

REVISION OF THE CORAL-INHABITING BARNACLES (CIRRIPEDIA: BALANIDAE)

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ABSTRACT.—The biogeography, growth, morphology and host specificity of all known taxa of coral-inhabiting barnacles in the Pyrgomatinae are reviewed. In addition to *Pyrgoma* and *Creusia*, among which all of the species were previously divided, we resurrect five genera and propose **Hoekia**, **Hiroa** and **Cantellius**. These 10 genera fall into three groups: *Boscia* (cosmopolitan), *Ceratoconcha* (Pliocene in the eastern Pacific, Mio-Pliocene in the Mediterranean Basin, and as Miocene relicts in the western Atlantic), and *Cantellius* and its derivatives (Miocene to Recent in the Indo-west Pacific). The Pyrgomatinae are apparently polyphyletic; *Cantellius* and possibly *Boscia* arose from different armatobalanid stocks, while *Ceratoconcha* arose from an indeterminate balanoid stock. *Cantellius* and *Ceratoconcha* first appeared in the Miocene during the break up of the Tethyan Sea and the initiation of faunal provincialism.

The reef coral community has been characterized by Cloud (1959: 387) as essentially a steady-state oasis of high population density, intense calcium metabolism, and complex nutrient cycling, generally surrounded by waters of relatively low nutrient and plankton content. Aside from interesting parallels with tropical rain forests and man-made megapolises, Newell (1971: 2) argued that the organisms comprising the coral reef community are "superlatively coadapted." One of the remarkably coadapted animal groups is the coralliophilic pyrgomatines.

Barnacles comprising the Pyrgomatinae are obligatory symbionts or parasites primarily of scleractinian corals. They occur in all regions of the world that support major growths of hermatypic corals, and they have been found in sediments dating from the early Miocene. Modern pyrgomatines were probably recognized by naturalists in the 18th century, but the group did not receive serious attention until the middle of the 19th century. The present study is the first general revision on a world-wide basis.

HISTORICAL ACCOUNT

Studies on pyrgomatine cirripeds may be grouped into three periods. The work of Leach (1817, 1818, 1825), Sowerby (1823), Gray (1825, 1831), and many other conchologists characterize the earliest period as one of describing new taxa and grouping these into a hierarchy.

The second period, covering about 70 years, began with the publication of Darwin's (1854) monograph of the Balanidae and Verucidae. Darwin attempted to embody the best features of earlier studies; however, he chose not to follow the generic divisions proposed by Leach and Gray, and retained only *Pyrgoma* and *Creusia*, and the latter he assigned subgeneric status. Leach and Gray had attempted to group a seemingly meager number of species into a maximum number of poorly defined genera. Consequently, Darwin's conservative approach was generally accepted; and such caution has proved a deterrent to unraveling the systematics of this group.

The third period began with the work of Annandale (1924), followed by Withers (1926, 1929), Hiro (1935, 1938), and Nilsson-Cantell (1938), and more recently, by Brooks and Ross (1960), Utinomi (1962, 1967), Baluk and Radwański (1967a, 1967b, 1967c), and Ross and Newman (1969). Annandale, Hiro, and Nilsson-Cantell provided names for the majority of Darwinian numerical varieties, and they added considerably to our knowledge of the Indo-Pacific members of the subfamily.

Of the many classifications proposed for this group, the earliest were taxonomic rather than phylogenetic, except that of Gray (1825: 102), which was based on an ecological concept. The most promising classification was proposed recently by Baluk and Radwański (1967c) who resurrected the generic groupings initiated by Leach, Gray and

Sowerby, and proposed several new names. The present study somewhat revises and greatly extends their classification.

BIOGEOGRAPHY

Modern pyrgomatines occur in all regions of the world that support major growths of hermatypic corals. Fossils occur predominantly in the Tertiary and Pleistocene of the western Atlantic and the Mediterranean Basin (Withers, 1929: 2; Brooks and Ross, 1961: 326; Baluk and Radwański, 1967c; Newman and Ladd, in press). The western Atlantic contains but a few morphologically primitive pyrgomatines, while the Indo-west Pacific has the greatest variety and abundance and the morphologically most advanced species. The disparity between these faunal realms may relate to the greater number of reef corals available as hosts in the Indo-Pacific, of which there are 80 genera and 500 species as compared to 20 genera and 65 species in the western Atlantic (Newell, 1971: 26), but the latter has also witnessed a general decline in the biota dating from the Miocene (Newell, 1971: 23).

Three major morphological groups of Pyrgomatinae are recognized in this paper (*Ceratoconcha*, *Boscia* and *Cantellius* and its derivatives), and these have interesting implications. The first and most generalized is the creusoid *Ceratoconcha*, which first appears in sediments of lower Miocene age. Based on studies by Brooks and Ross (1961: 362), Baluk and Radwański (1967c), and Newman and Ladd (in press), it is evident that during the Miocene *Ceratoconcha* was not only more diverse in terms of species than it is today, but also ranged throughout the tropical Atlantic and its eastern Pacific outpost, while it survives as a Miocene relict in the western Atlantic (Fig. 2). *Ceratoconcha* apparently never ranged into the Indo-Pacific, probably because communications between the Indian Ocean and the Mediterranean had ceased in early Miocene times (Ruggieri, 1967: 284) with the northward movement of the African land mass.

The Pliocene fauna in the Mediterranean Basin includes only *C. costata* (see Baluk and Radwański, 1967c: 483; Moroni, 1967: 17); apparently no Pleistocene ceratoconchoids are found there. The short stratigraphic range of *Ceratoconcha* in the Mediterranean Basin is not surprising, because climatic cooling which had already begun in the Oligocene (Wells, 1956; Ekman, 1953), coupled with isolation (Ruggieri, 1967: 284), resulted in a decline in, if not total destruction of, the hermatypic corals and other tropical elements of the fauna.

The Mediterranean ceratoconchoids are probably western Atlantic derivatives despite the great distance separating these two regions. Numerous other invertebrates presently have trans-Atlantic distribution patterns (Briggs, 1970), and apparently many of these animals have larvae that were transported eastward from the western Atlantic (Robertson, 1964: 21; Scheltema, 1971: 284).

Ceratoconcha was represented by at least five species in the western Atlantic in the early Miocene (Newman and Ladd, in press), and some time thereafter by a few species in the eastern Pacific. At least two species are found in Pliocene corals of the Imperial Formation of the Carrizo Creek and Coyote Mt. areas of southern California (Ross, unpubl.). There are no Pleistocene or living ceratoconchoids in the eastern Pacific. The western Atlantic Pliocene fauna contains only *prefloridanum*; the Pleistocene fauna contains *barbadensis*, possibly *prefloridanum*, and several undescribed species (Brooks and Ross, 1960: 362). The Recent western Atlantic contains two or possibly three species.

The second group, containing only the primitive pyrgomoid *Boscia* (Fig. 2), has been found in sediments of Pliocene age in the Mediterranean Basin (Baluk and Radwański, 1967c: 483) and England (Darwin, 1854b; Withers, 1926). Pleistocene occurrences include Italy (Alessandri, 1906) and Japan (Sakakura, 1938). Although Sakakura reported the individuals he found on an ahermatypic coral as *anglicum*, restudy of these may reveal that they represent either a new species or *oulastreae* (see Utinomi, 1967: 232), since *anglicum* appears to be restricted to the western Mediterranean and eastern Atlantic (Moyses, 1961: 384; Utinomi, 1967: 231; cf. Rees, 1962: 412). *Boscia* occurs on hermatypic corals in the western Atlantic (*madreporarum*) and western Pacific (*oulastreae*), whereas in the eastern Atlantic and Mediterranean (*anglicum*) it settles only on ahermatypic corals. There are no

records of *Boscia* in the eastern Pacific.

The third group is wholly Indo-west Pacific with species ranging from the Red Sea to the Great Barrier Reef and to the Line Islands (Fig. 2 and 3). There are but two Miocene records for the eight genera in this group, but the specimens have not yet been identified (Newman and Ladd, in prep.). *Nobia*, *Cantellius*, and *Savignium* are found throughout the Indo-Pacific, but only *Savignium* ranges as far south as the Great Barrier Reef and as far east as the Line Islands. *Pyrgoma*, *Creusia*, and *Hoekia* range from eastern India to Japan, although *Hoekia* has been reported from Mauritius (Ross and Newman, 1969). There is only one record for *Hiroa*, in the Caroline Islands.

From the foregoing, two provincial coral-barnacle faunas can be recognized, one centering in the Caribbean portion of the western Atlantic and the other in the Australasian portion of the Indo-Pacific. Comparable biogeographic patterns have long been recognized in other invertebrates and in fishes (see Briggs, 1970). The coral barnacles were evolving when the continuity of the Tethyan Sea was being destroyed, ultimately leading to faunal provincialism. In light of the geological history of these regions and considering the morphological features of these two groups, it is apparent that they developed independently in the two regions from different balanoid ancestors. *Boscia*, which appears to be a third independent group, may owe its widespread distribution to its ability to settle on deep-water ahermatypic corals.

GROWTH AND FORM

The early growth stages of pyrgomatines look much like those of ordinary balanids. It is in the later stages that their adaptations to an intracoralline life become evident. Knowledge of the larval stages is limited: Kolosváry (1950: 293) described typically balanoid nauplii of *Savignium milleporae* and Moyses (1961: 371) described all larval stages of *Boscia anglicum*. Duerden (1904: 39) suggested that the cyprid bores through the living tissue of the polyp and that in the process of growth the skeletons of the two become fused.

Utinomi (1943: 16) followed the ontogeny of the earliest juveniles of *Creusia indicum* Annandale, and found that the juvenile does not initially attach to the coral skeleton but remains imbedded in the coral tissue. While the four plates making up the wall and the opercular valves are calcified, the cup-shaped basis of the juvenile is wholly membranous. Even after the basis calcifies there is a period when the juvenile remains free in the coral tissue before the basis and corallites come into contact and fuse. Moyses (1971: 127) noted similar relationships in *Boscia anglicum*.

Subsequent growth is rapid, especially laterally, so that the shell reaches essentially maximum diameter early in life. This is well illustrated by Hiro (1938, fig. 11 and 12). In general, the wall becomes proportionately less conical as its diameter and basal height increase, the aperture enlarging by diametric growth in four-plated forms, or by corrosion and cirral rasping in single-plated forms. In the scatter diagram plotted by Hiro (1938, fig. 12) for *Creusia indicum*, after the period when the basal height and shell width increase uniformly, width stabilizes while basal height continues to increase, as it must throughout the life of the barnacle. During the early period of rapid increase in width, the barnacle may rotate its position by as much as 90° (Baluk and Radwański, 1967b, fig. 2, 1; Newman and Ladd, in press, pl. 2h).

Creusoids with well developed radii are commonly overgrown to some extent by the coral, and enlargement in both basal height and shell diameter requires breaking the overgrowth along the sutures. Creusoids with radii indicated by simple sutures, and pyrgomoids in general (except *Boscia*, see Moyses, 1971), have the ability to suppress coral skeleton deposition around the margin of the shell so that vertical growth can proceed without mechanical breakage. In some cases, the coral may lay down skeletal elements on the wall of the barnacle suggestive of normal septa, and the barnacle then takes on the appearance of a corallite (Duerden, 1904: 39); this is an unusual form of mimicry to say the least. In other cases, only coral tissue grows over the wall of the barnacle, and in *Hoekia* this tissue proliferates over the aperture where it is fed upon by the barnacle (Ross and Newman, 1969).

