larvae or cyprid stage, or both. Parasitic on crustaceans, primarily Decapoda. *Rec.*

Suborder KENTROGONIDA Delage, 1884

[Kentrogonidae HÄFELE, 1911; Kentrogonidea GUERIN-GANIVET, 1911; BOCQUET-VÉDRINE, 1961]

Rhizocephala with kentrogon stage establishing endoparasitic phase; development generally including naupliar stages. *Rec.*

Family PELTOGASTRIDAE Lilljeborg, 1861[1]

[Peltogastridae LILLJEBORG, 1861, p. 96; BOSCHMA, 1928, p. 3 *emend.*]

Peltogaster RATHKE, 1843, p. 244 [**P. paguri;* SD LILLJEBORG, 1861, p. 25]. Body elongate or ovoid, long axis parallel to long axis of host; colleteric glands and male-cell receptacles ("testes") paired; latter opening backward into mantle cavity. [Family divisible into gregarious (colonial) and nongregarious genera. Parasitic on pagurids and galatheids.] *Rec.*

Family SACCULINIDAE Lilljeborg, 1861[1]

[Sacculinidae LILLJEBORG, 1861, p. 96; BOSCHMA, 1928, p. 13 *emend.*]

Sacculina THOMPSON, 1836, p. 452 [**S. carcini;* SD BOSCHMA, 1955, p. 3]. Body laterally compressed; colleteric glands and male-cell receptacles paired; latter opening ventrally into mantle cavity. [Parasitic on anomurans (Hippidea and Galatheidea); brachyurans (Gymnopleura, Dromiacea, Brachygnatha and Oxyrhyncha).] *Rec.*

Family LERNAEODISCIDAE Boschma, 1928[1]

[Lernaeodiscidae BOSCHMA, 1928, p. 17]

Lernaeodiscus F. MÜLLER, 1862, p. 2 [**L. porcellanae;* SD VAN BAAL, 1935, p. 51]. Body dorsoventrally compressed; colleteric glands and male-cell receptacles ("testes") paired; latter opening into posterior part of mantle cavity. [Parasitic on galatheids and thalassinideans.] *Rec.*

Family CLISTOSACCIDAE Boschma, 1928

[Clistosaccidae BOSCHMA, 1928, p. 26]

Clistosaccus LILLJEBORG, 1861, p. 81 [**C. paguri* (=*Apeltes paguri* LILLJEBORG, 1861, p. 95); SD BOSCHMA, 1928, p. 26]. Body elongate or ovoid, long axis parallel to long axis of host; colleteric

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[1] Additional genera listed in Addendum to Cirripedia, p. R628.

gland and "testis" unpaired; the latter opening into anterior part of mantle cavity. [Parasitic on Paguridea.] *Rec.*, N.Atl.-N.Pac.

Family SYLONIDAE Boschma, 1928

[Sylonidae Boschma, 1928, p. 33]

Sylon Kröyer, 1855, p. 128 [**S. hippolytes* M. Sars, 1870; SD Boschma, 1928, p. 35]. Body ovoid, long axis parallel to long axis of host; colleteric glands unpaired, ?forming male-cell receptacle; mantle cavity with paired opening to exterior; development without free naupliar stages. Rec., N.Pac.-N.Atl. Inclusion of *Thompsonia, Duplorbis* and *Mycetomorpha* (Yanagimachi & Fujimaki, 1967) by *lapsus calami* (Yanagimachi, pers. comm.; Reischman, pers. comm.).

Suborder AKENTROGONIDA Häfele, 1911

[Akentrogonidae Häfele, 1911; Akentrogonidea Guerin-Ganivet, 1911; Bocquet-Védrine, 1961]

Rhizocephala without kentrogon stage; ectoparasitic penetration superficial or with moderate to extensively developed nutritive processes; development without free naupliar stage; no male-cell receptacles. [Genera other than *Chthamalophilus* included provisionally.] *Rec.*

Chthamalophilus Bocquet-Védrine, 1957, p. 1545 [**C. delagei;* OD]. Solitary rhizocephalan, with bulbous localized nutritive process; "testes" residing in mantle cavity. [Ectoparasite on cirriped *Chthamalus*]. *Rec.*, E.Atl. (vicinity of Roscoff).

Duplorbis Smith, 1906, p. 118 [**D. calathurae;* OD]. Solitary rhizocephalan; apparently without extensive nutritive processes, attached to host by tube opening into mantle cavity; ?male-cells residing in mantle cavity. [Parasitic on Isopoda.] *Rec.*, N.Atl.

Microgaster Bocquet-Védrine, 1967, p. 1630 [**M. balani;* OD]. Solitary, much like *Chthamalophilus* except for rootlike nutritive processes, invading tissue of host. [Parasitic on *Balanus*.] *Rec.*, E.Atl.

Mycetomorpha Potts, 1912, p. 591 [**M. vancouverensis;* OD]. Multilobed solitary rhizocephalan; nutritive processes not widely distributed; situated under abdominal nerve cord of host; male-cells residing in mantle. [Parasitic on Caridea.] *Rec.*, N.Pac.

Thompsonia Kossmann, 1873, p. 132 [**T. globosa;* OD] [=*Thylacoplethus* Coutière, 1902; Potts, 1915, p. 28, *emend.*]. Colonial rhizocephalan without mantle cavity; internal nutritive processes giving off numerous external reproductive sacs, male-cells residing in mantle. [Parasitic on Caridea, Galatheidea, Paguridea, Thalassinidea, Brachygnatha.] *Rec.*, N.Pac.-Carib.-Medit.

UNCERTAIN AFFINITIES

Sphaerothylacus Sluiter, 1884, p. 205 [**S. polycarpae;* OD]. Body containing reproductive organs and alimentary canal, covered by mantle. Attached to pharynx of tunicate by branching nutritive processes; ovaries opening near mouth suggesting cirriped affinities; nauplii without frontolateral horns suggesting ascothoracican or copepod; host selection suggests copepod. [Parasitic on *Polycarpa*.] *Rec.*, E.Indies.

Order ASCOTHORACICA Lacaze-Duthiers, 1880

[=Ascothoracida or Rhizothoracida Lacaze-Duthiers, 1880 (p. 580); Ascothoracica Gruvel, 1905 (p. 336)]

Cirripedia with prehensile first antennae; body enclosed in bivalved carapace; sexes separate or combined; mouth parts forming oral cone modified for biting and piercing; thoracic appendages basically natatory, first pair not conspicuously modified to form accessory mouth parts; fifth abdominal segment bearing furca. [Ectoparasitic and endoparasitic on coelenterates and echinoderms; generic definitions based on degree of reduction related to parasitic mode of existence.] *Cret.-Rec.*

Family SYNAGOGIDAE Gruvel, 1905

Six pairs of thoracic appendages; abdomen of four or five distinct somites and furca; carapace distinctly bivalved. [Ectoparasitic on antipatharians, crinoids, and ophiuroids.] *Rec.*

Synagoga Norman, 1887 (p. 87) [**S. mira;* OD]. Thorax of 6 distinct somites, each bearing pair of biramous natatory appendages. [Ectoparasitic on crinoids and Antipatharia.] *Rec.*, Medit.-Japan. [See Fig. 82,2.]

Ascothorax Djakonov, 1914 (p. 158) [**A. ophioctenis;* OD]. First thoracic somite fused with head; thoracic limbs somewhat reduced; 1st and 6th pairs biramous or uniramous; abdomen of 4 or 5 somites. [On ophiuroids.] *Rec.*, Arctic-Antarctic.

Parasothorax Wagin, 1964 (p. 271) [**P. synagogoides;* OD]. First thoracic somite fused with head, 1st thoracic limbs uniramous; abdomen of 5 somites, furca multiarticulate. [On ophiuroid.] *Rec.*, Okhotsk Sea-NW.Pac.

Family LAURIDAE Gruvel, 1905

Three to six pairs of uniramous unsegmented thoracic limbs; abdomen with four distinct somites (except *Gorgonolaureus*); carapace a sac (bivalved in *Baccalaureus maldivensis*). [On Octocorallia and Hexacorallia.] *Rec.*

Laura LACAZE-DUTHIERS, 1866 (p. 5) [**L. gerardiae;* OD]. Five pairs of thoracic limbs (5th one reduced) [On Antipatharia.] *Rec.*, Medit.

Baccalaureus BROCH, 1929 (p. 242) [**B. japonicus;* OD]. Thorax of 4 or 5 somites which bear 3 to 5 pairs of uniramous limbs, with lateral chitinous ridge. [On Zoantharia.] *Rec.*, IndoPac.

Gorgonolaureus UTINOMI, 1962 (p. 458) [**G. bikiniensis;* OD]. Thorax apparently unsegmented, bearing 6 pairs of uniramous limbs; abdomen unsegmented yet bearing furca. [Only member of order known from Octocorallia (on gorgonian).] *Rec.*, C.Pac.

Family PETRARCIDAE Gruvel, 1905

Unsegmented thorax bearing six pairs of unsegmented uniramous appendages; abdomen three-segmented; furca minute. *Rec.*

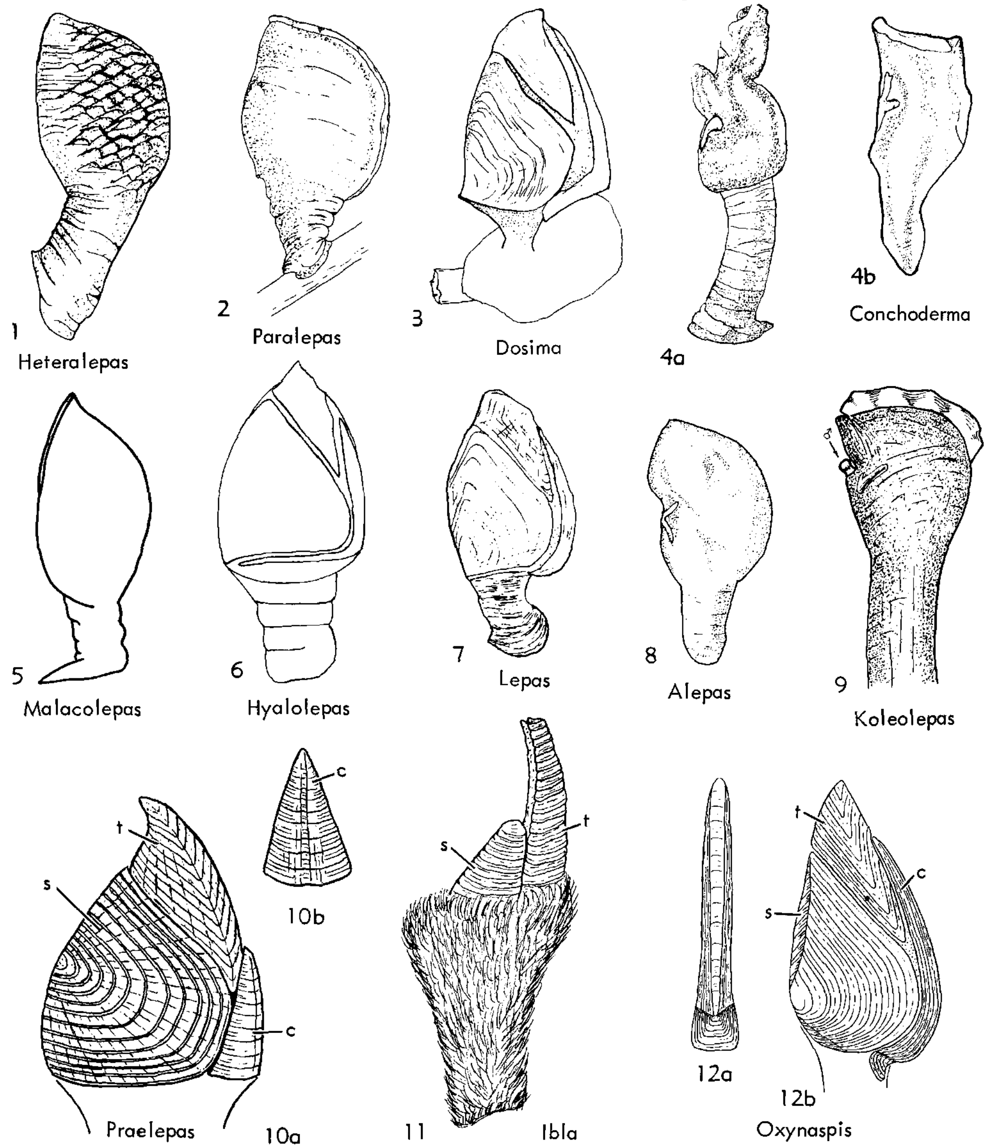

FIG. 114. Praelepadidae *(10)*, Heteralepadidae *(1-2)*, Iblidae *(11)*, Koleolepadidae *(9)*, Lepadidae *(3-4, 6-8)*, Malacolepadidae *(5)*, Oxynaspididae *(12)*, (p. *R275-R279*).