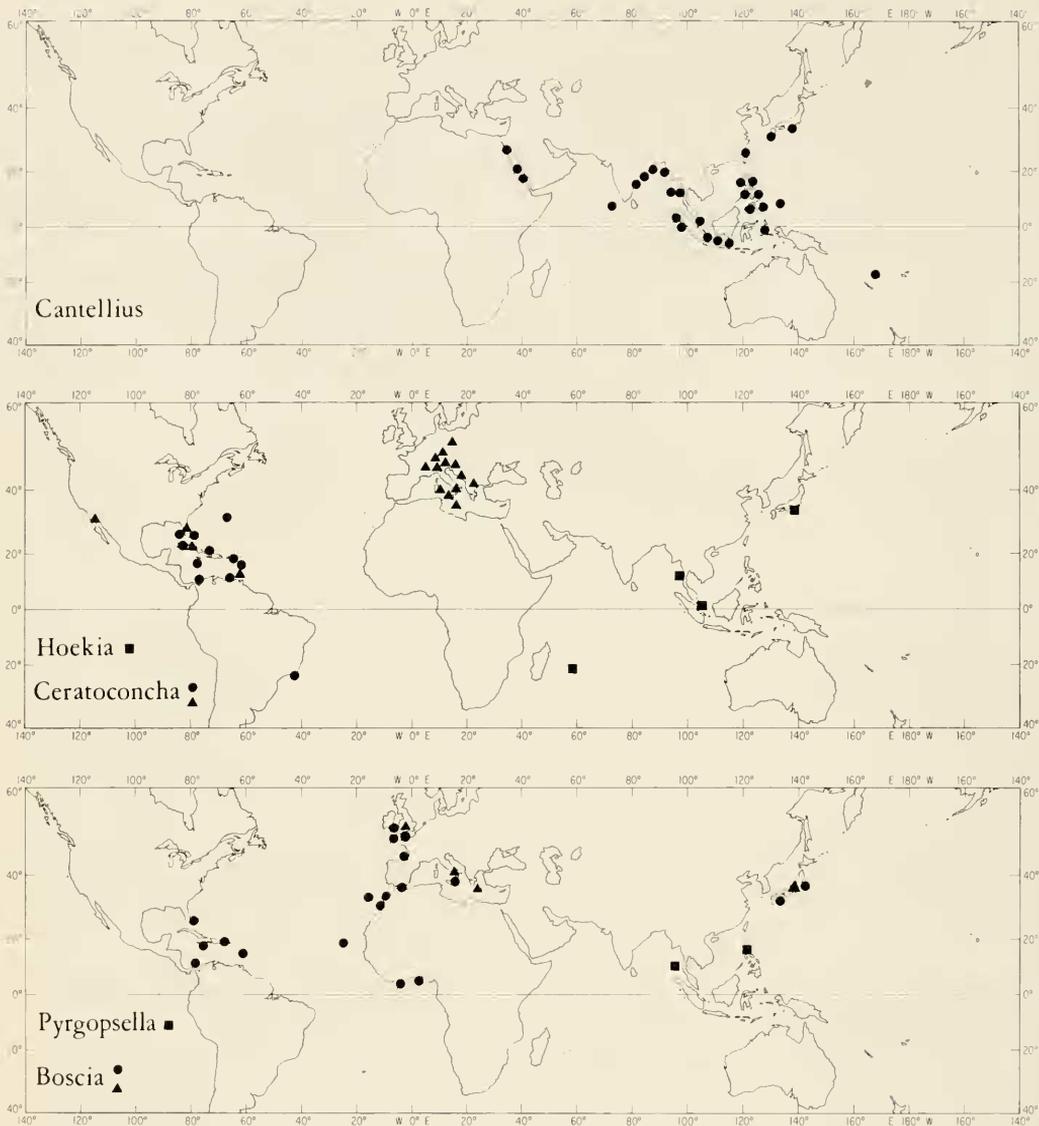


Figure 2. Distributional records for *Nobia*, *Pyrgoma*, *Hiroa*, *Savignium*, and *Creusia*. Data from same sources as Figure 3.

In specimens of *Savignium crenatum* that we have observed growing between low branches of the surface of *Merulina ampliata*, the rate of growth of the barnacle exceeds that of the coral so that the barnacle extends well above the general surface of the corallum. In most cases a thin layer of coral skeleton grows up onto the surface of the basis of the rapidly advancing barnacle, aiding in its support, but in some a fair proportion of the basis stands free of the coral. While it might appear that the barnacle's growth rate is simply out of phase with that of the coral, there is adaptive value in growing in this manner. The barnacles are growing up between branches of the coral which will eventually fuse laterally at higher levels. If the barnacles simply kept pace with the growth of the surface, they would more than likely be buried.

Boscia anglicum grows in a similar manner, but on solitary ahermatypic corals, along the margin of the corallite (Fig. 1). In this position there is relatively little interference with the normal feeding mechanism of the coral. Established individuals frequently serve as sites for subsequent generations. Cloud (1959: 392) suggested that the barnacles replace the coral polyps, and although this is certainly not true here, it may more frequently

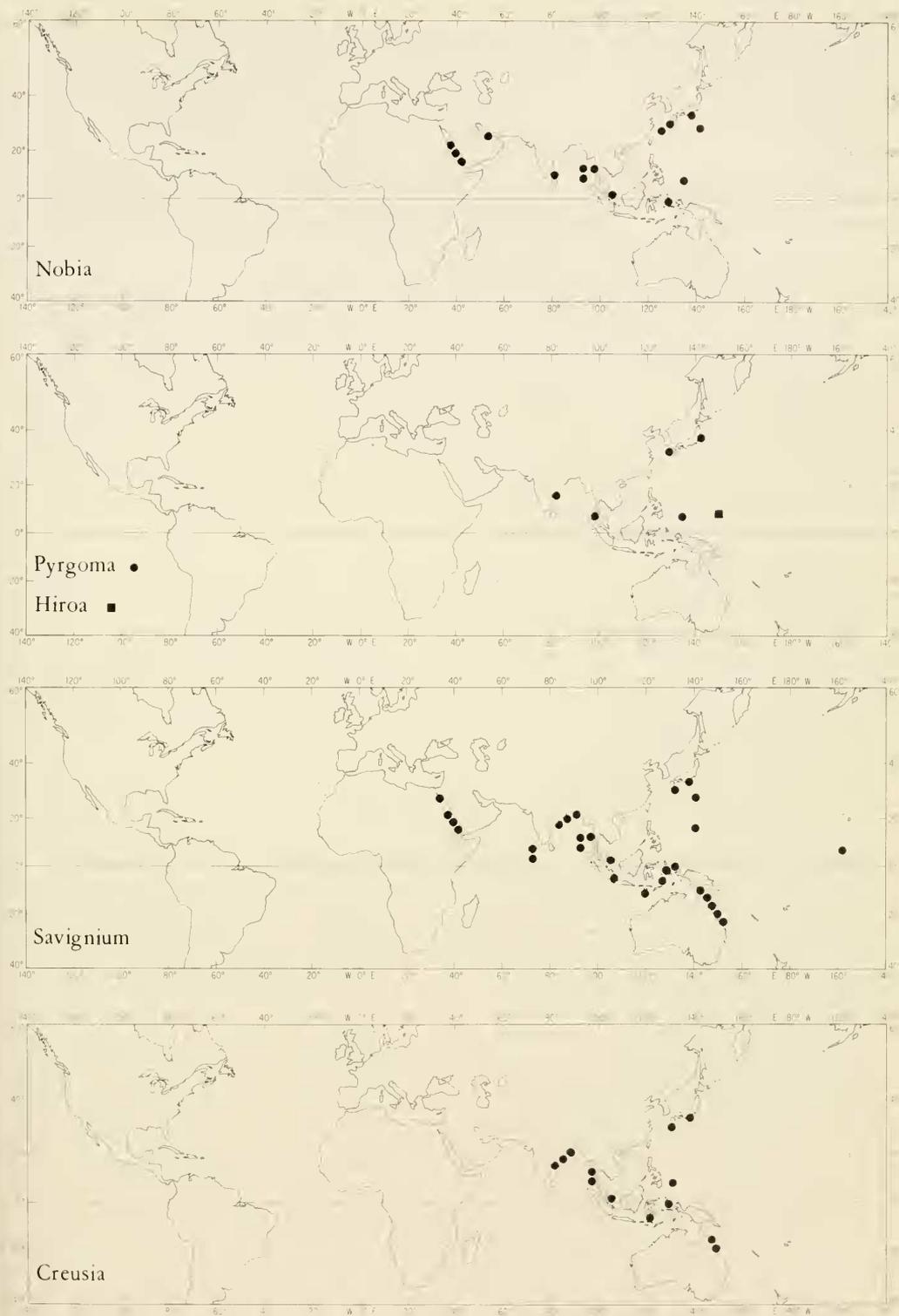


Figure 3. Distributional records for *Cantellius*, *Hoekia*, *Ceratoconcha*, *Pyrgopsella*, and *Boscia*. Circles and squares represent Recent records, triangles fossil records. Data based on specimens in the American Museum, San Diego Natural History Museum, Scripps Institution of Oceanography, Florida State Museum, British Museum (Natural History), Museum of Comparative Zoology, Harvard University, and available literature.

be true in those corals having smaller calices. Duerden (1904: 39) found that in *Siderastrea radians*, *Ceratoconcha* fixes itself in the calicinal cavity, never on the ridges connecting two calices and that the presence of the barnacle results in imperfections in the surrounding polyps.

The only pyrgomatine growing on the stinging hydrocoral *Millepora* is *Savignium milleporae*. It is not uncommon to find a thick-walled chimney of the host skeleton elevated about 5 mm above the general surface of the coral supporting the barnacle. The basis of the barnacle occupies the whole chimney, with the initial point of attachment essentially at the level of the surrounding colony. The top of the chimney is flush with the flat top of the barnacle. Evidently the general surface of the coral does not grow fast enough to accommodate the rapidly growing body chamber of the barnacle. Whether the barnacle is able to regulate the growth rate of the coral, so that the supporting chimney is formed, or the coral is simply reacting to the presence of a foreign object and attempting to bury it, has not been determined. Interestingly, *Balanus stultus*, the only other barnacle occurring on *Millepora*, likewise extends well above the general surface of the coral. It is also covered by a layer of coral skeleton, but it appears to be simply encrusted, rather than contained within a thick-walled chimney as is *S. milleporae*. *Balanus stultus* continues to grow diametrically by fracturing the coral skeleton along the sutures in the wall. Thus in both cases the coral is reacting in ways that favor the different growth habits of the barnacles, and this suggests that these barnacles are exercising some control over the growth habits and defense mechanisms of the coral.

In general, shell color in the pyrgomatines is white. *Boscia* juveniles have a white shell, but with later growth the shell takes on a pinkish or pinkish-purple hue. *Hoekia* has a pinkish-purple shell, while that of *Nobia* is white and splotted with pink or purple. In *Cantellius* some species are all white, whereas in others the apical portion of the opercular plates is tinted purple. The shell in *Savignium* is commonly pinkish red, and in *Pyrgoma* it is a pale pink. *Ceratoconcha* is invariably white. While the basis is never pigmented, the exposed shell of most genera is. Consequently, there must be some adaptive or functional significance to these colors. Since the colors do not match those of their hosts, they apparently do not serve as protective coloration.

Generalized creusoids have well developed radii, and undergo diametric growth during the better part of their lives. The radii range in form from triangular to rectangular, or they may be indicated externally simply by sutures. When the radii are triangular, the base of the isosceles triangle forms part of the apertural margin and indicates that the aperture has enlarged disproportionately to the total diameter of the shell. Rectangular radii indicate proportionate increments. Where radii are evidenced simply by sutures, diametric growth has all but terminated, and the total diameter of the wall can increase only by marginal increments. The aperture either remains the same or is enlarged by corrosion and (or) by the rasping effect of cirral movement; such forms have effectively reached the pyrgomoid level of organization.

The surface of the basis is commonly marked by longitudinal ribs, corresponding to the internal radiating ribs of the wall, and by transverse growth lines. The growth lines are generally very fine, ranging between 4 and 24 per mm (Newman and Ladd, in press), and are interrupted by discontinuities at more or less regular intervals (Baluk and Radwański, 1967a, fig. 2; Newman and Ladd, in press, pl. 1,b). The interruptions are frequently at intervals of 5 mm or so and probably correspond to the annual density bands in coral described by Knutson et al (1972: 270). This suggests that coral barnacles live for several years, which agrees with the age estimate given by Hiro (1938: 410). Unfortunately, the barnacles in which these bands have been observed are fossil forms that have been leached out of the coral so that the host species is unknown. With intact specimens, agreement between the bands in the coral and the barnacle probably could be determined by the x-ray techniques employed by Knutson et al (1972), but such work remains to be done.

Coral barnacles do not live as long as their hosts, and eventually they become entombed. In some cases the opercular parts of the entombed barnacles are cemented in the position they occupied in life, while in others they have fallen into the body chamber. In

the first case the coral undoubtedly overwhelmed the barnacle while alive. This could be true in the second case, although it may be that the barnacle died before the coral overgrew it. In any event, the coral usually forms a "stopper," growing into the aperture a short distance, before attaining a normal growth pattern over the barnacle (Baluk and Radwański, 1967c: 490).

To the best of our knowledge all pyrgomatines have solid walls, at least fundamentally. Some species develop parietal tubes where the longitudinal ribs on the interior of the wall become fused with the sheath, while others form tubes between external longitudinal ribs. In still others, where the sheath becomes fully fused to a much thickened wall, several rows of more or less regularly spaced tubes develop. In none of these cases are the tubes formed in the same way as in the tubiferous balanids (subgenera *Balanus* and *Megabalanus*) where interlaminar figures can be observed in the longitudinal septa separating the inner and outer laminae of the wall.

The ontogenetic and phylogenetic development of tubiferous walls has been analyzed in a number of cases (Costlow, 1956; Newman et al, 1967; Ross and Newman, 1967), but their function has only been a point of speculation. A few systematists have suggested applying the general engineering principle that, for a given amount of material, a properly designed tubiferous structure would be mechanically stronger than a solid one. If it were necessary for a barnacle to be economical in its use of calcium carbonate, then a tubiferous wall should be advantageous in high energy environments. Barnes et al (1972) tested the resistance of certain species to impaction and found that breakage occurred not in the plates themselves but at the sutures between them. They concluded that the strength of the plates generally exceeded the strength of the articulating joints. The nature of the articulation between the wall and calcareous basis is also of great importance (Newman et al, 1967: 170). These structural features are well developed in the pyrgomatines. However, wall strength in coral barnacles can hardly be related to withstanding impaction as in many free-living forms, but rather is related to the pressures required to sustain growth in an intracoralline habitat.

Considering the array and independent occurrences of tubiferous walls, and the secondary modifications found in them, e.g. sealing off into chambers, secondarily filling with calcareous material, or filling with chitin during construction, one might look for some adaptive value other than simply strength. Ross (1970: 9) and Newman and Ross (1971) suggested that such adaptations might include defensive mechanisms against borers, specifically against the drilling of gastropods. In this regard, Orton (1927: 653) noted that "oysters are frequently attacked and abandoned (by gastropods) . . . if either a chamber or loose horny layer is encountered . . ." It would be expected that free-living barnacles, which are frequently attacked by gastropods, would also have developed defense mechanisms against them. However, in the pyrgomatines predation by borers has not been reported. Their tubiferous walls, then, developing in different ways in different members of the group, undoubtedly have some other function. Strength is probably the important one, but it is also likely that these tubes allow for physiological interactions between the barnacle and its host. In many species the tubes are arranged so as to leave gaps around the margin of the shell, which appear to allow the uncalcified integument of the barnacle to come into intimate contact with the tissue of the coral. Moyses (1971) suggested that the barnacle may receive metabolic substances from the host by this route. However, we believe it more likely or important that these are the sites where physiological control of coral growth are initiated.

The opercular valves function to guard the aperture and range in form from wholly balanoid to highly modified. In *Cantellius* and *Ceratoconcha*, the two most generalized genera, the four-plated wall varies from high conic to virtually flat. Yet the valves are always tall and typically balanoid. The same can be said of *Boscia*, except that it has a concrescent shell. In these three genera the terga as well as the scuta occlude the aperture.

In the *Savignium* line (Fig. 5), the opercular valves are generally thin and fragile, and the wall is totally concrescent. The scuta are relatively elongate and the reduced terga become completely fused to them. Likewise, the aperture is elongate, and it is guarded primarily by the scuta. The epitome of modified valves is seen in *Hoekia*. However, it has

a minute orifice and this is related to its wholly parasitic way of life (Ross and Newman, 1969).

In the *Hiroa* lineage the opercular valves tend to remain balanoid, although the scuta alone occlude the aperture. Modifications within the lineage include elongation and narrowing of the terga and reduction of articular margins on one hand (*Hiroa*, *Pyrgoma*), and broadening and concrescence on the other (*Nobia*, *Creusia*). In *Hiroa*-*Pyrgoma* the opercular plates are relatively thin and fragile while in *Nobia*-*Creusia* they are thick and massive. This disparity correlates to some extent with size, but the difference probably also relates to the amount of protection each requires from predators. Baluk and Radwański (1967c: 463), with reference to Darwin's plate 13, fig. 1d, (Fig. 12, c herein), misunderstood the anatomical relationships between the opercular valves and the wall in *Nobia*, and concluded that the valves no longer guard the aperture. Apparently, they were not distinguishing between the scutal and tergal portions of the concrescent valves and thought that the occludent margins of the scutal portions were fused together and no longer functional.

In summary, cyprids of coral barnacles apparently first settle on coral tissue where they metamorphose into juveniles. A juvenile doesn't attach to the coral skeleton until after the cup-shaped basis has become calcified. During this period, and to some extent after attachment, the juvenile may undergo reorientation in relation to the host of as much as 90°. Unlike ordinary barnacles, subsequent growth is primarily through elongation of the basis rather than the wall. Species with radii generally undergo diametric growth and, in the process, frequently fracture the coral skeleton overgrowing them. Advanced species apparently gain a degree of control over coral tissue, and its ability to lay down new skeleton. While barnacles live for several years, they eventually become entombed.

HOST SPECIFICITY

Gray (1825: 102) proposed the Pyrgomatidae to accommodate several balanoid genera peculiar to certain zoophytes; *Pyrgoma* and *Creusia* imbedded in scleractinian corals, *Conopea* in gorgonians and *Acasta* in sponges. The unification of these genera under one family was based primarily on comparable habitats.

Figure 4 summarizes available data on distribution of the various genera of Pyrgomatinae among the scleractinian suborders. Of the ten genera all, except *Pyrgopsella* in sponges (not included in the figure) and *Savignium milleporae* on nine species of *Millepora*, occur exclusively on hermatypic and ahermatypic corals. Of these, seven genera occur on Faviina, five on Fungiina, five on Astrocoeniina, four on Dendrophylliina, and two on Caryophylliina. Faviina then, with the greatest diversity of genera, supports the greatest diversity of coral barnacles. Caryophylliina, while nearly equal to Faviina in numbers of genera, supports the least. This is no doubt because Faviina, Fungiina, and Astrocoeniina are hermatypic, while Dendrophylliina and Caryophylliina are ahermatypic with representatives ranging into deep water. Balanoids in general are shallow water organisms.

Only the cosmopolitan genus *Boscia* is known to inhabit all five scleractinian suborders and it is, as far as opercular valves are concerned, among the most generalized of the Pyrgomatinae. *Hoekia*, *Pyrgoma*, and *Hiroa* are each limited to but one scleractinian suborder, and each is monotypic. Of these, the first two are among the more specialized members of the subfamily, *Hoekia* being the most specialized balanoid known. *Hiroa* on the other hand resides at the stem of the other higher forms (*Creusia*, *Nobia*, and *Pyrgoma*) which, between themselves share all five scleractinian suborders, with *Nobia*, a relatively highly modified form, occurring on four of them.

Ceratocoelocoma is one of the most generalized forms, yet it inhabits but two of the scleractinian suborders. In being an Atlantic genus, it has survived in a situation where coral diversity has declined since the Oligocene or Miocene (see Biogeography). The remaining generalized genus, *Cantellius*, stands at the stem of the Indo-Pacific members of the subfamily and is well represented on the three principal shallow water suborders, Faviina, Fungiina, and Astrocoeniina.

From the foregoing, what can be said of host specificity among Pyrgomatinae at the

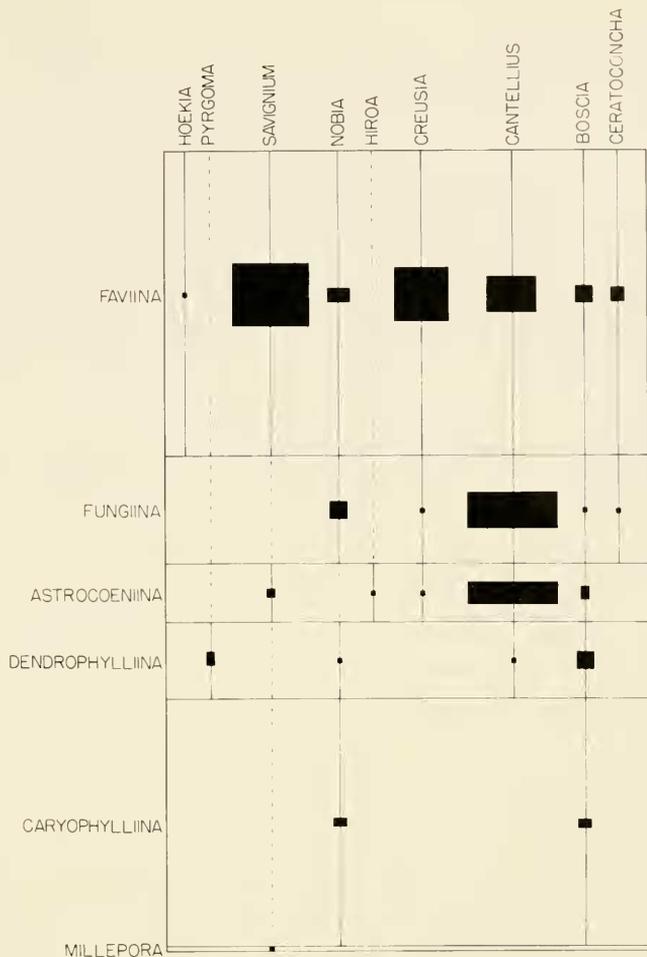


Figure 4. Distribution of genera of Pyrgomatinae among scleractinian coral suborders derived from the literature. Space for each coral suborder is proportional to the total number of coral genera within each suborder; bar width indicates number of occurrences of barnacles within each suborder; bar height represents the number of coral genera on which the barnacles are known to occur.

scleractinian subordinal level? One might expect highly modified forms to be highly host specific, and for such extremes as *Hoekia* this is indeed the case. However, *Nobia* is among the most modified forms, yet it occurs on all scleractinian suborders except Astrocoeniina, while *Hiroa*, an intermediate in the transition between *Cantellius* and *Creusia*, has been found only on Astrocoeniina. *Savignium* and *Creusia* exploit mainly Faviina while *Cantellius* exploits mainly Fungiina and Astrocoeniina, but the division is not precise as there is considerable overlap among the three.

What then seems to be the situation as regards host specificity at the specific level? Hiro (1935: 23) found that in Tanabe Bay, Japan, "A given species of *Pyrgoma* is practically confined to a single species of coral, whereas the same variety of *Creusia* may be found on various kinds of coral." In 1938 he reported on his findings in the more tropical Palau Islands. While expanding the number of corals playing host to species of *Pyrgoma* (1938: 404), he again came to the same general conclusion (1938: 392). Presently, his statement holds best for the monotypic genera.

The suborder Faviina plays host to most of the genera of Pyrgomatinae. Of the Faviina, *Porites* apparently has been selected most frequently as a host. Other balanids also have invaded *Porites*, the Recent armatobalanid *Balanus allium*, the Pliocene to Recent armatobalanid *Balanus durhami* and the Miocene balanid *Balanus duvergieri* are notable. Growth on *Porites* is independent of the growth of individual coral polyps and con-

sequently requires little specialization. This appears to us to be the reason why *Porites* plays host to a variety of barnacles. *Millepora*, on the other hand, does not, and one might suspect that this is due to its stinging ability.

In summary then—1) the greatest diversity of Pyrgomatinae in terms of numbers of genera is found among hermatypic suborders, particularly Faviina and this is probably because balanids in general are shallow water organisms; 2) there are no marked differences between the occurrences of pyrgomoids and creusoids as a whole on the various suborders of scleractinian corals—in both groups Faviina is preferred, with scattered occurrences between the other scleractinian suborders; and 3) the rule (Hiro 1938: 408), that the more peculiar the morphological characteristics of species, the more rigid their host specificity, holds in a general way. The same rule holds only weakly when applied to barnacle genera and scleractinian suborders, for some relatively specialized genera, such as *Nobia* and *Boscia*, occur on a wide variety of corals and are notable exceptions.

ORIGIN AND EVOLUTION

The Pyrgomatinae are a well defined group (Baluk and Radwański, 1967b: 465), but to what lineage of the Balaninae the subfamily owes its origin has not been resolved. Although the consensus is that the Pyrgomatinae are polyphyletic, only the broader outlines of their evolution have been elucidated (Withers, 1929: 564; 1935: 38; Hiro, 1938: 402, 412; Zullo, 1961: 72; 1967: 127; Baluk and Radwański, 1967c: 500). Existing problems stem from a lack of critical data on fossil and Recent forms, as well as from Darwin's (1854) conservative handling of genera and species. His treatment of *Creusia* as a subgenus of *Pyrgoma* has not been accepted by later workers. Also, his reluctance to recognize geographic populations of *Creusia* as species, even though a sample from a given locality showed markedly uniform characteristics (Darwin, 1854: 376), and the failure of subsequent workers to rectify this, resulted in a plethora of subspecific and infraspecific taxa that make little sense biologically. Therefore, before looking into the origins of these barnacles relationships within the subfamily are discussed.

Pyrgoma, in the broad sense, contains the most highly evolved members of the Pyrgomatinae (Darwin, 1854: 355, 375; Hiro, 1938: 402). Baluk and Radwański (1967b: 691; 1967c: 486) revised *Pyrgoma*, dividing it into *Pyrgomina* (= *Megatrema* of Utinomi, 1967: 232) and *Pyrgoma* with its subgenera *Nobia* and *Daracia*. We recognize somewhat similar groupings, with minor differences in the arrangement of species, but all at the generic level. The relationships of the genera are indicated in Figure 5.

Pyrgoma s. s., *Nobia*, *Savignium*, *Hoekia*, and *Pyrgopsella* are Indo-Pacific shallow-water pyrgomoids. *Boscia* is a cosmopolitan pyrgomoid, having both shallow and deep-water representatives. The Indo-Pacific pyrgomoids differ morphologically from *Boscia* in having highly modified opercular valves and in lacking paired fissures ('sutures') in the sheath; they can be derived readily from Indo-Pacific creusoids (*Cantellius*, *Creusia*, *Hiroa*), as will be discussed, but they cannot be derived readily from *Boscia*. We infer that *Boscia* has had a separate origin—that is, that the Pyrgomatinae are at the least diphyletic. In contrast, the Indo-Pacific pyrgomoids apparently are related through two major lines derived from different creusoid lineages. Hence, we infer that the pyrgomoid level of organization has been achieved at least four times (Fig. 5).