Petrarca Fowler, 1889 (p. 107) [**P. bathyactidis;* OD]. Characteristics of family. [On madreporarian, 4,200 m.] *Rec.,* Japan.

Family DENDROGASTRIDAE Gruvel, 1905

[*nom. correct.* Newman & Zullo, herein (*pro* Dendrogasteridae Gruvel, 1905)]

Thoracic somites more or less evident, limbs rudimentary stubs or absent; furca partially fused rudimentary stubs, or absent. [On asteroids and echinoids.] *Rec.*

Dendrogaster Knipowitsch, 1891 (p. 1) [**D. astericola;* OD]. Thorax of indistinct somites, without limbs; abdomen of ?4 somites, without furca. [On asteroids.] *Rec.,* White Sea-?NW.Atl.

Myriocladus Okada, 1925 (p. 370) [**Dendrogaster arborescens* LeRoi, 1905 (p. 400) (*non M. arborescens* Okada, 1925, p. 365, =*M. okadai* Yosii, 1931, p. 337); SD]. Like *Dendrogaster,* but abdomen coalesced with thorax. [On asteroids.] *Rec.,* IndoPac.-Calif.

Ulophysema Brattström, 1936 [**U. öresundense;* OD]. Thorax of ?6 more or less distinct somites bearing 4 or 5 limb stubs; ?3-segmented abdomen bearing rudimentary furca. [On irregular echinoids.] *Rec.,* NE.Atl.

Family UNCERTAIN

Endosacculus Voight, 1959 [**E. moltkiae;* M]. *U.Cret.(Maastricht.),* W.Ger.

Genus cf. Ulophysema Madsen & Wolff, 1965. *U. Cret.(Turon.-Maastricht.),* W.Ger.

Order THORACICA Darwin, 1854

Permanently attached cirripeds as adults; mantle usually strengthened by calcareous plates; with six pairs of biramous thoracic appendages or cirri (?except *Rhizolepas*), first usually associated closely with mouth parts, second through sixth evenly distributed along thorax; nauplii usually, cyprid larva always present, latter undergoing complex metamorphosis into adult form. *U.Sil.-Rec.*

Suborder LEPADOMORPHA Pilsbry, 1916

Usually differentiated into capitulum containing body with mouth parts and thoracic appendages and peduncle containing testes in males or ovaries in females or hermaphrodites; capitulum usually protected by calcareous plates of specific form; peduncle protected in some by calcareous plates, usually muscular, allowing changes in orientation. *U.Sil.-Rec.*

Family CYPRILEPADIDAE Newman & Zullo, new family

Capitulum distinct from peduncle, possibly weakly calcified, although lack of growth lines in cuticle indicates complete molting as in Acrothoracica; thickening along carinal and basal margins separates capitulum into single lateral plate on each side; appendages unknown. *U.Sil.*

Cyprilepas Wills, 1962, p. 567 [**C. holmi;* OD]. Characters of family. [Occurring on appendages of *Eurypterus fischeri* Eichwald.] *U.Sil.,* Estonia.——Fig. 111,*1*. **C. holmi; 1a,b,* large and small individuals from left side, ×17 (Wills).

Family PRAELEPADIDAE Chernyshev, 1930

[=Cirravidae Chernyshev, 1935]

Plates probably five, chitinous; scutal umbones subcentral; tergal umbones apical; carina short, semiconical, umbo apical. *M. Carb.*

Praelepas Chernyshev, 1930, p. 28 [**P. jaworskii;* SD Withers, 1953, p. 11] [=*Cirravus* Chernyshev, 1935, p. 36]. Characters of family. *M.Carb.;* USSR.——Fig. 114,*10*. **P. jaworskii; 10a,* reconstr., *10b,* carina, ×8 *(118).*

Family SCALPELLIDAE Pilsbry, 1916

Capitulum protected by more than five plates; peduncle armed with plates. *U.Trias. (Rhaet.)-Rec.*

Scalpellum Leach, 1817, p. 68 [**Lepas scalpellum* Linné, 1767, p. 1109 (=*Scalpellum vulgare* Leach, 1824, p. 170); SD Leach, 1824]. Carina bent, forming angle at position of umbo; scutal umbo usually subapical; inframedian latus usually large, umbo varying in position from middle to basal. *L.Eoc.-Rec.,* N.Atl.-Medit.——Fig. 115,*3*. *S. fischeri* Bertrand, M.Eoc.(Lutet.), France.; reconstr., ×3 *(120).*

Aporolepas Withers, 1953, p. 116 [**Scalpellum recurvatum* Bertrand, 1891, p. 694; OD]. Capitular plates 21 or more, umbones all apical, with at least 8 pairs of comparatively large modified lower latera; rostrum and subcarina present; upper latus long and narrow, extending well up between scutum and tergum. *M.Eoc.(Lutet.)-L.Oligo. (Lattorf.);* Eu.(France-Eng.)-USA.

Archaeolepas Zittel, 1884, p. 581 [**Pollicipes redtenbacheri* Oppel, 1862, p. 116; SD Withers, 1928, p. 83]. Capitular plates 6; scutum triangular, with tergal slip; tergum with base widely truncated; carina comparatively small; rostrum much smaller than carina. *U.Jur.-L.Cret.*, Eu. (Eng.-France-Ger.)-S.Am.——Fig. 115,*6*. **A. redtenbacheri* (Oppel), U.Jur.(Kimmridg.), Ger.; reconstr., ×2 *(116)*.

Arcoscalpellum Hoek, 1907, p. 59, 85 [**Scalpellum*

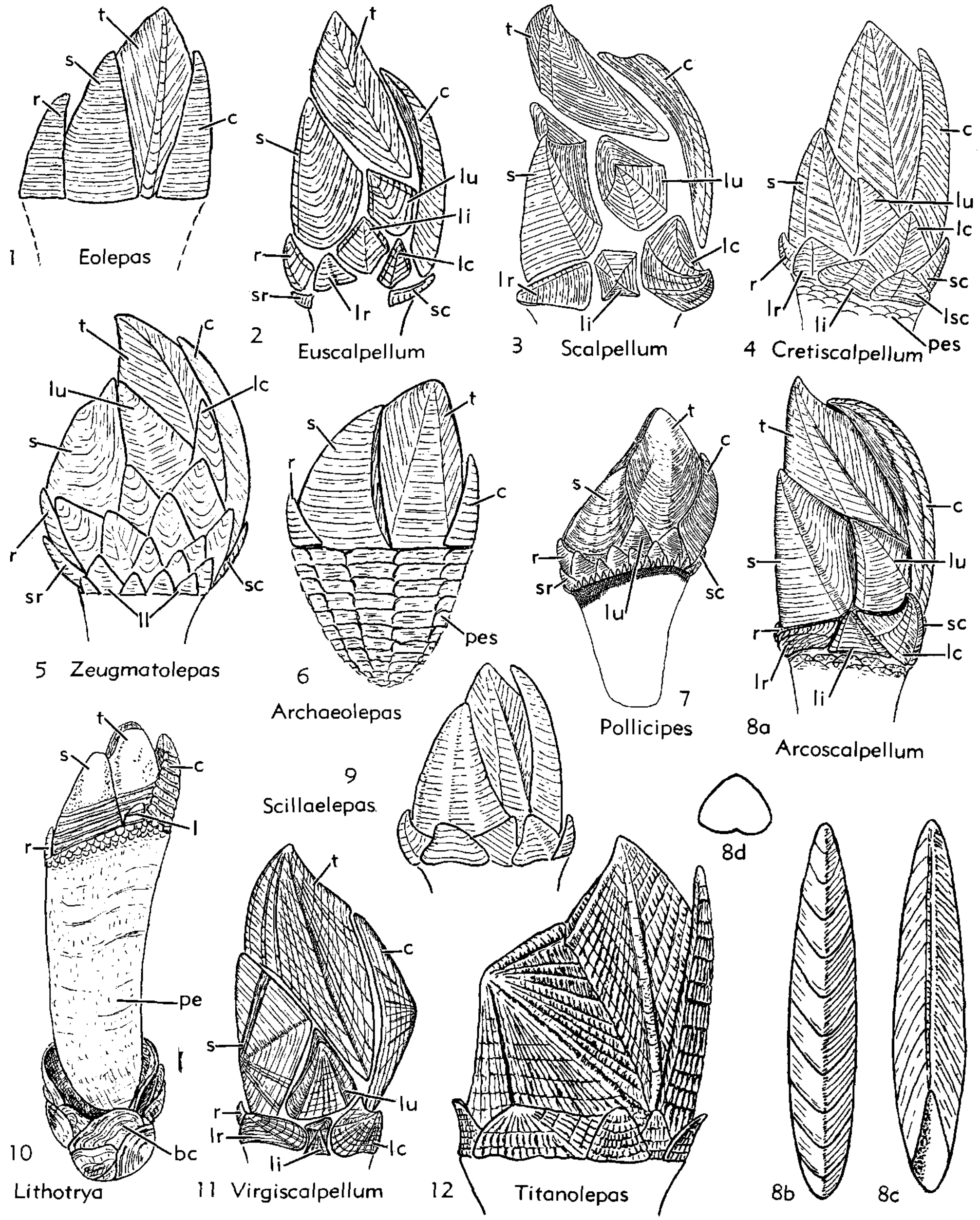

Fig. 115. Scalpellidae (p. *R*275-*R*278).

[Explanation: *bc,* basal cup (calcareous); *c,* carina; *l,* latus; *lc,* latus (carinal); *li,* latus (inframedian); *ll,* latus (lower); *lm,* latus (median); *lr,* latus (rostral); *lsc,* latus (subcarinal); *lu,* latus (upper); *pe,* peduncle; *pes,* peduncle scale; *r,* rostrum; *s,* scutum; *sc,* subcarina; *sr,* subrostrum; *t,* tergum.]

michelottianum Seguenza, 1876, p. 381, 464 (=*S. velutinum* Hoek, 1883, p. 96); OD] [=*Holoscalpellum* Pilsbry, 1907, p. 25]. Capitular plates 15 in fossil and ?13-14 in Recent forms; rostral latus low and wide, larger than inframedian latus; carina with umbo apical. *U.Cret. (Senon.)-Rec.,* cosmop.——Fig. 115,*8a. A. fossula* (Darwin), U.Senon.; reconstr., ×2 *(116).*——Fig. 115,*8b-d. A. maximum solidulum* (Steenstrup), U.Cret.(Senon.), *B. mucronata* Zone, E. Ger. (I. of Rügen); *8b-d,* carina (reconstr.), outer side, inner side, cross sec., ×2 *(116).*

Calantica Gray, 1825, p. 100 [**Pollicipes villosus* Leach, 1824, pl. lvii; OD]. Capitulum with 2 whorls of plates; upper whorl comprising paired scuta, terga, and carina; tergum occupying entire space between scutum and carina; lower whorl comprising rosrtum, subcarina, subrostrum in some species, and 3 pairs of latera (2 pairs in subgenus *Paracalantica;* umbones all apical (scutal umbo subcentral in subgenus *Paracalantica,* central in subgenus *Titanolepas*). *U.Jur.-Rec.,* Eu.-S.Am.-N. Z.-Australia-N.Am.-?E.Indies.

C. (Calantica). Plates of lower whorl low and wide, small, barely concealing bases of upper whorl, scales of peduncle minute. *?U.Jur., Mio.-Rec.,* Eu.-N.Z.——Fig. 85,*1. *C. (C.) villosa* (Leach), Rec., N.Z.; *1a,b,* ×1 (Withers).

C. (Paracalantica) Utinomi, 1949, p. 93 [**C. (P.) ikedai,* p. 93; OD]. Only 2 pairs of latera, scutum with subcentral umbo. *Rec.,* Japan.

C. (Scillaelepas) Seguenza, 1876, p. 390 [**Pollicipes carinatus* Phillipi, 1835, p. 512; OD]. Plates of lower whorl large, high, concealing bases of upper whorl; scales of peduncle large. *?U.Jur., Paleoc.-Rec.,* N.Atl.-Eu.-Australia.——Fig. 115,9. *C. (S.) dorsata* (Steenstrup), Paleoc., Denm.; reconstr., ×2 *(120).*

C. (Titanolepas) Withers, 1913, p. 943 [**Scalpellum tuberculatum* Darwin, 1851, p. 43; OD]. Like *C. (Scillaelepas),* but with scutal umbo subcentral. *U.Cret.(Cenoman.-U.Senon.),* Eu.-N. Am.——Fig. 115,*12. *C. (T.) tuberculata* (Darwin), Cenoman, Eng.; reconstr., ×10 (Withers, 1913).