Creusia, in the broad sense, contains the most generalized members of the Pyrgomatinae. Baluk and Radwański (1967c: 484) attempted a modest revision of *Creusia*, which they divided into the nominate subgenus and a new subgenus, *Withersia*. Their revision was based mainly on fossil forms, thereby considering only the Atlantic fauna and thus failed to come to grips with the Indo-Pacific *Creusia spinulosa* complex; and the natural groupings that exist within *Creusia* were overlooked. All of the Atlantic species, both living and fossil, form a natural unit for which the name *Ceratoconcha* is available. *Ceratoconcha* has relatively unmodified balanoid opercular valves of a characteristic type that differ markedly in form from what would be considered generalized balanoid valves of the Indo-Pacific forms contained within our newly proposed genus *Cantellius*. This indicates that the generalized or primitive creusoids are not closely related and if the creusoids descended from a common balanoid stock, they did so independently in the

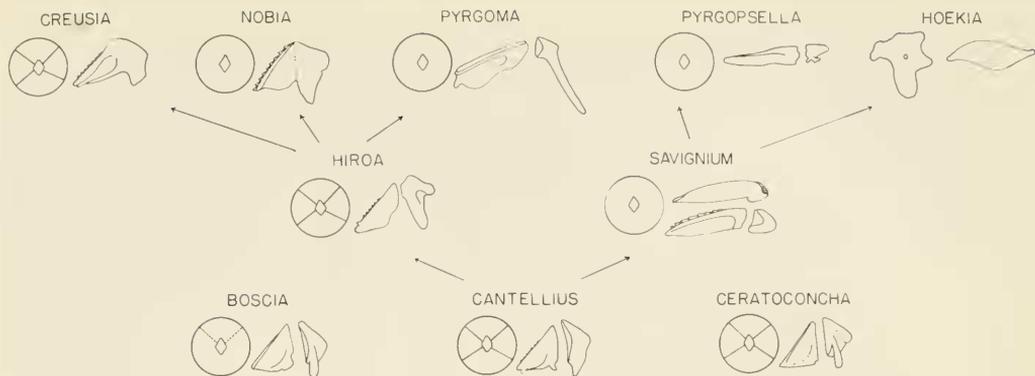


Figure 5. Diagram depicting inferred phylogenetic relationships within the Pyrgomatinae. The group or groups from which *Boscia*, *Ceratoconcha*, and *Cantellius* evolved remain unknown. The solid lines radiating from the orifice of the shell, shown in plan view, indicate relative position of the sutures separating the compartments; the dotted lines in *Boscia* indicate the position of the pseudoalae. Dotted lines on the opercular plates indicate a structures present in only a few species of that group.

Atlantic and the Indo-Pacific. Thus we set *Ceratoconcha* from the Atlantic apart and independent from the Indo-Pacific creusoid genus *Cantellius*, and consider the subfamily to be triphyletic (see Fig. 5).

Although *Ceratoconcha* has remained much the same throughout its history, the Indo-Pacific creusoids have undergone marked diversification. There is no fossil record to document the lineages leading to contemporary forms, but among Recent representatives there are sufficient forms upon which to draw inferences. First, there presently appears to be no reason to suggest that the Indo-Pacific creusoids are other than a natural group since they can be derived readily from one another. *Cantellius* is the most generalized and is envisaged as the stem from which the remaining genera evolved. Secondly, there are apparently two major lineages, one stemming from *Hiroa*, the other from *Savignium*;—that is, two parallel lines, each leading independently from *Cantellius* to pyrgomoid forms (Fig. 5). *Pyrgopsisella*, occurring in sponges, appears to be an offshoot of the *Savignium-Hoekia* line. The modifications that ensue in each line concern alterations in the form of the opercular valves and conrescence of the wall plates, presumably better adapting the barnacles to different host corals. Interestingly, the most modified form, *Hoekia*, has the most reduced wall plate, aperture, and opercular valves of any pyrgomoid. It has also modified its nutritional source, shifting from setose feeding to feeding directly on the tissues of the host coral (Ross and Newman, 1969: 255).

Baluk and Radwański (1967c: 465) believed that *Pyrgopsis annandalei* Gruvel (= *Pyrgopsisella* nom. nov., Zullo, 1967), dredged from 90m off the Andaman Islands, should not be assigned to the Pyrgomatinae because the basis is membranous. Gruvel (1907: 8) had three specimens, but the habitat and (or) actual relationship of the barnacle to the substratum were unknown. He inferred that the membranous elongate basis functioned as a peduncle or stalk, analogous to the fleshy stalk of *Xenobalanus*, by which the animal attached to the substratum. Indeed, Zullo (1967: 123) referred to *Pyrgopsisella* as an "unusual pedunculate balanid." Recently, however, Rosell (pers. comm., 1971) reported finding a new species of *Pyrgopsisella* imbedded in a sponge from the Philippines, and we believe that this explains the peculiar anatomical structure of the genus. The membranous stalk is not a "peduncle" in the sense used by Gruvel, but rather it is an elongate basis comparable to and serving the same function as the elongate basis of other Pyrgomatinae. In inhabiting sponges, rather than a coral, the basis is membranous rather than calcareous, analogous to the situation seen in *Membranobalanus* also inhabiting sponges. The single plate making up the wall and the pyrgomoid valves suggest that *Pyrgopsisella* is an off-shoot of the coral-inhabiting pyrgomatines. Indeed the valves are similar to those of *Savignium*, and it is from this genus that we infer it has evolved.

In summary then, the Pyrgomatinae are a diverse group of coral-inhabiting balanids, dominated by a central group of eight wholly Indo-Pacific genera stemming from *Can-*

tellius, and flanked by the cosmopolitan genus *Boscia* and the Atlantic genus *Ceratoconcha*. *Cantellius*, *Boscia*, and *Ceratoconcha* have rather generalized balanoid opercular valves, but there is no indication that one gave rise to the other. Rather it is inferred that they descended independently from balanoid ancestors, and therefore the subfamily is considered triphyletic. We can now ask from which balanines these three lines may have evolved.

There is ample evidence that the Pyrgomatinae have been derived from balanines; the rostrum overlaps the laterals, the opercular plates are balanoid, the labrum is notched, and the intromittant organ bears a basidorsal point. While the most primitive living balanid (*Chelonibia*) has eight plates making up the wall, it is apparently a specialized survivor of an ancient stock that presumably gave rise to the more typical balanines. The vast majority of typical balanines have six plates making up the wall, and it has generally been assumed that the Pyrgomatinae descended from some six-plated ancestor (Withers, 1929: 564; 1935: 38; Hiro, 1938: 402; Zullo, 1967: 127; Baluk and Radwański, 1967c: 504). Withers (1935: 38) suggested that *Balanus* (*Balanus*) *duvergieri* (Alessandri) might be such a form, and Zullo (1961: 72) proposed the subgeneric name *Hexacreusia* for *Balanus durhami*, a species he thought also likely to be such a form.

Balanus duvergieri, with its tubiferous wall and basis, appears to belong to the subgenus *Balanus*, where Withers placed it. The wall of all known pyrgomatines is solid; while tubes may be found in some species, they are formed between the sheath and the internal ribs or between external ribs of the wall and therefore are not homologous with the tubes of *Balanus*. All generalized pyrgomatines, except *Boscia anglicum*, have a solid basis. The opercular valves of *B. duvergieri* are generalized, resembling those of *Cantellius* more than those of *Boscia* and *Ceratoconcha*, but this is no doubt simply because *Cantellius* has the most generalized valves of any of the pyrgomatines. In light of the differences in the wall between *B. duvergieri* and the Pyrgomatinae, and in light of the evidence indicating that the Pyrgomatinae had a solid-walled ancestry, we must agree with Baluk and Radwański (1967c: 504) that *B. duvergieri* is not an ancestor of the Pyrgomatinae as Withers suggested, nor is it closely related to the stock from which the Pyrgomatinae must have been derived.

Balanus durhami appears closer than *B. duvergieri* to the stem line of the Pyrgomatinae since it has a solid wall and basis, and since the opercular valves are superficially comparable. If *B. durhami* had but four wall plates rather than six, would it then belong to the Pyrgomatinae, and if so, to which of the three major groups would it be assigned? It would belong to the Pyrgomatinae as presently defined, but it is not readily assignable to any one of the three existing divisions. The tergum, with broad spur and strongly developed depressor muscle crests, and the scutum, with a broadly developed adductor ridge descending from the occludent margin, differ markedly from the generalized types seen in the subfamily, so that *B. durhami* would have to be placed as a fourth and independent line. Although for different reasons, we agree with Baluk and Radwański (1967c: 504) that *B. durhami* is not a surviving ancestor of the Pyrgomatinae. Yet it is much closer to what must have been the balanine stock from which one or more of the Pyrgomatinae lines were derived, and it is therefore necessary to look closely at the affinities of *B. durhami*.

Zullo (1961: 75) stated that *B. durhami* resembles species of the subgenus *Armatobalanus* but differs from them in having the anterior margin of cirrus III toothed rather than only cirrus IV, and he placed it in a new subgenus, *Hexacreusia*.¹ However, when Zullo (1963: 590) described *B. (Armatobalanus) nefrens* from California, he noted that this species lacks hooks or spines on cirrus IV, as does *B. (A.) oryza* Broch from the southwest Pacific. Zullo (1967: 127) later noted that Darwin (1854) confused specimens of *B. durhami* with *B. (A.) allium* from the southwest Pacific. He stated that such species of *Armatobalanus*, as *terebratus* Darwin are so similar to *B. durhami* that it appears reasonable to assume that the armatobalanids were the ancestral stock from which the coral barnacles

¹We wholly concur that *Hexacreusia* and *Armatobalanus* are similar, and in fact, except for the development of the scutal adductor ridge in the former, there are no diagnostic differences between them. Rather than elevate *Hexacreusia* to generic rank as did Zullo, et al (1972: 72), we consider it synonymous with *Armatobalanus*. If *Armatobalanus* were raised to generic rank, it would be reasonable to consider *Hexacreusia* subgenerically distinct.

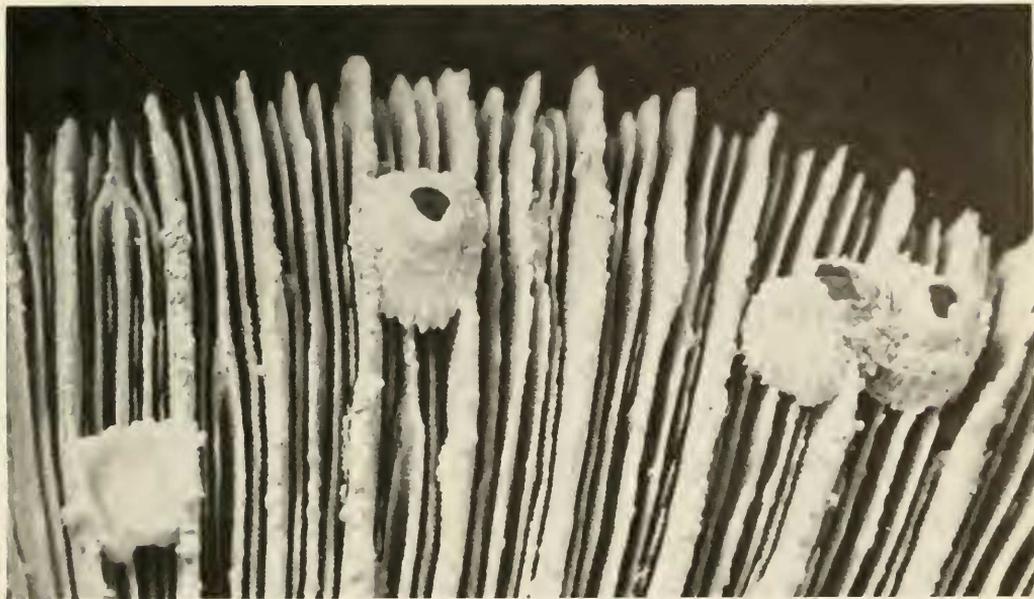


Figure 6. *Cantellius pallidus* on *Fungia fungites* (Linnaeus). Indo-west Pacific. Zoologisk Museum, Copenhagen.

were derived.

Darwin (1854: 282), Hiro (1938: 402), and Zullo (1967: 127) looked to *Armatobalanus* as the stem line from which the Pyrgomatinae evolved. Members of the subgenus are found in both the Atlantic and the Indo-Pacific, some occur exclusively on corals, and one is known from the late Miocene of the United States (Ross, 1965: 337). There is a fair diversity of opercular valves, and in general these bear a closer resemblance to those of *Cantellius* than to those of *Boscia* or *Ceratoconcha*. If the lines within the Pyrgomatinae have in fact evolved three times, it seems likely that at least the Indo-Pacific *Cantellius* and its derivatives and perhaps *Boscia* have an *Armatobalanus* ancestry. The affinities of *Ceratoconcha* are still too obscure to conjecture (see Newman and Ladd, in press).

SYSTEMATICS

Descriptions of the 54 or more species in this subfamily are not included here, because many require redescription and adequately preserved material is unavailable. To obviate the problem of deciding on the author's intent in relegating subspecific or infraspecific rank to a taxon (ICZN, Art. 45), we have blanketly endorsed all known nominal taxa, and accordingly assigned them appropriate rank. Our reasons for placing a nominal species or genus in synonymy are given in the remarks section under the respective taxon. For each species, following citation of the author and date of publication, we cite type locality and host-coral. A list of species incertae sedis follows the systematics section.

Family Balanidae, Leach, 1817

Subfamily Pyrgomatinae Gray, 1825

Balanidae Leach, 1817: 68, in part; Darwin, 1854a: 33, in part.

Pyrgomatidae Gray, 1825: 102, in part; Reichenbach, 1828: 89, in part.

Bifora Latreille, 1825: 234, in part.

Pyrgomacea Menke, 1830: 92, in part; Philippi, 1853: 424, in part.

Sessilia: Philippi, 1836: 247, in part.

Tetrameridae Gruvel, 1903: 159, in part; Alessandri, 1922: 226, in part.

Creusiinae Baluk and Radwański, 1967c: 468.

Definition.—Shell of four parietal plates with radii and alae, or totally con crescent, with or without carinal “pseudoalae” discernible in sheath; walls solid or tubiferous, the tubes occurring in one or more rows either between the sheath and internal ribs or between external ribs of wall; scutum and tergum either separate, cemented, or calcified together; basis membranous or calcareous, when calcareous cup-shaped and shallow or cylindrical and deep; labrum with deeply incised notch; intromittant organ with basi-dorsal point. Obligatory symbionts or parasites primarily of scleractinian corals. (One species occurs on a hydrocoral, another on a sponge.) Type genus: *Pyrgoma* Leach, 1817.

Key to Genera of Pyrgomatinae

1. Basis membranous (1 sp.) *Pyrgopsella*
1. Basis calcareous 2
2. Shell con crescent 3
2. Shell separable into 4 plates 7
3. Scutum at least twice as long as high 4
3. Scutum as long as high 5
4. Tergal spur well developed (1 sp.) *Pyrgoma*
4. Tergal spur rudimentary 6
5. Opercular plates balanoid, separable; tergum triangular (4 spp.) *Boscia*
5. Opercular plates modified, fused together; tergum quadrate (6 spp.) *Nobia*
6. Shell irregular in outline; aperture minute (1 sp.) *Hoekia* n. gen.
6. Shell regular in outline; aperture large (4 spp.) *Savignium*
7. Opercular valves fused (3 spp.) *Creusia*
7. Opercular valves not fused 8
8. Opercular valves highly modified (1 sp.) *Hiroa* n. gen.
8. Opercular valves balanoid 9
9. Scutum with basal margin entire, depressor muscle pit present, but no rostral tooth; tergum with broad pad in area normally occupied by depressor muscle crests (16 spp.) *Ceratoconcha*
9. Scutum with basal margin notched near basi-tergal angle, commonly with depressor muscle pit, and a rostral tooth; tergum without broad pad (17 spp.) *Cantellius* n. gen.

Cantellius n. gen.

Definition.—Wall of four plates, conical to flat; compartments separated by well defined radii; scutum varies from high triangular to transversely elongated, and bearing prominent adductor ridge and lateral depressor muscle depression; scutum commonly with rostral tooth and notch in basal margin near basitergal angle; spur of tergum essentially confluent with scutal margin, and about ½ width of basal margin; crests for tergal depressor muscles feebly developed or wanting.

Type species.—*Cantellius transversalis* (Nilsson-Cantell), 1938; Recent, Andaman Islands.

Etymology.—Named in honor of Carl August Nilsson-Cantell.

Species assigned to genus:

Cantellius acutum (Hiro), 1938: 398 (syn.: *Creusia spinulosa* var. 6 subvar. 2 Darwin, 1854: 379); Palao Islands, Caroline Islands; on *Acropora formosa*.

Cantellius arcuatum (Hiro), 1938: 395; Palao Islands, Caroline Islands; on *Porites capricornis*.

Cantellius brevitergum (Hiro), 1938: 397; Palao Islands, Caroline Islands; on *Acropora* sp.

Cantellius euspinulosum (Broch), 1931: 118 (syn.: *Creusia spinulosa* var. 1 Darwin, 1854: 377); Amboina, Molucca Islands; on *Herpetolitha* sp.

Cantellius gregarea (Sowerby), 1823 [no pagination] (syn.: *Creusia spinulosa* var. 3 Darwin, 1854: 378; *Creusia spinulosa pseudoseptima* Kolosváry, 1948: 362; *Creusia spinulosa pseudoseptima* [sic]: Kolosváry, 1951 lb: 292); near Kei Islands (5°31'S., 132°47'E.); on *Acropora cytherea*, type host here designated.

Cantellius iwayama (Hiro), 1938, p. 393; Palao Islands, Caroline Islands; on *Porites iwayamaensis*.

Cantellius madreporae (Borradaile), 1903: 443 (syn.: *Pyrgoma madreporae* [sic]: Nilsson-Cantell, 1938: 65); Hulule, Male Atoll, Maldive Islands; on *Madrepora* sp.

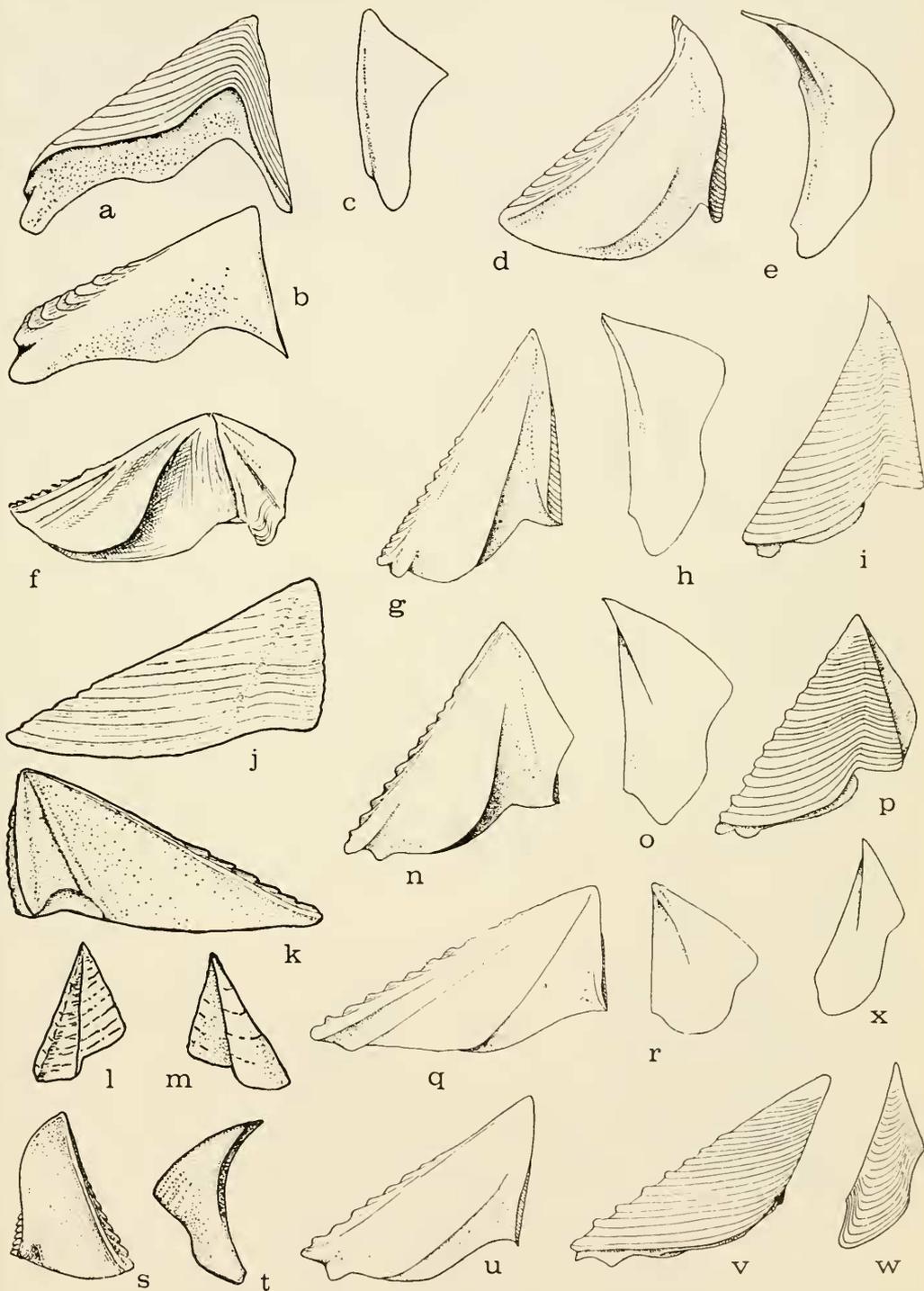


Figure 7. Opercular plates of *Cantellius*. a-c, *C. sextus*, after Hiro, 1938; d, e, *C. arcuatus*, after Hiro, 1938; f, *C. madreporarae*, after Borradaile, 1903; g-i, *C. euspinulosum*, after Hiro, 1938; j-m, *C. transversalis*, after Nilsson-Cantell, 1938; n-i, *C. iwayama*, after Hiro, 1938; q, r, *C. brevitergum*, after Hiro, 1938; s, t, *C. tredecimus*, after Kolosváry, 1947; u-x, *C. acutum*, after Hiro, 1938.

Cantellius octavus Ross and Newman, n. sp. (syn.: *Creusia spinulosa* var. 8 Darwin, 1854a: 380); type locality, distribution and host coral not known.

Cantellius pallidus (Broch), 1931: 118; Banda Sea (5°32'S., 132°37'E.); on *Pocillopora damicornis*, type host here designated.

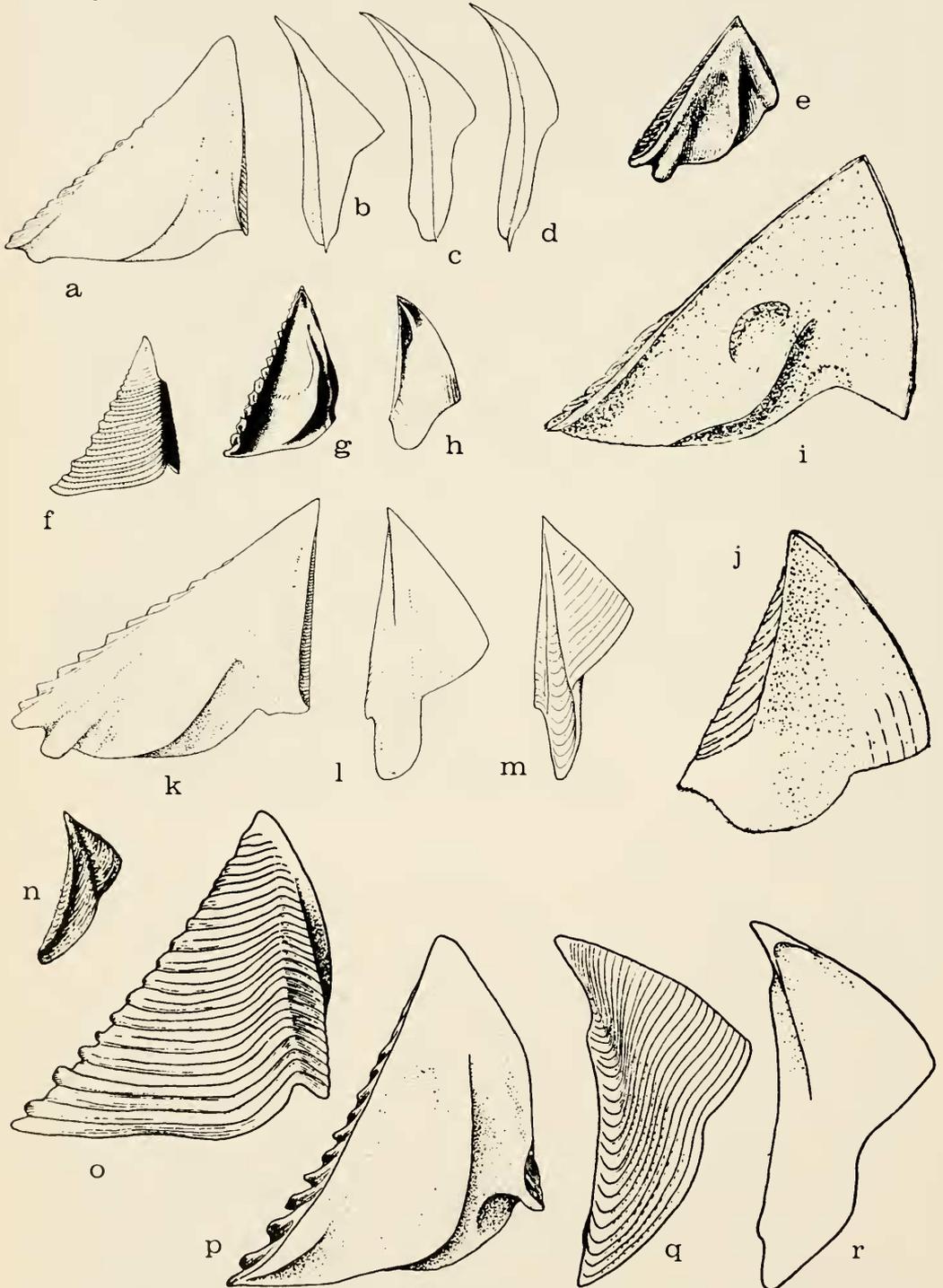


Figure 8. Opercular plates of *Cantellius*. a-d, *C. secundus*, after Hiro, 1938; e, *C. septimus*, after Darwin, 1854; f-h, *C. sumbawae*, after Hoek, 1913; i, j, *C. gregarea*, after Nilsson-Cantell, 1938; k-m, *C. septimus*, after Hiro, 1938; n, *C. quintus*, after Darwin, 1854; o-r, *C. pallidus*, after Hiro, 1935.