Cretiscalpellum Withers, 1922, p. 374 [**Pollicipes unguis* J. de C. Sowerby, 1836, p. 335; OD]. Capitular plates 17, including 4 pairs of large, overlapping and little-modified lower latera; subcarina much larger than rostrum; all umbones apical. *L.Cret.-U.Cret.(Apt.-Maastricht.),* Eu.——Fig. 115,*4. *C. unguis* (J. de C. Sowerby), Alb., Eng.; reconstr., ×1.5 *(118).*

Eolepas Withers, 1928, p. 65 [**Pollicipes rhaeticus* Moore, 1861, p. 512, 497; OD]. Capitular plates 6, scutum without tergal slip and apicobasal ridge; tergum not truncated at base; rostrum large, almost equaling carina in size. *U.Trias.(Rhaet.)-U. Jur.(Kimmeridg.),* Eu.(Eng.-France-Ger.).——Fig. 115,*1. E. quenstedti* (Von Ammon), U.Jur. (Kimmeridg.), Ger.; reconstr., ×1.5 *(116).*

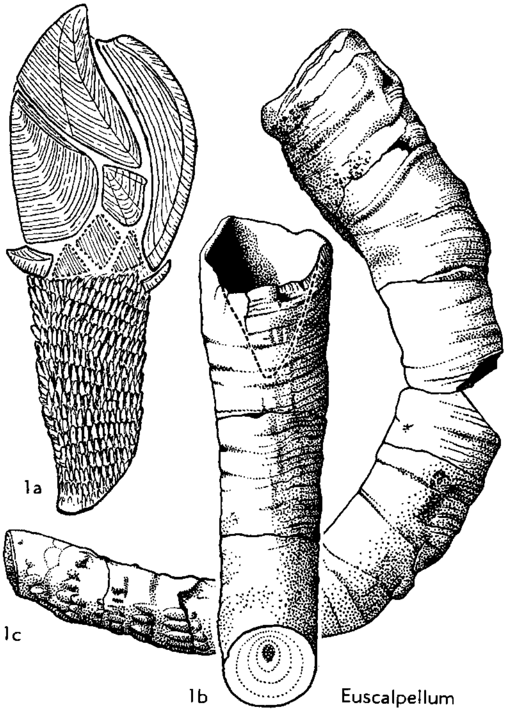

Fig. 115A. Scalpellidae, shells showing secretion of calcium carbonate; *1a, Euscalpellum eocenense* (Meyer); *1b,c, E. zelandicum* Withers (p. *R*277).

Euscalpellum Hoek, 1907, p. 59, 65 [**Scalpellum rostratum* Darwin, 1851, p. 259; SD Pilsbry, 1908, p. 107]. Capitular plates 15; rostrum large and prominent; subcarina well developed; inframedian latus diamond-shaped. *U.Cret.-Rec.,* Eu.-USA-S. Am.-N. Z.-Antarctica-Malay Arch.——Fig. 115,2. *E. minutum* (T. Brown), L.Eoc.(Ypres.; London Clay), Eng.; reconstr., ×3.5 *(120).*——Fig. 115A,*1a. E. eocenense* (Meyer), M.Eoc. (Claiborne), USA; side view of shell, reconstr., ×1.5 *(120).*——Fig. 115A,*1b,c. E. zelandicum* Withers, U.Cret.(Senon.), N.Z.; *1b,* whole peduncle, ×1.4; *1c,* upper half of peduncle showing cavity above and cross section below, ×1.4 (Withers, 1951).

Lithotrya G. B. Sowerby, 1822, no. 8 [**Lepas dorsalis* Ellis & Solander, 1786, p. 197; OD]. Capitulum of 8 plates, umbones apical; scuta, terga and carina large; rostrum and pair of latera small; peduncle with small scales, those of upper row crenated; base terminating in calcareous cup; inhabits cavities bored in calcareous substrata. *Rec.,* E.Atl.-IndoPac.——Fig. 115,*10. *L. dorsalis* (Ellis & Solander), Rec., W.Indies; ×2 *(37).*

Mesoscalpellum Hoek, 1907, p. 39, 73 [**Scalpellum javanicum* Hoek, 1907, p. 78; SD Pilsbry, 1908, p. 110] [Includes *Neoscalpellum* Pilsbry, 1907, p. 69, 1908, p. 110]. Juveniles typically arcoscalpelloid, adults with capitular plates variously reduced; tergum V-shaped, carinal umbo apical. [Deep sea.] *U.Cret.(M.Senon.)-Rec.,* cosmop.——Fig. 94,*11.* *M. dicheloplax* (Pilsbry), Rec., W. Atl., ×1 (Pilsbry).

Pisiscalpellum Utinomi, 1958, p. 113 [**P. withersi;* OD]. Similar to *Calantica (Scillaelepas)* but lacking subcarina and males attached in different position. *Rec.,* Japan.

Pollicipes Leach, 1817, p. 68 [**Lepas pollicipes* Gmelin, 1790, p. 3213; OD]. Capitular plates 18 or more, all umbones apical; lower latera numerous, arranged in one or more whorls. *?U.Jur., L. Eoc. - Rec.,* Eu.-Greenl.-Medit.-Indo Pac.-E. Pac. ——Fig. 115,*7.* **P. pollicipes* (Gmelin), Rec., N. Atl.-Medit.; ×1 *(120).*

Protomitella Broch, 1922, p. 246 [**P. paradoxa,* p. 247; OD]. Similar to *Pollicipes,* capitular plates nearly identical to some variants of *P. spinosus,* except lower latera digitiform rather than pointed and complemental males present. *Rec.,* N.Z.

Scalpellopsis Broch, 1922, p. 243 [**S. striatociliata,* p. 243; OD]. Like *Arcoscalpellum* but with inframedian latera highly reduced and rostral latera wanting. *Rec.,* Philip.Is.

Smilium Leach, 1825, p. 209 [**S. peronii* Gray, 1825, p. 100; SD Pilsbry, 1907, p. 13]. Similar to *Calantica* but with pair of upper latera interposed between carina and scuta. *?U.Cret. (Cenoman.-Turon.), Rec.,* cosmop.

Virgiscalpellum Withers, 1935, p. 283 [**Scalpellum beisseli* Bosquet & Miller, 1857, p. 7; OD]. Capitulum as in *Arcoscalpellum,* but with carinal umbo subapical to subcentral and scutal umbo subcentral or lower; rostrum long and narrow; 14 plates known. *L. Cret.-U. Cret. (Apt.-Maastricht.),* Eu.-N.Am.-S.Am.——Fig. 115,*11.* *V. darwinianum* (Bosquet), Maastricht., Neth.; reconstr., ×2 *(118).*

Zeugmatolepas Withers, 1913, p. 938 [**Z. mockleri,* p. 939; OD] [=*Cretaspis* Joleaud, 1916, p. 43]. Capitulum like that of *Scalpellum,* but with at least 34 plates, including 3 or more whorls of lower latera; scutal umbo apical in Jurassic forms, subcentral in Cretaceous forms. *U.Jur.-Paleoc.,* Eu.-S. Am.-W. Australia.——Fig. 115,*5.* **Z. mockleri,* U.Cret.(Cenoman.), Eng.; reconstr., ×10 *(118).*

Family HETERALEPADIDAE Nilsson-Cantell, 1921

Capitulum without calcareous plates; position of scuta (attachment of scutal adductor muscle) marked by small chitinous thickening on each side and below aperture; multiarticulate caudal appendages present; one or more filamentary appendages at base of first cirrus; no ovigerous frena. *Rec.*

Heteralepas Pilsbry, 1907, p. 100 [**Alepas rex* Pilsbry, 1907, p. 186, 1911, p. 171; OD]. Cirri ctenopod or lasiopod; outer rami of 2nd through 6th pairs normal; inner rami of 5th and 6th moderately to very much reduced. *Rec.,* cosmop. ——Fig. 114,*1.* **H. rex* (Pilsbry), Hawaii; ×1.5 *(80,* mod.).

Paralepas Pilsbry, 1907, p. 100 [**Alepas percarinata* Pilsbry, 1907, p. 185; 1911, p. 171; OD]. Cirri acanthopod; outer rami of 2nd through 6th stout; inner rami somewhat more slender but not reduced. *Rec.,* cosmop.——Fig. 114,*2.* **P. percarinata* (Pilsbry), Hawaii; ×2 *(80,* mod.).

Family IBLIDAE Leach, 1825

Capitulum of female or hermaphrodite supporting two pairs of weakly calcified plates; scuta and terga, with apical umbones. Peduncle not separated from capitulum, clothed with blunt chitinous spines. *Rec.*

Ibla Leach, 1825, p. 209 [**I. cumingi* Darwin, 1851, p. 183; SD]. Diagnosis as for family. *Rec.,* W.Afr.-IndoPac.——Fig. 114,*11.* **I. cumingi* Darwin, IndoPac.; ×4 *(37).* [Also see Fig. 86,*2.*]

Family KOLEOLEPADIDAE Hiro, 1937

Capitulum of female or hermaphrodite without calcareous plates; scuta chitinous, small, left usually better developed than right; mouth parts well developed, mandible atypical; cirri biramous, short, posterior pairs acanthopod, filamentary appendage at base of first cirrus; caudal appendage uniarticulate. Male much reduced, attached at base of aperture. [Living attached between pedal disc of anemone on gastropod shell inhabited by hermit crab.] *Rec.*

Koleolepas Stebbing, 1900, p. 677 [**K. willeyi;* OD]. Characters of family. *Rec.,* IndoPac.(Loyalty Is.-Japan-Hawaii).——Fig. 114,*9.* *K. tinkeri* Edmondson, Hawaii; ×2 (Newman, n).

Family LEPADIDAE Darwin, 1851

Capitulum with five approximate plates *(Lepas),* five or two reduced plates *(Conchoderma),* two reduced plates *(Alepas),* or naked *(Anelasma);* scutal and carinal umbones fundamentally basal; caudal appendages continuous with thorax, simple points without long setae; first maxillae with steplike cutting edge; ovigerous frena present; peduncle naked. *?U.Trias., M.Eoc.-Rec.*

Lepas Linné, 1758, p. 667 [**L. anatifera* Linné, 1785, p. 668; SD Pilsbry, 1907]. Capitular plates

5, approximate. [Pelagic.] *?U.Trias., M.Eoc.-Rec.,* Eng.-France-Italy-Australia-all seas.

L. (Lepas). Plates well calcified; basal portion of carina forming small fork or knob. [On floating objects.] *M.Eoc.-Rec.,* Eng.-France-Italy-Australia-N.Z.——Fig. 114,*7*. **L. (L.) anatifera* Linné, L.Mio. (Southland Series), N.Z.; ×0.5 *(80)*.

L. (Dosima) Gray, 1825, p. 100 [**Lepas fascicularis* Ellis & Solander, 1786, p. 197; SD Annandale, 1909, p. 72]. Plates weakly calcified; basal portion of carina forming large disc. [Pelagic; larvae attached to floating objects, subsequently forming floats of their own.] *Rec.,* all seas.——Fig. 114,*3*. **L. (D.) fascicularis* (Ellis & Solander), W.Atl.; ×1 (after *80*).

L. (Hyalolepas) Annandale, 1909, p. 72 [**Dichelaspis tenuivalvata* Annandale, 1906, p. 193; OD]. Plates weakly calcified; arms of basal fork of carina long, slender, running about parallel to each other along basal margins of scuta. [On sea snakes, feathers.] *Rec.,* Ind.O.——Fig. 114, *6*. *L. (H.) begalensis* Daniel, Ind.O.; ×14 (Daniel, 1952, mod.).

Conchoderma Olfers, 1814, p. 177 [**Lepas virgata* Spengler, 1790, pl. 6, fig. 9; OD]. Capitulum generally striped, typically with 5 vestigial plates or two pair of scuta in some species. [Attached to floating objects and organisms.] *Rec.,* all seas.——Fig. 114,*4a*. *C. auritum* (Linné), Cape Hatteras; ×0.5 (after *80*).——Fig. 114,*4b*. **C. virgatum* (Spengler), Woods Hole; ×1 (after *80*).