Cantellius quintus Ross and Newman, n. sp. (syn.: *Creusia spinulosa* var. 5 Darwin, 1854a: 379); type locality, distribution and host coral not known.

Cantellius pseudopallidum (Kolosváry), 1948: 362; Pacific area; on *Pavona varians*.

Cantellius secundus (Broch), 1931: 118 (syn.: *Creusia spinulosa* var. 2 Darwin, 1854: 378); off Naira, Banda Islands; on *Pavonia* sp.

Cantellius septimus (Hiro), 1938: 395 (syn.: *Creusia spinulosa* var. 7 Darwin, 1854: 380; *Creusia spinulosa duodecima* Kolosváry and Wagner, 1941: 9); Palao Islands, Caroline Islands; *Montipora* sp. cf. *M. cactus*.

Cantellius sextus (Hiro), 1938 (syn.: *Creusia spinulosa* var. 6 subvar. 3 Darwin, 1854: 379); Palao Islands, Caroline Islands; on *Pachyseris rugosa*.

Cantellius sumbawae (Hoek), 1913: 265; east of Dangar Besar, Saleh Bay; on *Heteropsammia* sp.

Cantellius transversalis (Nilsson-Cantell), 1938: 61 (syn.: *Creusia spinulosa* var. 6 subvar. 1 Darwin, 1854: 379); North Bay, Port Blair, Andaman Islands; on *Madrepora* sp.

Cantellius iredecimus (Kolosváry), 1947: 426; Island of Singapore; on *Tridacophyllia lactuca*.

Remarks.—*Cantellius* is proposed for those Indo-Pacific creusoids with unfused opercular valves of which the scutum commonly possesses a notch in the basal margin near the basi-tergal angle, a rostral tooth, an adductor ridge, and a lateral depressor muscle pit. The tergum has either feebly developed crests for the depressor muscles, or no crests.

In critically comparing the illustrations and brief description of *Creusia spinulosa duodecima* Kolosváry (1941: 9) with that of *Cantellius septima*, the authors find no differences that warrant continued recognition of *duodecima*. We also find, for the same reasons, that *C. spinulosa pseudoseptima* is synonymous with *C. gregarea*.

Hiroa n. gen.

Definition.—Wall of four plates, small, flat or low conical; parietal tubes present; sheath occupying whole inner wall; basis cylindrical and deep; triangular scutum high and elongated transversely; adductor ridge projecting below basal margin of valve; tergum narrow, with spur about ½ or less height of valve, lacking crests for depressor muscles; overall height of tergum greater than that of scutum and about equal in bulk to scutum.

Type species.—*Hiroa stubblingsi*, new species.

Etymology.—Named in honor of Dr. Fijio Hiro (= Huzio Utinomi), in appreciation of his numerous studies on the Pyrgomatinae.

Remarks.—*Hiroa* bridges the gap between *Cantellius* and the morphologically advanced Indo-Pacific creusoids and pyrgomids. In having a shell with four distinct plates, it is readily separable from *Nobia* and *Pyrgoma*. The bizarre development of the opercular plates, which are separate, distinguishes it from *Cantellius* on one hand, and from *Creusia* on the other.

Hiroa stubblingsi n. sp.

Diagnosis.—Because there is but a single known species, the diagnosis is the same as that for the genus.

Material.—Numerous specimens in *Stylophora* sp., type host; Ollan Island, Truk Islands, 7°14'N, 151°38'E, type locality; CARMARSEL Exped. sample CRS 811; 25 February 1967; coral blasted from base of seaward reef front at 8 m; c¹⁴ dating indicates age of less than 500 BP.

Description.—Specimens were entombed in coral so that the external surfaces of the wall could not be observed; wall of four plates, flat or low conic; outline ovate; rostracarinal diameter less than 5 mm, lateral diameter less than 3 mm; parietes non-tubiferous and thickened marginally, thinning toward aperture; sutural surfaces of radii strongly denticulate; sheath extending to basal margin of wall with basal edge depending freely.

Basis deep (greater than 26 mm); cylindrical; strongly ribbed internally; non-tubiferous; gradually expanding from point of initial growth.

Scutum high and transversely elongated (1.7 mm high x 1.6 mm wide); exterior surface sculptured with irregular, high, growth ridges; tergal margin about ½ length of basal; occludent margin coarsely toothed; internal surface smooth; slight indication of adductor muscle depression; adductor plate extends well below basal margin of valve proper; rostral angle of adductor plate slightly produced.

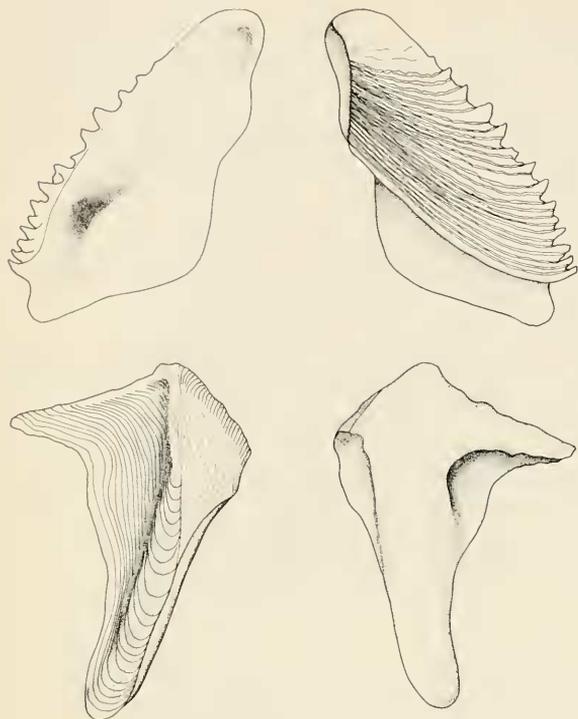


Figure 9. Opercular plates of *Hiroa stubbingsi* n. gen., n. sp.

Tergum T-shaped or narrowly triangular (2.3 mm high x 1.6 mm wide); external surface ornamented with irregular low growth ridges; external longitudinal furrow deep, steep-walled and open throughout its length; internal surface smooth, lacking crests for depressor muscles, deep depression present in area bordering basi-carinal angle.

Disposition of types.—The holotype and two paratypes are deposited in the collections of the National Museum of Natural History. The remaining paratypes are housed in the collections of Scripps Institution of Oceanography.

Etymology.—Named in honor of H. G. Stubbings, long-time student of the Cirripedia, on the occasion of his retirement.

Genus *Creusia* Leach

Creusia Leach, 1817: 68. Genus without originally included nominal species; first species assigned to genus: *Creusia spinulosa* Leach, 1818, Recent, type locality unknown, *ipso facto* type species by subsequent monotypy (Leach, 1818: 171).

Cerusia (error for *Creusia* Leach, 1817): Ranzani, 1818: 92; Ranzani, 1820: 56.

Creusa (error for *Creusia* Leach, 1817): Catlow, 1843: 39.

Definition.—Shell flat, ribbed, compartments separated by narrow radii; parietal tubes absent in small species, rarely present in larger ones; scutum and tergum calcified together without visible indication of line of juncture; adductor “plate” commonly extending below basal margin of valve; where plate extends below margin it is produced as basi-rostral tooth; no distinct lateral depressor muscle depression on scutum; tergal portion of valve somewhat quadrate, occupying $\frac{1}{2}$ or more of total area; basis oval, or nearly circular in outline and commonly deep.

Species assigned to genus:

Creusia decima Ross and Newman, n. sp. (syn.: *Creusia spinulosa* var. 10 Darwin, 1854: 381); type locality, distribution, and host coral not known.

Creusia indicum (Annandale), 1924: 64 (syn.: *Creusia spinulosa* var. 11 Darwin, 1854: 381; *Pyrgoma indicum* phase *merulinae* Annandale, 1924: 65; *Pyrgoma indicum* phase *symphylliae* Annandale, 1924: 65; *Creusia spinulosa angustiradiata* Broch, 1931: 118; *Creusia spinulosa angustiterga* [sic] Nilsson-Cantell, 1938: 63); Padaw Bay, King-Island, Mergui Archipelago; on *Favia valenciennesii*.

Creusia spinulosa Leach, 1818: 171 (syn.: *Creusia spinulosa* var. 9 Darwin, 1854: 380); type locality, distribution, and host coral not known.

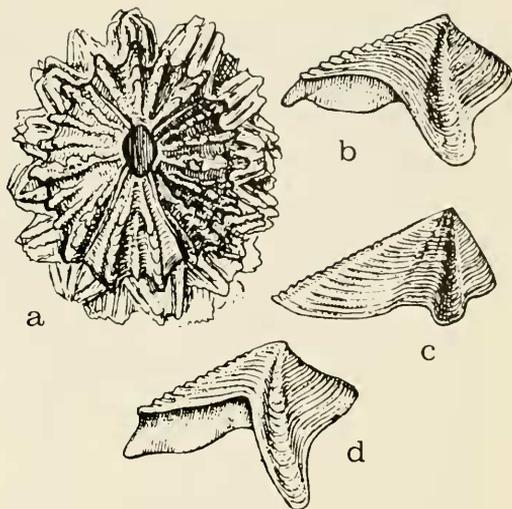


Figure 10. *Creusia*. a, b, shell and opercular plate of *C. indicum*; c, opercular plate of *C. spinulosa*; opercular plate of *C. decima*; all figures after Darwin, 1854.

Remarks.—The original definition of *Creusia* follows: “Testa quadripartita; operculum valvis unipartitis” (Leach, 1817: 68). This was later given by Leach (1818: 171) as: “Shell quadripartite; parts equal. Valves of the operculum unipartite. Base infundibuliformis.” In reference to Leach’s statement that the opercular valves are fused, Gray (1825: 103) stated, in his discussion of *C. spinulosa*, “Dr. Leach describes the valves of the operculum as soldered two and two, but they are not so in the Museum specimens.” Probably the opercular valves of the specimens in question, which are not necessarily a species of *Creusia (sensu stricto)*, are only cemented together, rather than calcified together, and this would account for the discrepancy between the two descriptions.

Of the 13 numbered varieties and sub-varieties of *C. spinulosa* described by Darwin (1854a), three have not been redescribed nor assigned formal names. For “variety 5” we propose the name *Cantellius quintus*; for “*C. spinulosa* var. 8,” the name *Cantellius octavus*; for “*C. spinulosa* var. 10,” the name *Creusia decima*.

Nilsson-Cantell (1938: 63) considered Annandale’s phase *merulinae* and phase *symphylliae* to be synonymous with *Creusia spinulosa angustiradiata*. This taxon is a junior subjective synonym of *C. indica*, as noted by Utinomi (1962: 227), who also followed Nilsson-Cantell’s suggestion in synonymizing Annandale’s several “phases.”

Genus *Nobia* Sowerby

Nobia Sowerby (ex Leach), 1839: 71. Type species: *N. [obia] grandis* Sowerby, Recent, Island of Singapore (type locality here designated), by monotypy.

Definition.—Shell flat or conical, ribbed or smooth, composed of one piece lacking all evidence of radii and alae; shell perched on basis; sheath applied directly to wall, extending to, or nearly to basis; opercular valves nearly of equal size and fused, with line of fusion invisible, or visible either externally, internally, or both; scutal portion of valve quadrate to subquadrate in outline; basis deep, cylindrical, and either exerted or flush with corallum.

Species assigned to genus:

Nobia conjugatum (Darwin), 1854: 364; Red Sea; on *Cyphastraea chalcidicum*.

Nobia grandis Sowerby, 1839: 71; Singapore; on *Galaxea musicalis*.

Nobia halomitrae (Kolosváry), 1948: 363; type locality and distribution unknown; on *Halomitra* sp.

Nobia kuri (Hoek), 1913: 259; near Kei Islands (5°28.4’S., 132°0.2’E.); on *Caryophyllia* sp.

Nobia orbicellae (Hiro), 1934: 367; Tanabe Bay, Japan; on *Goniopora* sp.

Nobia projectum (Nilsson-Cantell), 1938: 70; Persian Gulf; on *Caryophyllia* sp.

Remarks.—Sowerby’s (1839: 71) original definition of *Nobia* is: “This genus resembles *Pyrgoma*, Auct. consisting of a conical paries supported upon a funnel-shaped cavity in the madreporic, but differs in its operculum, which consists of two valves; whereas that of *Pyrgoma* has four.”



Figure 11. *Nobia grandis* on *Euphyllia fimbriata* (Spengler); Warrior Reef, Torres Straits, Australia; Museum Comparative Zoology coral 5685.

Genus *Pyrgoma* Leach

Pyrgoma Leach (ex Savigny MS), 1817: Genus without originally included nominal species; first species assigned to genus: *Pyrgoma cancellata* Leach, 1818, Recent, Indo-Pacific, *ipso facto* type species by subsequent monotypy (Leach, 1818, 171; and by subsequent designation of Brooks and Ross, 1960: 354).

Pyrgone (error for *Pyrgoma* Leach, 1817): Ferrusac, 1822: 144.

Pyrgona (error for *Pyrgoma* Leach, 1817): Catlow, 1843: 39.

Pyrgomum (error for *Pyrgoma* Leach, 1817): Darwin, 1854: 364 (footnote).

Pyrogoma (error for *Pyrgoma* Leach, 1817): Kolosváry and Wagner, 1941: 12; Kolosváry, 1943: 95.

Pyigoma (error for *Pyrgoma* Leach, 1817): Johnson, 1963: 95.

Definition.—Shell large, flat to sub-conical, plates totally fused; short adpressed sheath covers about 1/5 height of inner wall; parietal tubes present; triangular scutum high and elongated transversely; adductor ridge projecting below basal margin of valve; tergum extremely narrow, with spur $\frac{2}{3}$ to $\frac{3}{4}$ height of valve; lacking crests for depressor muscles; overall height of tergum greater than that of scutum, but about $\frac{1}{2}$ bulk of scutum.

Species assigned to genus:

Pyrgoma cancellata Leach, 1818: 171 (syn.: *Pyrgoma lobata* Gray, 1825: 102; *Pyrgoma cancellatum* var. *japonica* Weltner, 1897: 255); Sirahama, Honshu Island, Japan, type locality here designated; on *Turbinaria contorta*.

Remarks.—Leach's (1817: 68) original definition of *Pyrgoma* is: "Testa unipartita; operculum valvis bipartitis." In subsequent publications Leach (1818, 1825) neither enlarged nor amplified this description.

Pyrgoma cancellata is the only species assigned to this genus. The unusual development of the opercular valves, especially the tergum, and the concrescent shell, serve to distinguish it from those species previously referred to *Pyrgoma*.

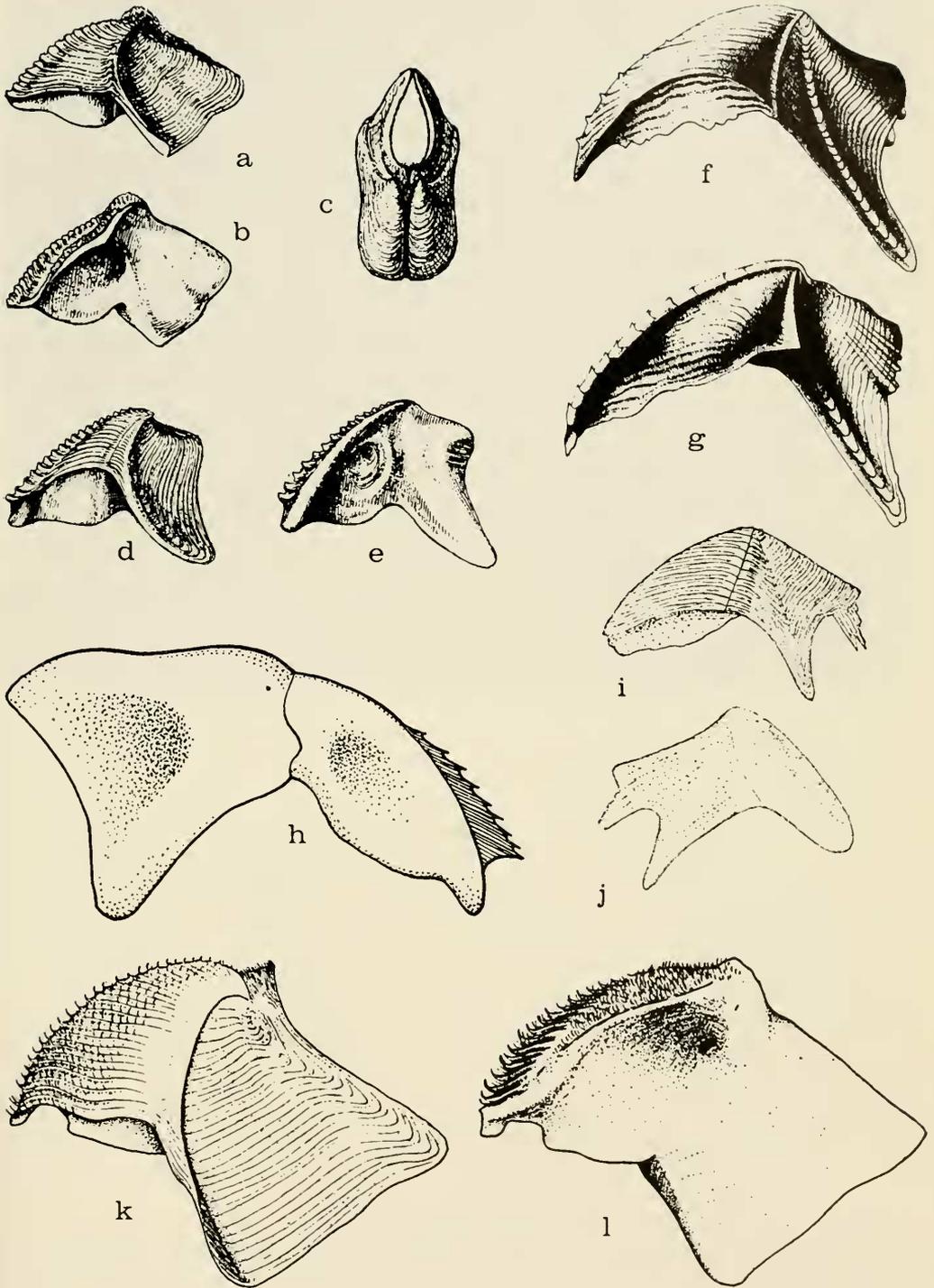


Figure 12. Opercular plates of *Nobia*. a-c, *N. grandis*, after Darwin, 1854; d, e, *N. conjugatum*, after Darwin, 1854; f, g, *N. kuri*, after Hoek, 1913; h, *N. halomitrae*, after Kolosváry, 1948; i, j, *N. projectum*, after Nilsson-Cantell, 1938; k, l, *N. orbicellae*, after Hiro, 1935.



Figure 13. *Pyrgoma cancellata* Leach on *Dendrophyllia micranthus grandis* Crossland; Great Barrier Reef, Australia; Zoologisk Museum, Copenhagen.

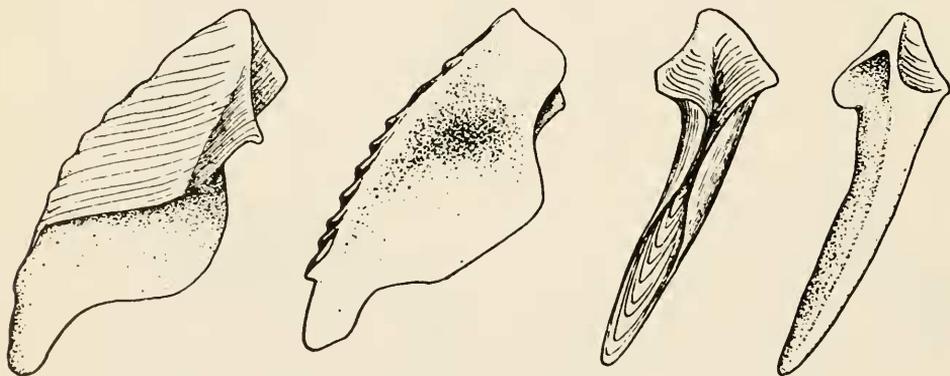


Figure 14. Opercular plates of *Pyrgoma cancellata*, after Hiro, 1935.

Genus *Savignium* Leach

Savignium Leach, 1825 (not Sowerby, 1823, *nomen nudum*): 210. Genus without originally included nominal species; first species assigned to genus: *D. [aracia] linnaei* Gray, 1825 [= *Savignium crenatum* Sowerby, 1823], Recent, Island of Singapore (type locality here designated), *ipso facto* type species by subsequent monotypy (Gray, 1825: 102).

Daracia Gray, 1825: 102. Type species: *D. [aracia] linnaei* [= *Savignium linnaei* = *Savignium crenatum* Sowerby, 1823], Recent, Philippine Archipelago, by monotypy.

Doracia (error for *Daracia* Gray, 1825): Weltner, 1897: 278.

Definition.—Shell totally fused, flat, oval in outline; lower margin of sheath free, extending nearly to basal edge of wall; opercular valves separate, cemented, or fused to-

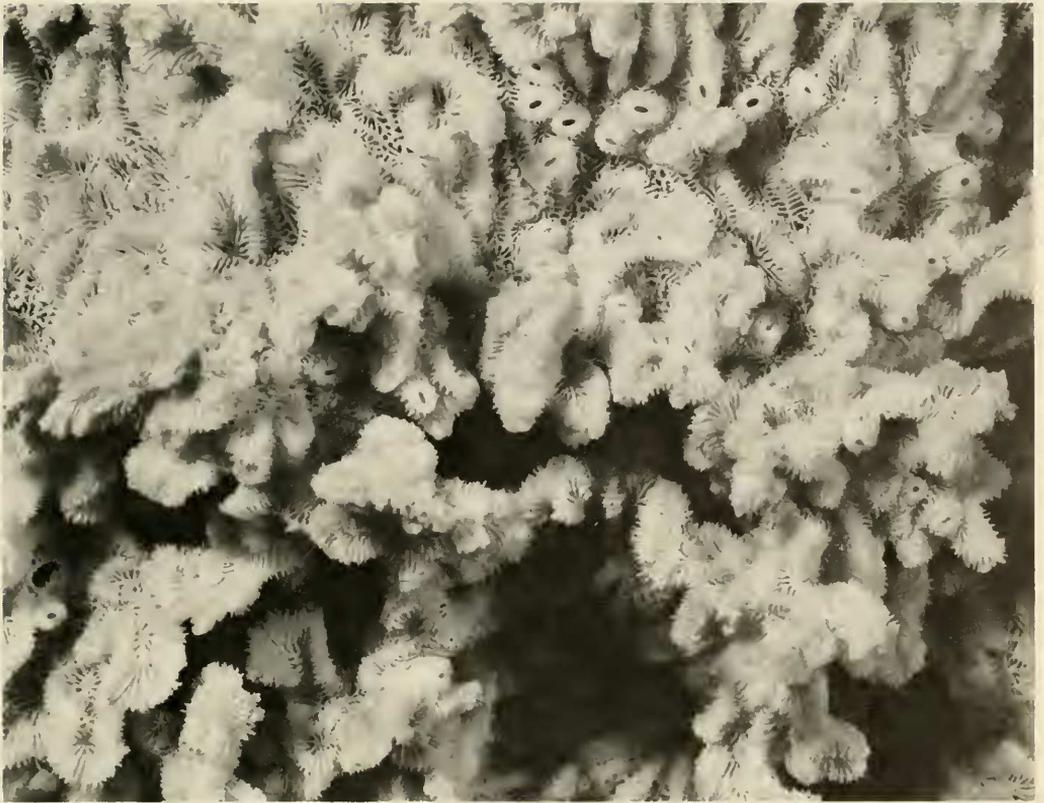


Figure 15. *Savignium crenatum* on *Merulina ampliata* Ellis and Solander; Singapore; American Museum coral 1868.

gether; scutum transversely elongated, its overall length exceeding that of tergum; tergum variable, commonly lacking definitive spur and lacking crests for depressor muscles; scutum comprising bulk of operculum; basis commonly deep and cylindrical.

Species assigned to genus:

Savignium crenatum Sowerby, 1823, no pagination (syn.: *Pyrgoma crenatum* phase *tridacophylliae* Annandale, 1924: 66; *Pyrgoma crenatiformis* Kolosváry, 1951: 287); Singapore, type locality here designated; on *Tridacophyllia lactuca*.

Savignium dentatum Darwin, 1854: 369; Red Sea; on *Meandrina spongiosa*.

Savignium elongatum Hiro, 1931: 154; Sirahama, Honshu Island, Japan; on *Madrepora* sp.

Savignium milleporae Darwin, 1854: 367 (syn.: *Pyrgoma millepora* [sic]: Nilsson-Cantell, 1938: 65; *Pyrgoma milleporae* forma *typica* Kolosváry, 1950: 292; *Pyrgoma milleporae* forma *snelliusi* Kolosváry, 1950: 292); Mindoro Island, Philippine Archipelago; on *Millepora complanata*.

Remarks.—After Leach (1817, 1818) published his first two studies on the Cirripedia he subdivided *Pyrgoma* and proposed the genera *Savignium*, *Megatrema*, and *Adna*. Although he did not publish these names until 1825, he did leave labeled specimens in the British Museum (Natural History) collections (see Sowerby, 1823; Gray, 1825: 107). Sowerby (1823) found “. . . upon examining the collection of Cirripedes, in the British Museum, as it now remains arranged by Leach himself, that since the publication of the ‘Supplement to the Encyclopedia Britannica,’ where the characters of the genus [*Pyrgoma*] first appear in print, he [Leach] had divided into four; upon what grounds we must acknowledge ourselves entirely ignorant, except it be from some differences in the form of the shell, and the valves of the operculum . . . We do not consider . . . these four genera . . . sufficiently distinct to constitute several genera . . . wherefore we still include all above enumerated [*Megatrema*, *Savignium*, and *Adna*] under the denomination of *Pyrgoma*.”

Sowerby is not considered the author of *Megatrema*, *Savignium*, or *Adna*, although his publication has priority, because, “A name first published as a synonym is not thereby



Figure 16. *Savignium milleporae* on *Millepora* sp.: Heron Island, Great Barrier Reef, Australia.

made available unless prior to 1961 it has been treated as an available name with its original date and authorship, and either adopted as the name of a taxon or used as a senior homonym" (Article 11 (d), ICZN). Sowerby's use of the specific names, *Savignium crenatum* and *Adna anglica*, suggested by Leach, on the other hand, entitles him to the authorship of these.