Alepas Rang, 1829, p. 364 [**Anatifa univalvis* Quoy & Gaimard, 1827, p. 234; (=*Alepas parasita* Rang, 1829, p. 364); SD Pilsbry, 1907]. Capitulum thin, translucent, typically with small, lobed, weakly calcified scuta. [On large medusae.] *Rec.,* cosmop.——Fig. 114,*8*. *A. pacifica* Pilsbry, Calif.; ×0.7 (after *80*).

Anelasma Darwin, 1851, p. 169 [**Alepas squalicola* Lovén, 1844, p. 192; OD]. Capitulum without valves; trophi and cirri apparently functionless; peduncle with root system invading host tissues. [Parasitic on dogfish, *Etmopterus,* and *Squalus.*] *Rec.,* N.Sea.——Fig. 112,*2*. **A. squalicola* (Lovén); ×2 (est.) (after Darwin).

Family MALACOLEPADIDAE Hiro, 1937

Capitulum thin, membranous, without plates; mouth parts and ctenopod cirri well developed, mandible with six or seven teeth; filamentary and caudal appendages absent. [Inhabiting calcareous tubes between mantle and shell of living bivalve mollusks.] *Rec.*

Malacolepas Hiro, 1933, p. 233 [**M. conchicola;* OD]. Characters of family. *Rec.,* Japan.——Fig. 114,*5*. **M. conchicola;* ×4 (Hiro, 1933, mod.).

Family OXYNASPIDIDAE Pilsbry, 1907

Capitulum with five plates; scutal umbo subcentral; tergal umbo usually apical; carina extending upward between terga, umbo subapical to subbasal, basal portion sometimes formed into broad plate or fork. Caudal appendages minute, uniarticulate; ovigerous frena absent. [Extant forms (except *O. connectens* Broch) on antipatharians.] *M.Eoc.-Rec.*

Oxynaspis Darwin, 1851, p. 133 [**O. celata;* OD]. Characters of family. *Eoc.-Rec.,* Atl.O.-Ind.O.-W.Pac.-E.Pac.——Fig. 114,*12*. *O. eocenica* (Withers), M.Eoc., Eng.; *12a,b,* reconstr. ×8 *(120)*.

Family POECILASMATIDAE Nilsson-Cantell, 1921

[=Trilasmatidae Nilsson-Cantell, 1934]

Capitulum typically with five calcified, approximate plates or plates five, three, or two, in varying degrees of reduction; scutum may be divided into two calcified portions, but parts always connected by chitinous ligament, having developed from common primordial plate; scutal and carinal umbones fundamentally basal; caudal appendages well developed, uniarticulate, provided with long setae; cutting edge of first maxilla not steplike; peduncle naked or with chitinous thickenings. *U. Eoc. (Barton.)-Rec.*

Trilasmis Hinds, 1844, p. 71 [**T. eburneum;* SD Pilsbry, 1928, p. 308]. Capitulum typically with 5, in one case 3, well-calcified plates; scutum entire or divided into 2 parts, umbo at rostral or basal angle. *U.Eoc.-Rec.,* Atl.-IndoPac.-Medit.

T. (Trilasmis). Capitulum with 3 well-calcified plates; terga wanting; scuta with internally visible, fused suture; carina with base expanded into large disc. *Rec.,* IndoPac.——Fig. 116,*9*. **T. (T.) eburneum* Hinds, New Guinea; ×8 *(37)*.

T. (Poecilasma) Darwin, 1851, p. 99 [**Poecilasma kaempferi* Darwin, 1851, p. 102; SD Pilsbry, 1907]. Capitulum with 5 approximate plates; scutum not split into 2 parts; carina not expanded laterally at base. *U.Eoc.(Barton.)-Rec.,* Atl.-IndoPac.——Fig. 116,*5*. **T. (P.) kaempferi* (Darwin), Rec., Japan; ×5 *(37)*.

T. (Temnaspis) Fischer, 1884, p. 357 [**Poecilasma fissa* Darwin, 1851, p. 109; OD]. Capitulum with 5 approximate plates; scutum split into 2 parts. *L.Mio.-Rec.,* IndoPac.-Medit. (Malta I.).——Fig. 116,*8*. **T. (T.) fissus* (Darwin), Rec., Philip. Is.; ×5 (after Darwin).

Megalasma Hoek, 1883, p. 50 [**M. striatum;* OD]. Capitulum with 5, approximate, heavily calcified plates; carina progressively larger towards base, with internal transverse shelf; scutal umbo subcentral; peduncle very short. *Rec.,* Atl.-IndoPac.-E. Pac.

M. (Megalasma). Basal margin of scutum nearly continuous with occludent margin. *Rec.,* Indo-Pac.-E.Pac.——FIG. 116,*12*. *M. (M.) bellum* (PILSBRY), ×5 *(80)*.

M. (Glyptelasma) PILSBRY, 1907, p. 87 [**Megalasma subcarinatum* PILSBRY, 1907, p. 91; OD].

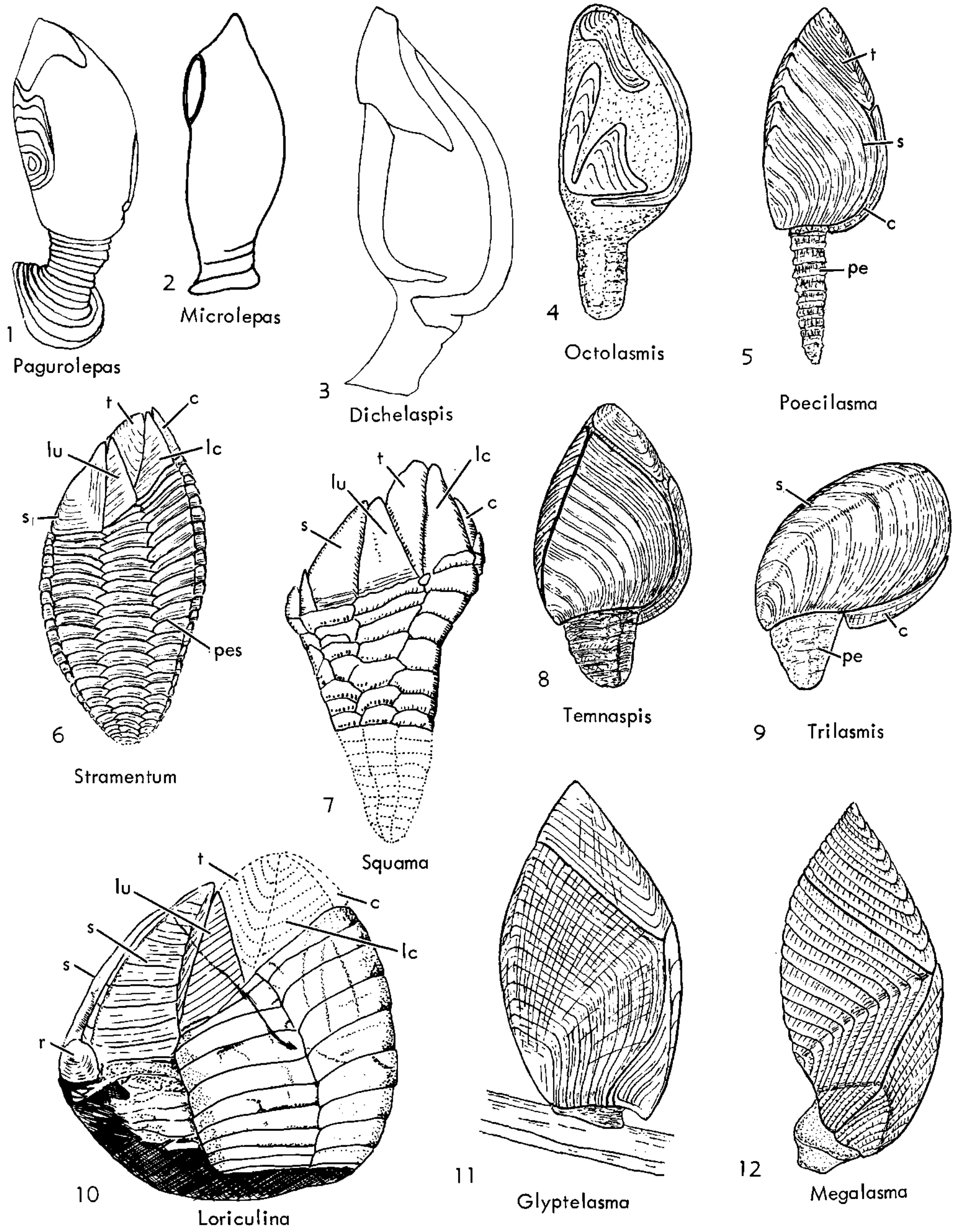

FIG. 116. Poecilasmatidae *(3-5, 9, 11-12)*, Stramentidae *(6-7, 10)*, Family Uncertain *(1-2)* (p. *R*279-*R*281). [Explanation: *c,* carina; *lc,* latus (carinal); *lu,* latus (upper); *pe,* peduncle; *pes,* peduncle scale; *r,* rostrum; *s,* scutum; *t,* tergum.]

Basal margin of scutum nearly at right angles with occludent margin. *Rec.,* Atl.-IndoPac.——FIG. 116,*11.* **M. (G.) subcarinatum* PILSBRY, USA(N.J.); ×5 *(80).*

Octolasmis GRAY, 1825, p. 100 [**O. warwickii;* OD]. Capitulum with 5, 3 or 2 incompletely calcified plates; carina extending up between terga when present. *Rec.,* cosmop., all warm seas.

O. (Octolasmis). Plates very incompletely calcified; scutum usually with 2 principal arms, connected by chitinous ligament; carina, when present, usually with slender basal fork; tergum, when present, usually with 2 or more diverging points. *Rec.,* cosmop., all warm seas and in deep water.——FIG. 116,*4.* **O. (O.) warwickii* GRAY, Borneo; ×10 *(37).*

O. (Dichelaspis) DARWIN, 1851, p. 115 [**D. orthogonia;* SD PILSBRY, 1907, p. 94]. Plates 5, incompletely calcified; scutum usually with 2 principal arms calcified together at their junction; carina terminating in basal disc; tergum usually triangular, commonly with projecting points. *Rec.,* Atl.-IndoPac.——FIG. 116,*3.* *O. (D.) hawaiiense* (PILSBRY), Hawaii; ×10 (after *80*).

Family STRAMENTIDAE Withers, 1920

[=Loriculidae PILSBRY, 1916]

Capitulum short, composed of single whorl of nine to 12 plates; upper latus interposed for its whole length between scutum and tergum; carinal latus placed between carina and tergum. Peduncle composed on each side of five vertical rows of closely imbricating plates, two outer rows in free apposition. *Cret.(Alb.-Senon.).*

Stramentum LOGAN, 1897, p. 188 [**Pollicipes haworthi* WILLISTON, 1896, p. 243; SD WITHERS, 1920, p. 68] [=*Loricula* G. B. SOWERBY, JR., 1851, p. 81]. Capitulum of 9 plates; no rostrum; carina split longitudinally into 2 halves; scutal umbo subcentral. *Cret.(?Alb.-U.Senon.),* Eu.-Syria-N.Am.——FIG. 116,*6.* *S. pulchellum* (SOWERBY), Turon., Eng.(Kent); ×6 *(116).*

Loriculina DAMES, 1885, p. 155 [**Loricula noetlingi* DAMES, 1885, p. 152; SD WITHERS, 1935, p. 303]. Capitular plates 10; paired scuta, upper latera, carinal latera, carina and entire rostrum; scutum elongate, umbo apical. *U.Cret.(Cenoman.-U.Senon.),* Eu.-Syria-USA.——FIG. 116,*10.* **L. noetlingi* (DAMES), U.Senon., Syria; ×6 *(118).*

Squama LOGAN, 1897, p. 187 [**S. spissa;* SD WITHERS, 1935, p. 309]. Capitular plates probably 12, subcarina, rostrum and subrostrum in addition to plates in *Stramentum;* carina probably entire. *U.Cret.(Senon.),* N.Am.——FIG. 116,*7.* **S. spissa,* U.Niobrara, USA(Kans.); ×1.5 *(118).*

Family UNCERTAIN

Microlepas HOEK, 1907, p. 43 [**M. diademae;* OD]. Capitulum continuous with short peduncle, without calcareous plates; mouth parts and cirri peculiar; 1st cirrus single article, 2nd through 6th biramous, rami uniarticulate, unequal in length; no caudal appendages. [On sea urchin spines.] *Rec.,* Ind.O.(Savu Sea).——FIG. 116,*2.* **M. diadema,* Savu Sea; ×10.5 (*54,* mod.).

Pagurolepas STUBBINGS, 1940, p. 383 [**P. conchicola;* OD]. Capitulum with 5 calcified, reduced plates; carinal umbo basal; scutal umbo subcentral; mandible normal, 1st maxilla atypical; cirri biramous, rami each of 3 articles; caudal appendage well developed, uniarticulate. [In gastropod shells inhabited by hermit crab.] *Rec.,* Ind.O.(Zanzibar)-W.Atl.(Fla.).——FIG. 116,*1.* **P. conchicola,* Zanzibar; ×8 (Stubbings, 1936, mod.).

Rhizolepas DAY, 1939, p. 64 [**R. annelidicola;* OD]. Capitulum without plates; not completely covering thorax; with chitinous ribs supporting occludent margins; peduncle long, forming root system in host; cirri uniramous, weakly developed, rami multiarticulate; ?caudal appendages multiarticulate. [Parasitic on polychaete annelid.] *Rec.,* S.Afr.——FIG. 112,*3.* **R. annelidicola,* S. Afr.; ×8.5 (after Day).

Suborder VERRUCOMORPHA Pilsbry, 1916

Cirripeds lacking peduncle; with asymmetrical shell composed of rostrum, carina, scutum, tergum, and in some forms carinal and rostral latera; remaining scutum and tergum reduced in size, forming movable lidlike top to shell; basis membranous or calcareous. *U. Cret.(?Cenoman.-U.Senon.)-Rec.*

Family VERRUCIDAE Darwin, 1854

Characters of suborder. *U.Cret.(?Cenoman.-U.Senon.)-Rec.*

Verruca SCHUMACHER, 1817, p. 35 [**Lepas stroemia* MÜLLER, 1776, p. 251; OD]. Wall composed of 4 compartmental plates. [PILSBRY (1916) divided *Verruca* into four sections. BROCH (1922) elevated a subgroup of one of these, forming a fifth. He and other authors have used the sections as subgenera.] [Littoral-bathyal.] *U.Cret.(Senon.)-Rec.,* temp. and tropic seas (except *Rec.* in N.Pac.).

V. (Verruca) [=*Euverruca* BROCH, 1924, p. 63]. Top of movable plates flat, plane nearly parallel to that of base; radioalar area between parietes of fixed scutum and tergum narrow and linear.

U.Cret.(Senon.)-Rec., cosmop.——FIG. 117,*4.* *V. (V.) prisca* BOSQUET, U.Senon., Eng.; *4a,b,* ×20 *(118).*

V. (Altiverruca) PILSBRY, 1916, p. 40 [**V. hoeki* PILSBRY, 1907, p. 113; OD]. Top nearly vertical; fixed scutum without adducor ridge; no internal recesses of general cavity. *Rec.,* cosmop.

V. (Cameraverruca) PILSBRY, 1916, p. 39 [**V.*

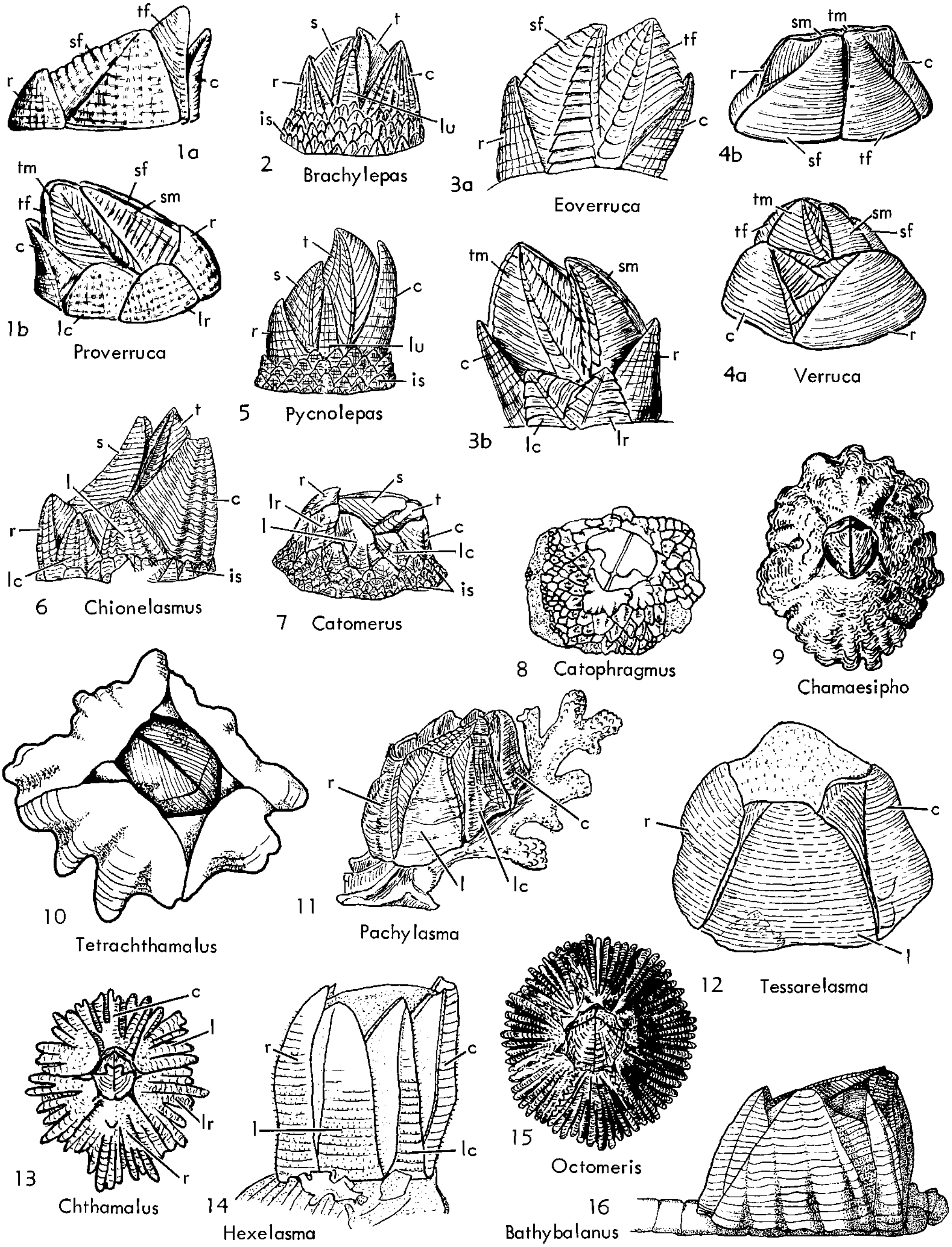

FIG. 117. Verrucidae *(1,3-4);* Brachylepadidae *(2,5);* Chthamalidae *(6-15);* Balanidae *(16)* (p. *R*281-*R*285). [Explanation: *c,* carina; *is,* imbricating scales; *lc,* latus (carinal); *lr,* latus (rostral); *lu,* latus (upper); *r,* rostrum; *s,* scutum; *sf,* scutum (fixed); *sm,* scutum (movable); *t,* tergum; *tf,* tergum (fixed); *tm,* tergum (movable).]

euglypta Pilsbry, 1907, p. 108; OD]. Top steeply sloping; adductor ridge of fixed scutum forming vertical partition-like myophore; partitioned off apical cavities in fixed tergum and rostrum forming recesses of general cavity. *Rec.*, USA(Fla.).

V. (Metaverruca) Pilsbry, 1916, p. 21 [**V. coraliophila* Pilsbry, 1916, p. 21; OD]. Top flattened; basal border of wall plates inflected; adductor ridge of fixed scutum forming tongue-shaped myophore. *Rec.*, cosmop.

V. (Rostratoverruca) Broch, 1922, p. 297 [**V. nexa* Darwin, 1854, p. 522; OD]. As *V. (Verruca)*, but with apex of rostrum removed from upper edge of the plate. *Rec.*, IndoPac.

Eoverruca Withers, 1935, p. 388 [**E. hewitti;* OD]. Two lateral plates on rostrocarinal side; rostrum and carina nearly symmetrical; interlocking ribs present on fixed and movable scuta and terga. *U.Cret.(M.Senon.)*, Eng.——Fig. 117,*3*. **E. hewitti: 3a,b,* reconstr., ×20 *(118)*.

Proverruca Withers, 1914, p. 946 [**P. vinculum;* OD]. Two lateral plates on rostrocarinal side; rostrum and carina asymmetrical; plates without interlocking ribs. *U.Cret.(Turon.-U.Senon.)*, Eu. ——Fig. 117,*1*. **P. vinculum,* L.Senon., Eng.; *1a,b,* reconstr., ×15 *(118)*.

Suborder BRACHYLEPADOMORPHA Withers, 1923

Cirripeds lacking peduncle; with laterally flattened or circular, bilaterally symmetrical shell composed of rostrum and carina; with up to four whorls of smaller imbricating plates at base of wall; operculum formed of paired scuta and terga separated by long, narrow upper latus; basis membranous or calcareous. *U. Jur. (Tithon.) U. Mio. (Helvet.)*.

Family BRACHYLEPADIDAE Woodward, 1901

Character of suborder. *U.Jur.(Tithon.)-U.Mio.(Helvet.)*.

Brachylepas Woodward, 1901, p. 150 [**Emarginula(?) naissanti* Hebert, 1855, p. 374; OD]. Shell laterally flattened or circular; carina cylindrical or semiconical; outer whorls of imbricating plates with inwardly projecting ledge which fits into median basal notch on plates of inner whorl; basis membranous, except in *B. quascoi*. *U.Cret.(Turon.-Maastricht.)*, Eu.——Fig. 117,*2*. **B. naissanti* (Hebert), U.Senon., Eu.; reconstr., ×1.3 (Withers).

Pycnolepas Withers, 1914, p. 170 [**Pollicipes rigidus* Sowerby, 1836, p. 335; OD]. Shell laterally flattened; carina cylindrical; outer whorls of imbricating plates with inwardly projecting ledge bearing median basal socket (?muscle pit); basis probably membranous. *U.Jur.(Tithon.)-U. Mio.(Helvet.)*, Eu.——Fig. 117,*5*. **P. rigida* (Sowerby), L.Cret.(Alb.), Eng.; reconstr., ×3 (Withers).

Suborder BALANOMORPHA Pilsbry, 1916

Cirripeds lacking peduncle; with bilaterally symmetrical shell composed of carina, rostrum, and one to three pairs of lateral compartmental plates variously fused or totally concrescent; opercular valves when present paired, members of each pair separate, articulated or concrescent; with but one or two exceptions in the Balaninae, purely hermaphroditic. *U.Cret.(U.Senon.)-Rec.*

Family CHTHAMALIDAE Darwin, 1854

[*nom. transl.* Pilsbry, 1916 (*ex* Chthamalinae Darwin, 1854)]

Wall of eight, six, or four distinct, solid compartmental plates; some forms with one or more whorls of smaller accessory plates encircling base of wall; rostrum free or fused with rostrolaterals; carinolaterals absent in six- and four-plated groups with free rostra; inner surface of parieties without regular longitudinal ribs; cirrus *III* usually more similar in structure to cirrus *IV* than to cirrus *II*, or intermediate in structure between cirri *II* and *IV;* labral crest straight or concave, not notched, labrum usually swollen externally. *U.Cret. (U.Senon.)-Rec.*

Chthamalus Ranzani, 1817, p. 276 [**Lepas stellata* Poli, 1791, p. 29; OD]. Six compartmental plates in wall; rostrum free; carinolaterals absent; basis membranous or calcareous. [The genus falls into two natural divisions *(C. stellatus, C. hembeli)*, primarily on the form of the mandible and opercular parts (Nilsson-Cantell, 1921, p. 279, 290). These will no doubt eventually receive at least subgeneric status.] *Plio.(Piacenz.)-Rec.*, warm temp.-tropic seas.——Fig. 117,*13*. **C. stellatus* (Poli), Rec., Madeira Is.; ×4 *(39)*.

Catophragmus Sowerby, 1826, no. 28 (June 28) [**C. imbricatus* Sowerby, 1827, plate; OD]. Eight compartmental plates in wall, including rostrum, carina, 2 laterals, 2 rostrolaterals, and 2 carinolaterals; 2 or more basal whorls of accessory plates present; basis membranous or calcareous; scutum without adductor ridge. *U.Cret.(U.Senon.),* Sweden; *Rec.,* Australia-E.Pac.(Panama)-Carib.-Bermuda.

C. (Catophragmus). Plates of basal whorls few, not keeled, imbricating over sutures of inner whorls; basis calcareous, small caudal appendages present. *Rec.,* E.Pac.(Panama)-Carib.-Bermuda.—Fig. 117,*8*. *C. (C.) pilsbryi* Broch, Panama; ×1.3 (after *18*).

C. (Catomerus) Pilsbry, 1916, p. 335 [**Catophragmus polymerus* Darwin, 1854, p. 487; OD]. Plates of basal whorls numerous, carinate, imbricating over sutures of each preceding whorl, basis membranous; caudal appendages absent. *Rec.,* SE.Australia.——Fig. 117,*7*. **C. (C.) polymerus* Darwin; ×1.2 *(118)*.

C. (Pachydiadema) Withers, 1935, p. 389 [**Catophragmus cretaceus* Withers, 1935, p. 390; OD]. Basal plates arranged in more than 2 whorls, not keeled or toothed; articular ridge and furrow of both scutum and tergum weakly developed. *U.Cret.(U.Senon.),* Sweden.

Chamaesipho Darwin, 1854, p. 470 [**Lepas columna* Spengler, 1790, p. 192; SD Pope, 1965, p. 63]. Four compartmental plates in wall, including rostrum, carina, and composite lateral-rostrolaterals; basis membranous. *Rec.,* SE.Australia-N.Z.-?China seas.——Fig. 117,*9*. **C. columna* (Spengler), Australia; ×2.2 *(39)*.

Chionelasmus Pilsbry, 1911, p. 82 [**Catophragmus darwini* Pilsbry, 1907, p. 188; OD]. Six compartmental plates in shell wall, including free rostrum, carina, 2 laterals, and 2 rostrolaterals; single basal whorl of accessory plates present; basis calcareous; caudal appendages present. *Rec.,* Hawaiian Is.-Ind.O.——Fig. 117,6. **C. darwini* (Pilsbry), Ind.O.; ×3 *(118)*.

Hexelasma Hoek, 1913, p. 157, 244 [**H. velutinum;* SD Utinomi, 1965, p. 13]. Six compartmental plates in shell wall as in *Pachylasma,* but compound rostral plate showing no sign of fusion; radii absent; basis membranous or thinly calcareous; cirrus *III* intermediate in structure between cirri *II* and *IV;* caudal appendages absent. *?L.Oligo., L.Mio.-Rec.,* W.Pac.-SW.Pac.-Anarctic-N.Atl.——Fig. 117,*14*. **H. velutinum,* Rec., Malay Arch.; ×3.2 *(54)*.

Octomeris Sowerby, 1825, no. 26 (Nov. 8) [**O. angulosa;* OD]. Eight compartmental plates in shell wall as in *Catophragmus;* without basal whorls of accessory plates; basis membranous; caudal appendages absent. *?Pleist., Rec.,* S.Afr.-IndoPac.-Japan.——Fig. 117,*15*. *O. brunnea* Darwin), Rec., Philip. Is.; ×3 *(39)*.

Pachylasma Darwin, 1854, p. 475 [**Chthamalus giganteus* Philippi, 1836, p. 250; SD Pilsbry, 1916]. Six compartmental plates in shell wall, including tripartite rostral plate formed by partial or complete fusion of rostrum with adjoining rostrolaterals, 2 laterals, 2 carinolaterals, and carina; radii rudimentary or absent; basis calcareous; cirrus *III* similar to cirri *IV-VI;* caudal appendages present. *Mio.(Helvet.)-Rec.,* Medit.-W.Pac.-IndoPac.——Fig. 117,*11*. **P. giganteum* (Philippi), Rec., Medit.; ×2 *(39)*.

Tessarelasma Withers, 1936, p. 591 [**T. pilsbryi;* OD]. Four compartmental plates in shell wall, including compound rostral plate, 2 laterals, and carina; radii absent; basis possibly calcareous; indistinct longitudinal ribs on inner surface of parietes; opercular valves as in balanids. *L.Mio. (?Burdigal.),* India.——Fig. 117,*12*. **T. pilsbryi,* E.Bengal; ×2 *(39)*.

Tetrachthamalus Newman, 1967, p. 425 [**T. oblitteratus;* OD]. Wall composed of 4 compartments (rostrum compound, carinolaterals lacking); basis membranous; opercular parts, trophi and cirri similar to species of the *Chthamalus stellatus* group. *Rec.,* Red Sea (Gulf of Aqaba)-W.Ind.O.——Fig. 117,*10*. **T. oblitteratus;* ×10 (Newman, n).

Family BALANIDAE Leach, 1817

Wall of four or six distinct compartmental plates, or single fused plate; rostrum apparently fused with rostrolaterals, (?) or absent, forming compound rostral plate; carinolaterals usually present. Radii usually developed; parietes either solid or with parietal tubes; inner surface of parietes usually longitudinally ribbed; cirrus *III* similar in structure to cirri *I* and *II;* labrum not swollen externally; labral crest usually notched centrally, penis usually with basidorsal point. *L.Eoc.-Rec.*

Subfamily BALANINAE Leach, 1817

[*nom. transl.* Darwin, 1854 (*ex* Balanidae Leach, 1825)]

Wall of hermaphrodites composed of six, four, or single compartmental plates; parietes solid or with parietal tubes; basis membranous or calcareous; labral crest with deep, V-shaped notch; paired scuta and terga present, articulated, and filling orifice. Males, when present, variously reduced, located on interior of rostral plate. *L.Eoc. (Auvers.)-Rec.*

Balanus da Costa, 1778, p. 248 [**Lepas balanus* Linné, 1758, p. 667 (=*B. porcatus* da Costa, 1778, p. 249); SD Pilsbry, 1916, p. 49]. Wall of 6 usually rigidly articulated compartmental plates. *M.Eoc.(Auvers.)-Rec.,* all seas.

B. (Balanus). Parietes with parietal tubes; radii solid; basis calcareous. *Oligo.-Rec.,* all seas.——Fig. 118,*1*. **B. (B.) balanus* (Linné), Plio., Eng.; *1a,* shell, ×0.75; *1b,* part of basal margin, *1c,* part of basis, enl. *(39)*.——Fig. 118,*2*. *B. (B.) laevis* Bruguière, Pleist., Coquimbo, Chile; lower part of basal cup filled with bubble-like septa, ×2.5 *(40)*.

B. (Armatobalanus) Hoek, 1913, p. 159 [**B. quadrivittatus* Darwin, 1854, p. 284; SD Pilsbry, 1916]. Parietes and radii solid; radii well developed with denticulate sutural edges; basis calcareous; interior of parietes with sharp, longitudinal ribs; tergal spur wide, one third to more than one-half width of basal margin, teeth on anterior margins of some cirri. *Mio.,* USA(Md.); *Rec.,* Japan-Australia-W. Indies-USA(Calif.)-Eng. ——Fig. 118A,*6*. **B. (A.) quadrivittatus* Darwin, Rec., ×3.5 *(39)*.

B. (Austrobalanus) Pilsbry, 1916, p. 218 [**B. imperator* Darwin, 1854, p. 288; OD]. Parietes and radii (when present) solid; radii without denticles on sutural edges; internal basal edge of parietes with irregular points, ridges, or strong, irregular ribs; basis calcareous; scutum with adductor ridge and crest for lateral depressor muscle. *?Oligo.,* Chatham I.; *Rec.,* W.S.Am.-N.Z.-SE.Australia.——Fig. 118A,*7*. *B. (A.) flosculus* Darwin, Rec, S.Am.; ×1.5 *(39)*.

B. (Chirona) Gray, 1835, p. 37 [**Lepas hameri* Ascanius, 1767, p. 8; OD]. Characterized by thin, solid parietes and radii; basis calcareous; sutural edges of radii smooth or weakly crenulate; tergal spur narrow, moderately long. *Mio.-Rec.,* N. Pac.-Bering Sea-N. Atl.-Ind. O.-W. Pac.-Medit.——Fig. 118A,*9*. **B. (C.) hameri* (Ascanius), Rec., Sweden; ×1 *(39)*.

B. (Conopea) Say, 1822, p. 323 [**Lepas galeata* Linné, 1771, p. 544; OD]. Parietes of hermaphrodites(?) with or without parietal tubes; radii solid, well developed; basis calcareous, elongate along carinorostral axis, boat-shaped; shell attached to gorgonians. Males, when present, occurring on inner surface of rostral plate. *Mio.-Rec.,* Ind.O.-W.Pac.-S.Calif.-Gulf Calif.-E.C.Am.-SE. USA-W. Afr.-Medit.-N.S. Am.——Fig. 118A, *12*. *B. (C.) cymbiformis* Darwin, Rec., E.Indies; ×7 *(22)*.

B. (Hesperibalanus) Pilsbry, 1916, p. 192 [**B. hesperius;* OD]. Parieties and radii solid; basis calcareous; radii narrow with denticulate sutural edges; scutum ridged between adductor muscle scar and articular ridge; juncture between tergal spur and basal margin angulate. [*See B.(Solidobalanus).*] *Eoc.-Oligo.,* G.Brit.-France-USA; *Rec.,* N.Pac.——Fig. 118A,*8*. **B. (H.) hesperius* Pilsbry, Rec., Alaska (Bering Sea); ×2.7 *(83)*.

B. (Hexacreusia) Zullo, 1961, p. 72 [**B. durhami;* OD]. Parietes and radii solid; radii broad, with thick, denticulate sutural edges; sheath extending nearly to basal margin; lower edge of sheath free, continuous; basis calcareous, cup-shaped to subcylindrical; opercular valves as in *Creusia;* embedded in corals. *U.Plio.-Rec.,* Gulf Calif.-Tres Marias Is.——Fig. 118A,*5*. **B. (H.) durhami* Zullo, Rec., Gulf Calif.; ×10 (after Ross).

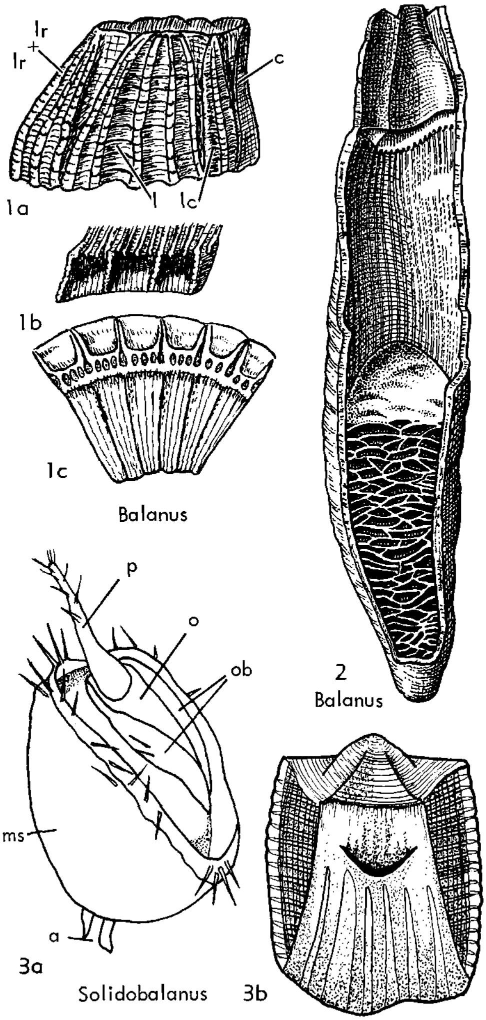

Fig. 118. Balanidae (Balaninae) (p. *R*285-*R*287). [Explanation: *a,* first antennae; *c,* carina; *l,* latus; *lc,* latus (carinal); *lr,* latus (rostral); *ms,* mantle sac; *o,* orifice; *ob,* opercular bars; *p,* penis.]

B. (Megabalanus) Hoek, 1913, p. 158 [**Lepas tintinnabulum* Linné, 1758, p. 668; OD]. Both parietes and radii with tubes; basis calcareous. *Oligo.-Rec.,* temp. and tropic seas.——Fig. 118A, *2*. **B. (M.) tintinnabulum* (Linné), Plio., Eng.; *2a,* shell, ×1.5; *2b,* basal margin of wall, enl. *(40)*.

B. (Membranobalanus) HOEK, 1913, p. 159 [**B. declivus* DARWIN, 1854, p. 275; SD PILSBRY, 1916]. Parietes and radii thin, solid; sutural edges of radii not crenulate; basis membranous; rostrum extending below and nearly twice as long as other compartmental plates; tergal spur short, broad. *Pleist.-Rec.,* E.Indies-S.Japan-W.Indies-S.Calif.-Gulf Calif.——FIG. 118A,*10.* **B. (M.) declivus* DARWIN, Rec., W.Indies; ×4.5 *(39).*

B. (Metabalanus) PILSBRY, 1916, p. 200 [**B. hoekianus* PILSBRY, 1911, p. 77; OD]. Parieties solid; radii absent; adductor ridge of scutum absent; tergal spur well differentiated from tergal

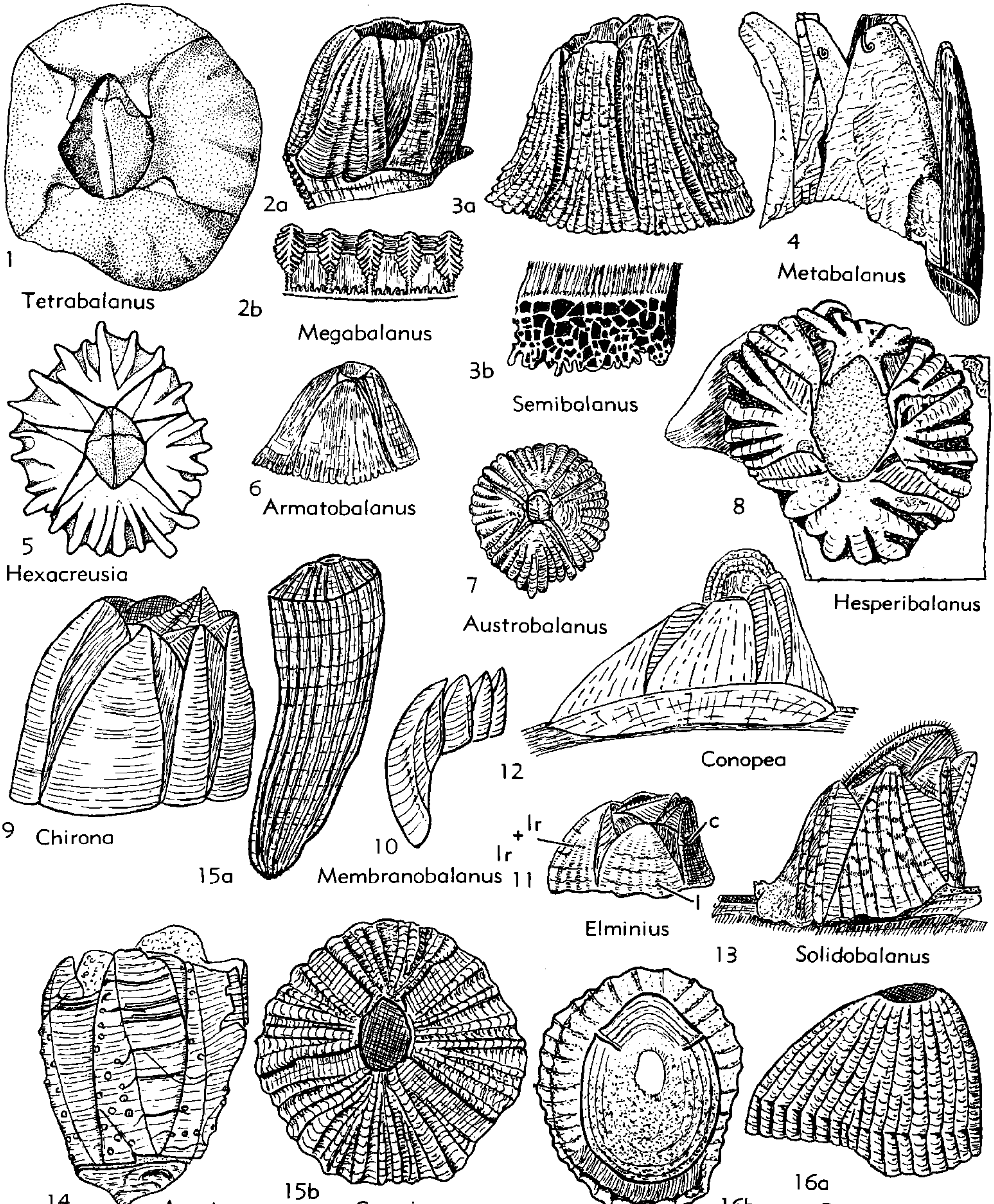

FIG. 118A. Balanidae (Balaninae) (p. *R*285-*R*287). [Explanation: *c,* carina; *l,* latus; *lr,* latus (rostral).]

margin. *Rec.,* Bering Sea.——Fig. 118A,*4.* **B. (M.) hoekianus* Pilsbry; ×4 *(83).*

B. (Semibalanus) Pilsbry, 1916, p. 182 [**Lepas cariosa* Pallas, 1788, p. 234; OD]. Parietes with one or more rows of parietal tubes; radii solid; basis membranous; rostrum not extending downward below other compartmental plates. *M.Plio.-Rec.,* N.Pac.-N.Atl.——Fig. 118A,*3.* **B. (S.) cariosus* (Pallas), Rec., NE.Pac.; *3a,* shell, ×1.5; *3b,* basal view of wall, enl. *(39).*

B. (Solidobalanus) Hoek, 1913, p. 159 [**B. auricoma;* SD Pilsbry, 1916]. Hermaphrodite with parietes and radii solid; radii well developed, with denticulate sutural edges; basis calcareous; adductor ridge of scutum reduced or absent; sides of tergal spur curving into basal margin. Complemental male, when present, may be found in pit inside rostral plate of hermaphrodite. [Includes *Hesperibalanus, fide* Henry & McLaughlin, 1967.] *Rec.,* RedSea-Ind.O.-W.Pac.-Hawaiian Is.-SE.Pac.-SE.Atl.——Fig. 118A,*13.* **B. (S.) auricoma* Hoek, N.Z.; ×3.3 *(18).*——Fig. 118, *3. B. (S.) masignotus* Henry & McLaughlin, Rec.; *3a,* complemental male, ×135; *3b,* int. view of rostrum, ×1.7 (from Henry & McLaughlin, 1967).

Acasta Leach, 1817, p. 69 [**Lepas spongites* Poli, 1795, p. 25 (=*A. montagui* Leach, 1817); OD] [=*Pseudacasta* Nilsson-Cantell, 1930]. Six solid compartmental plates arranged as in *Balanus;* radii well developed; compartmental plates weakly articulated; form of shell globose; basis solid, rounded or cup-shaped; shell not elongate along carinorostral axis; cirrus *IV* with or without recurved teeth or hooks; commonly embedded in sponges. *L. Oligo.-Rec.,* Ind. O.-W. Pac.-Red Sea-Medit.-W.Afr.-Eng.-SE.USA-Cuba.——Fig. 118A, *14. A.* sp. *cf. cyathus* Darwin, Rec., Cuba; ×2 (Withers, ?n).

Bathybalanus Hoek, 1913, p. 230 [**Balanus pentacrini* Hoek, 1913, p. 230; OD]. Six compartmental plates solid, ribbed internally; radii well developed; basis calcareous, solid; labrum with notch; cirrus *III* more like cirri *I* and *II* than cirri *IV-VI;* caudal appendages absent. Penis with basidorsal point. *Rec.,* Moluccas.——Fig. 117,*16.* **B. pentacrini* (Hoek); ×4.4 *(54).*

Creusia Leach, 1817, p. 68 [**C. spinulosa* Leach, 1818, p. 171; OD]. Four solid compartmental plates in shell wall, including rostral plate, carina, and 2 laterals; radii present or absent; sutural edges distinct or interlocked so as to appear to have become concrescent; basis cup-shaped to cylindrical, solid; embedded in corals. *L.Mio.-Rec.,* Medit.-Ind.O.-W.Pac.-W.Indies.——Fig. 118A,*15a.* **C. spinulosa,* Rec.; ×7 (Withers, after Darwin).——Fig. 118A,*15b. C. barbadensis* Withers, Pleist., Barbados; top view, ×6 *(115).*

Elminius Leach, 1825, p. 210 [**E. kingii* Gray, 1831, p. 13; SD Pilsbry, 1916, p. 260]. Wall composed of 4 solid compartmental plates, including rostral plate, carina, and 2 laterals; basis membranous. *Rec.,* W. S. Am.-N. Z.-Australia-Azores-(introduced by ships into NE.Atl.).——Fig. 118A,*11.* **E. kingii* Gray, Rec., S.Am.; ×1.5 *(39).*

Kathpalmeria Ross, 1965, p. 61 [**K. georgiana;* OD]. Wall form of 6 solid compartmental plates; basis calcareous, solid; reentrant buttresses forming ribs on inner surface of parietes; radii narrow or wanting; scutum without adductor ridge. *L. Eoc.,* SE.USA; *M.Eoc.,* Eu.(Hung.).

Pyrgoma Leach, 1817, p. 68 [**P. cancellata* Leach, 1818, p. 161; OD]. Shell wall composed of single plate; although carinolateral sutures may be seen in sheath in some species; basis calcareous, cup-shaped or cylindrical. *Plio.-Rec.,* Medit.-Ind.O.-W. Pac.-Carib.——Fig. 118A,*16.* **P. anglicum* G. B. Sowerby, Rec., W.Indies; *16a,* shell, side view, ×7; *16b,* shell, top view, ×7 *(115).*

Pyrgopsella Zullo, 1967 [*nom. subst. pro Pyrgopsis* Gruvel, 1907 (*non* Rochebrune, 1884)] [**Pyrgopsis annandalei* Gruvel, 1907, p. 8; OD]. Shell wall composed of single plate; basis membranous, in form of short peduncle. *Rec.,* Andaman Is.

Tetrabalanus Cornwall, 1941, p. 227 [**T. polygenus;* OD]. Shell wall of 4 plates including rostral plate, carina, and 2 laterals; parietes with single row of parietal tubes; radii solid, well developed; basis calcareous with radial tubes; inner surface of parietes ribbed. *Rec.,* Ecuador.——Fig. 118A,*1.* **T. polygenus,* Puna I.; ×5.5 (after Cornwall, 1941).

Subfamily TETRACLITINAE Gruvel, 1903

[*nom. transl.* Nilsson-Cantell, 1921 (*ex* Tetraclitinae Gruvel, 1903)]

Wall composed of four compartmental plates, including rostral plate, carina, and two laterals; parietes with one row, or more commonly with many irregular rows of parietal tubes; basis usually membranous; labrum with or without moderately developed notch. *Oligo.-Rec.*

Tetraclita Schumacher, 1817, p. 91 [**Balanus squamosus* Bruguière, 1789, p. 170 [=*Tetraclita squamulosa* Schumacher, 1817); OD] [=*Conia* Leach, 1817; *Asemus* Ranzani, 1817; *Polytrema* Férussac, 1822]. Characters of subfamily. *Oligo.-Rec.,* all seas.

T. (Tetraclita). Two or more irregularly arranged rows of parietal tubes; radii inconspicuous; adult shell externally concrescent in some specimens; scutum with prominent adductor ridge, and crests for lateral depressor muscle; tergum narrow, elongate. *?Mio.-?Plio., Pleist.-Rec.,* W. Ind.O.-W. Pac.-E. Pac.-SW. Atl.-S. Afr. —— Fig.

119,*2*. *T. (T.) squamosa rubescens* Darwin, 1854, Rec., USA(Calif.); *2a,* shell, ×1.5; *2b,* basal edge of wall, enl. *(39)*.

T. (Tesseropora) Pilsbry, 1916, p. 259 [**Conia rosea* Krauss, 1848, p. 136; OD]. Parietes of adult usually with single row of large parietal tubes; some with 1 or 2 secondary rows of small tubes; radii solid. *Oligo.(Lattorf.)-Rec.,* W.Pac.-Carib.-Medit.-E.Afr.——Fig. 119,*1*. **T. (T.) rosea* (Krauss), Rec., ?S.Afr.; *1a,* shell, ×1; *1b,* basal edge of wall, enl. *(39)*.

T. (Tetraclitella) Hiro, 1939, p. 273 [**Lepas purpurascens* Wood, 1815, p. 55; OD]. Parietes with more than one row of irregularly arranged parietal tubes; radii broad, with nearly horizontal summits and interseptal tubes; scutum broad with poorly developed adductor ridge and without crests for lateral depressor muscles; tergum short, broad. *Rec.,* W.Pac.-Hawaiian Is.-W. Indies-Madras.——Fig. 119,*4*. *T. (T.) divisa* Nilsson-Cantell, Hawaii; *4a,* shell from above, ×12; *4b,* view from below of basal margin on interior, enl. (Newman, n).

Subfamily CHELONIBIINAE Pilsbry, 1916

Six compartmental plates in shell wall, including tripartite rostral plate, two laterals, two carinolaterals, and carina; sheath extending to base of shell, forming inner wall of body chamber; sutures uniting rostrum and rostral plate; compartmental plates

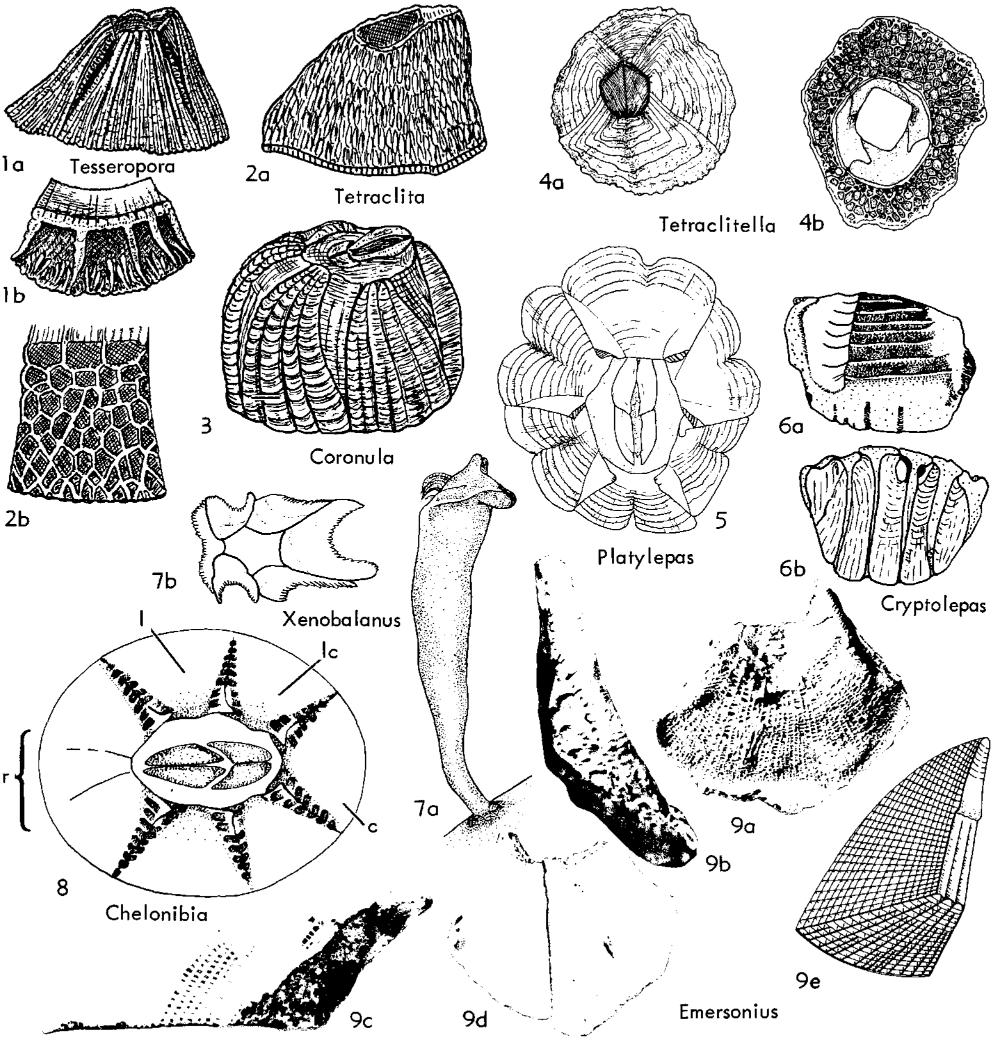

Fig. 119. Balanidae (Tetraclitinae) *(1-2, 4)*, (Chelonibiinae) *(8)*, (Coronulinae) *(3, 5-7)*, (Emersoniinae) *(9)* (p. *R*287-*R*290). [Explanation: *c,* carina; *l,* latus; *lc,* latus (carinal); *r,* rostrum.]

with cavity between outer lamina and sheath partially filled by lamellar plates normal to shell wall; basis membranous; opercular valves smaller than orifice; articular ridge of scutum chitinous. *L.Mio.-Rec.*

Chelonibia Leach, 1817, p. 68 [**Lepas testudinaria* Linné, 1757, p. 668; SD Pilsbry, 1916]. Diagnosis as for subfamily. [On turtles, sea snakes, manatees, and crabs.] *L.Mio.(Aquitan.)-Rec.,* temp. and tropic seas.——Fig. 119,*8*. **C. testudinaria* (Linné), Rec., Baja Calif.; ×1 (Newman, n).

Subfamily CORONULINAE Leach, 1825

[*nom. transl.* Pilsbry, 1916 (*ex* Coronuladae Leach, 1825)]

Six compartmental plates in shell wall, including rostral plate, two laterals, two carinolaterals, and carina; opercular valves, when present, smaller than orifice, not articulating; sheath extending nearly to base, but with inner lamina present below; basis membranous; shell attached to marine animals. *U.Mio.-Rec.*

Coronula Lamarck, 1802, p. 464 [**Lepas diadema* Linné, 1767, p. 1108; SD Pilsbry, 1916] [=*Diadema* Schumacher, 1817; *Diadema* Ranzani, 1817; *Cetopirus* Ranzani, 1817; *Polylepas* Klein, 1825; *Coronulities* Parkinson, 1833; *Polylopas* Mörch, 1852; *Ceteopirus* Mörch, 1852; *Flabelcorona* de Gregorio, 1895]. Body contained in shell wall composed of 6 equal-sized compartmental plates; opercular valves present; parieties with similar structure throughout, without internal midribs; radiating accordion-like folds of parietes (ribs) ending in T-shaped flanges forming exterior of wall; radii well developed; sheath smooth. [On cetaceans.] *U.Mio.-Rec.,* cosmop.

- **C. (Coronula).** Orifice of body chamber larger than basal openings; sheath as long as inner wall; radiating ribs on either side of sutures unbranched or asymmetrically branched; opposed sides of terminal flanges crenulate; radii less than half thickness of compartmenal plates, leaving cavity between radii and adjacent alae. *U.Mio.-Rec.,* N. Am.-S.Am.-Eu.-Australasia-Japan.——Fig. 119,*3*. **C. (C.) diadema* (Linné), Rec., Arctic; ×1 *(39)*.
- **C. (Cetopirus)** Ranzani, 1817, p. 276 [**Ceteopirus complanatus* Mörch, 1852, p. 67 (=*Cetopirus balaenaris* Ranzani, 1817); OD]. Orifice of body chamber equal to or smaller than basal opening; sheath shorter than inner wall; branches of sutural ribs symmetrical; opposed sides of terminal flanges not crenulate; radii almost as thick as compartments, filling cavity between adjacent plates. *Pleist.,* USA(Ore.); *Rec.,* S. Hemis.-Norway-?USA(Calif.).

Cryptolepas Dall, 1872, p. 300 [**C. rachianecti;* OD]. Body contained in shell wall; opercular valves present; parietes with similar sculpture throughout, without internal mid-ribs; radiating ribs of parietes with or without terminal T-shaped flanges; radii well developed; sheath transversely grooved. *U.Pleist.-Rec.,* N.Pac.——Fig. 119,*6*. *C. murata* Zullo, U.Pleist., Baja Calif.; *6a,* inner view of compartmental plate showing grooved sheath, ×3; *6b,* bottom view of same showing T-shaped terminal flanges, ×3 (Zullo, 1961).

Cylindrolepas Pilsbry, 1916, p. 287 [**C. darwiniana;* OD]. Cylindrical shell with orifice and basal opening of same size; bases of compartmental plates obtusely dentate, with median tooth in each compartmental plate largest, slightly inflected; sheath long; basis and opercular valves as in *Platylepas*. *Rec.,* ?W.Indies-USA(Hawaii)-E.Pac.

Platylepas Gray, 1825, p. 105 [**Lepas hexastylos* Fabricius, 1798, p. 35; OD] [=*Columellina* Bivona, 1832]. Conic shell wall composed of 6 compartmental plates, each with internal, downward projecting median rib; basis membranous, supported by median ribs; sheath short; opercular valves occupying entire orifice. *U.Pleist.,* USA (Fla.-Calif.); *Rec.,* warm temp. and tropic seas.——Fig. 119,*5*. **P. hexastylos* (Fabricius), Rec., Baja Calif.; ×17 (Newman, n).

Stephanolepas Fischer, 1886, p. 193 [**S. muricata;* OD]. Body contained in globoconic (young) or tubular (adult) shell wall composed of 6 compartmental plates; opercular valves not distinctly articulated; parietes with median, longitudinally ridged area flanked by spinose areas bearing horizontally flattened projections irregularly arranged in transverse rings; basal opening smaller than orifice; sheath 0.7 length of inner wall. *Rec.,* Indochina-Ceylon-USA(Calif.).

Stomatolepas Pilsbry, 1910, p. 304 [**S. praegustator;* OD]. Wall bowl-shaped, with orifice larger than basal opening; composed of 6 compartmental plates, each with external median sulcus; sheath long, transversely grooved, without distinct lower edge; opercular valves thin, long, narrow; basis membranous. *Rec.,* Medit.-W.Indies-Japan.

Tubicinella Lamarck, 1802, p. 461 [**T. major;* OD]. Body contained in elongate, tubular shell wall composed of 6 equal compartmental plates; parietes similar in structure throughout, without internal mid-ribs or radial ribs or parietal folds on exterior of parietes; radii narrow; sheath transvesely grooved. [On whales.] *Rec.,* S.Hemis.-Faroe Is.

Xenobalanus Steenstrup, 1851, pl. 3, fig. 11-15 [**X. globicipitis;* OD] [=*Siphonicella* Darwin, 1852]. Lengthened body not contained in shell wall; shell star-shaped, small, composed of 6 compartmental plates embedded in skin of host; opercular valves absent. *Rec.,* Atl.-NE.Pac.——Fig. 119,*7*. **X. globicipitis,* Calif.; *7a,* shell, ×2 (Newman, n); *7b,* wall plates embedded in skin of cetacean seen from above, enl. (Newman, n).

Subfamily EMERSONIINAE Ross, 1967

[*nom. correct.* NEWMAN & ZULLO, herein (*pro* Emersoninae Ross, 1967)]

Known from single rostral plate, paries and radii of which are permeated by tubes divided into cubes by uniformly spaced transverse septa. Unique, regularly spaced, intercalated laminae occurring between inner and outer laminae, distinguish this from other known Balanomorpha. *U.Eoc.*

Emersonius Ross, 1967, p. 7 [**E. cybosyrinx;* OD; in Ross & NEWMAN, 1967]. Characteristics of subfamily. *U.Eoc.*, USA(Fla.).——FIG. 119,9. **E. cybosyrinx; 9a,* internal surface of rostrum, ×1.6; *9b,* lateral view of articulating surface of left radius, showing arborescent teeth, ×3; *9c,* cross section taken at primary septum showing transverse septa, intercalated laminae, inner and outer laminae, ×2; *9d,* external surface of rostral plate showing radii slightly below surface of parietes and the exposed transverse septa in tubes of right radius, ×1.5; *9e,* schematic projection of wall portion depicting relationships of transverse and longitudinal septa *(90a).*

Order APODA Darwin, 1854

Single specimen of a parasitic crustacean described by DARWIN (1851-54), not encountered since. Body markedly segmented, but bearing only two pairs of appendages; mandibles, with fused first and possible ?second maxillae; and ?first antennae. Presumed hermaphroditic. Attached by mouth parts within the mantle cavity to prosoma of a barnacle. [Assignment to Cirripedia questioned by KRÜGER (1940); interpreted as a copepod, or more likely an epicaridean isopod *(74).*] *Rec.*

Proteolepas DARWIN, 1854; p. 589 [**P. bivincta;* OD]. Parasitic within mantle cavity of *Heteralepas cornuta* (DARWIN), *Rec.*, W.Indies [Fig. 84, *1a-d*].

Y-larvae. Metanauplii inferred to be those of Apoda. If Cirripedia, equally and likely of Ascothoracica; if not, possibly of Branchiura.

Y-larvae HANSEN, 1899, p. 41. Metanauplii lacking frontolateral horns but otherwise resembling those of cirripeds. [Not assignable to any group in which larval forms are well known, and therefore, relegated to Apoda by HANSEN.] *Rec.*, North Sea-W.Indies-S.Atl. [Fig. 85,*2*].

Y-larvae STEUER, 1904, p. 3. Metanauplii comparable to HANSEN's *Y-larvae,* considered to be those of Apoda and named *Proteolepas hanseni* by STEUER. *Rec.*, Medit.

Y-larvae MCMURRICH, 1917, p. 50. Metanauplii apparently identical to certain of those of HANSEN. Recognized as probably of cirripeds, but assignment to Apoda considered highly speculative. *Rec.*, E.Atl.

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MALACOSTRACA

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