Leach's second synopsis of the Cirripedia, published in July of 1825, contained brief descriptions of *Savignium*, *Megatrema*, and *Adna*. At the same time Leach was working on his manuscript, Gray (1825) was also preparing a synopsis of the Cirripedia, which was published in the August issue of the *Annals of Philosophy*. In his synopsis, Gray (1825: 102) described the genus *Daracia* as follows: "*Daracia*, Gray, *Savignium*, Leach, without character. Valves of the body of the shell, four, soldered together." This description compares favorably with Leach's abbreviated description of *Savignium*: "Testa indivisa: basis immersa, valvae indivisae" (1825: 210). The only species mentioned by Gray in connection with the definition of *Daracia* is *linnaei*, which is not described. In the discussion of *Pyrgoma*, Sowerby (1823) made reference to *Savignium crenatum*, which he attributed to the authorship of Leach. That Gray referred to the same specimens as did Sowerby, who figured them, seems probable at this time, and Gray more than likely based his concept of *D. linnaei* on these specimens. Therefore, we believe that Gray's *D. linnaei* is actually a junior objective synonym of *Savignium crenatum*. It should also be noted that Gray, proposed *Daracia* as a replacement name for *Savignium* (see Gray 1825: 102, footnote).

Based on the general aspects of barnacles overgrown by a milleporine, Darwin (1854: 366) suspected Chenu's (1843) *Creusia madreporarum* to be synonymous with his *Pyrgoma milleporae*. Chenu, questionably, ascribed this taxon to the authorship of Leach, and his illustration speaks favorably of its being the same as Darwin's taxon. So far as we have been able to determine, the only pyrgomatid reported from a milleporine is *P. milleporae*. In the interests of stability, although recognizing that *C. madreporarum* has priority, Darwin's name is used here.

Two forms of *Pyrgoma milleporae* were designated by Kolosváry (1951: 292), *typica* (= *P. milleporae milleporae*) and *snelliusi*. These are not recognized here because the morphological variations recorded fall within the limits of variation assumed to correlate with different infrageneric milleporine associations.

In the coral collections of the American Museum there are two large specimens of *Merulina ampliata* (cat. no. 1868 and 3214) from the Island of Singapore infested with pyrgomatids. Our study of these indicated that they are conspecific with *Pyrgoma crenatum*. In 1951 Kolosváry described *P. crenatiformis* from the coral *Merulina ampliata*, col-

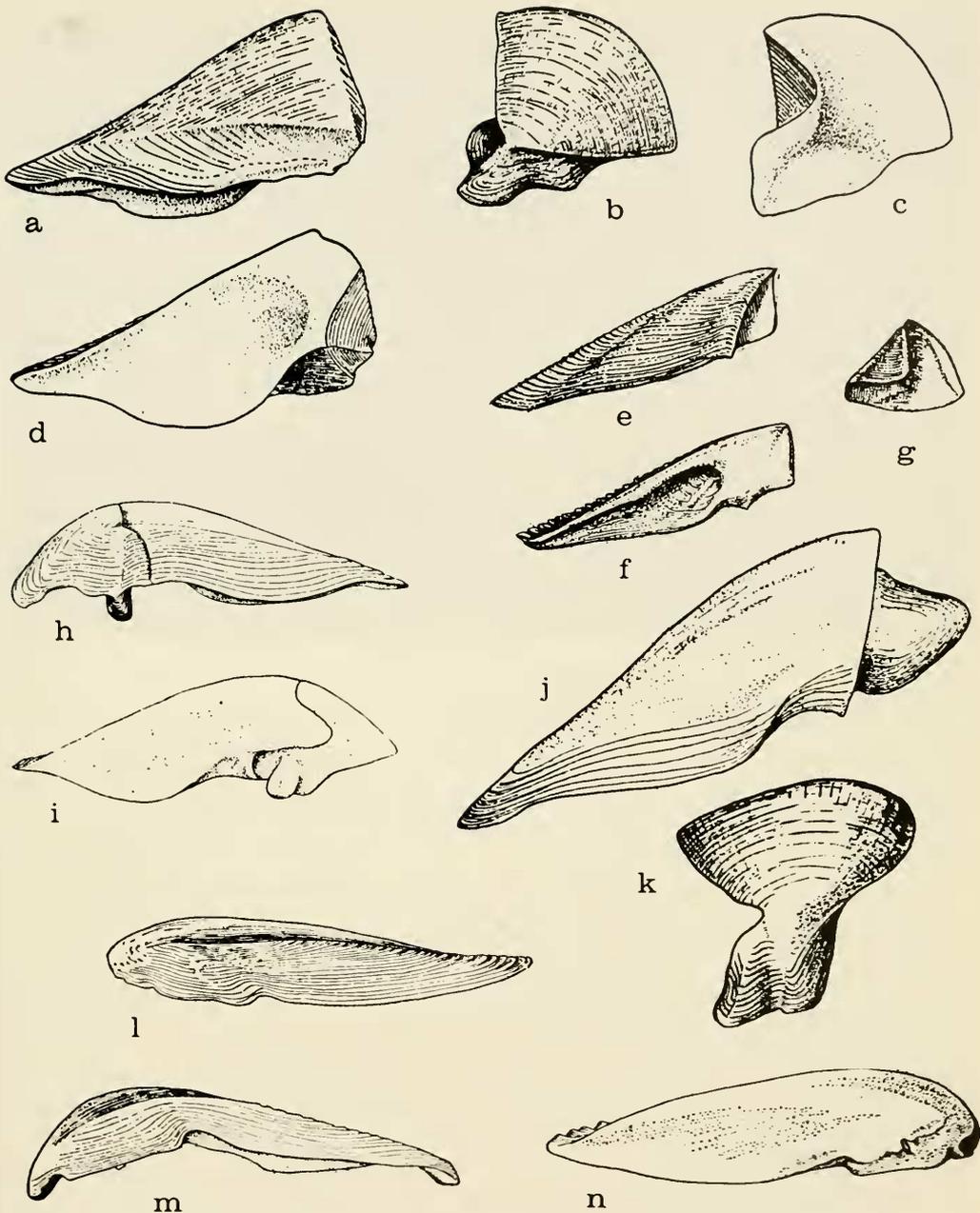


Figure 17. Opercular plates of *Savignium*. a-d, *S. crenatum*, after Hiro, 1935; e-g, *S. milleporae*, after Darwin, 1854; h-k, *S. dentatum*, after Hiro, 1935 and 1938; l-n, *S. elongatum*, after Hiro, 1938.

lected in the vicinity of the Island of Singapore. Comparison of our specimens with Kolosváry's illustrations and brief description does not reveal differences that enable one to separate these two species.

Hoekia n. gen.

Definition.—Shell totally con crescent, irregularly lobate in outline, and exhibiting no definitive peripheral shape; region surrounding minute ovate orifice elevated above externally flat or undulatory surface of shell; sheath short, adpressed, basal margin not depending freely; irregularly scattered wall tubes occur at varying distances from shell

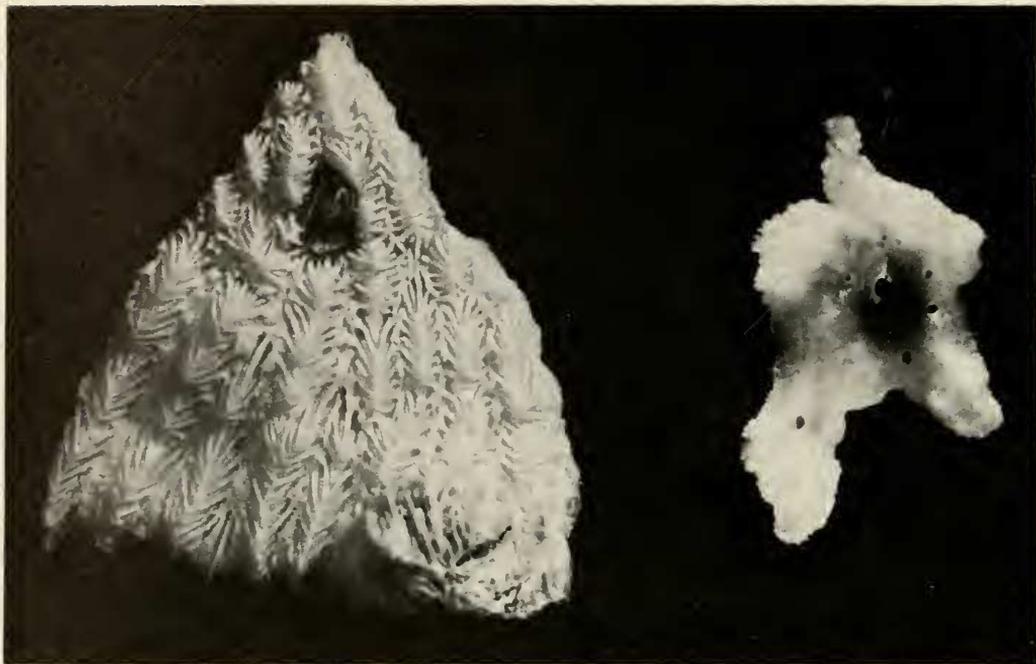


Figure 18. *Hoekia monticulariae*. Left, on *Hydnophora exesa* (Pallas); Mortensen Java-South Africa Expedition 1929-30; Station 44, Flat Island, Mauritius; Zoologisk Museum, Copenhagen. Right, internal view of shell from *Hydnophora exesa*; Singapore; American Museum coral 1883.

margin; operculum minute; scutum and tergum fused without evidence of suture, forming elongate valve with broad occludent ledge; tergal end of valve lacking spur.

Etymology.—This taxon honors the late Dutch cirripedologist Paulus Peronius Cato Hoek (1851-1914).

Type species.—*Pyrgoma monticulariae* Gray, 1831, Recent, Island of Singapore.

Species assigned to genus:

Hoekia monticulariae (Gray), 1831: 6; Singapore; on *Hydnophora exesa*.

Remarks.—The gross differences between the shell and opercular valves of *monticulariae* and those of other Pyrgomatinae are of sufficient magnitude to warrant its separation as a distinct genus (see Ross and Newman, 1969).

Although Baluk and Radwański (1967b: 487) resurrected the name *Daracia* to include *Pyrgoma monticulariae* and *P. elongatum*, it is readily apparent that not only was *Daracia* proposed as a replacement name for *Savignium* (see Gray, 1825: 102, footnote), but also the type species *D. linnaei* appears to be a junior objective synonym of *S. crenatum*. Consequently, we feel justified in proposing a new taxon.

Hoekia is allied morphologically to *Savignium* in that the fused opercular valves show some affinity to those of *S. crenatum*, *S. dentatum*, and less so to *S. milleporae*, as pointed out by Darwin (1854a: 374). But, in these species the valves are separate or only cemented together.

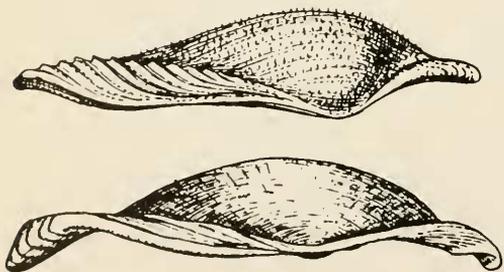


Figure 19. Opercular plate of *Hoekia monticulariae*: top, after Darwin, 1854; bottom, after Hiro, 1935.

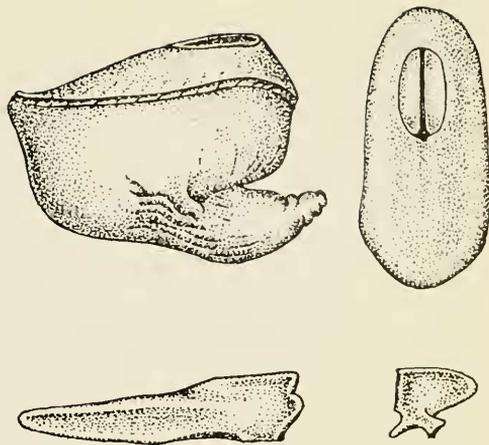


Figure 20. Shell and opercular plates of *Pyrgopsella annandalei*, redrawn after Gruvel, 1907.

Aside from the fact that *H. monticulariae* is the only known wholly parasitic balanid, the trophi of this species depart radically from those of other pyrgomatines (Ross and Newman, 1969: 255). Apparently, critical study of the mouth field should provide additional and independent criteria for recognition of pyrgomatine generic groups. Our preliminary studies of species having morphologically primitive shells indicate that the trophi of these depart little from that of many primitive balanids (see Broch, 1924, fig. 10).

Genus *Pyrgopsella* Zullo

Pyrgopsis Gruvel, 1907: 8. Type species: *Pyrgopsis annandalei* Gruvel, Recent, Andaman Islands, by monotypy.

Pyrgopsella Zullo, 1967: 109 (substitute name for *Pyrgopsis* Gruvel, 1907, not Rochebrune, 1884).

Definition.—Wall subconical, rostro-carinally elongate, smooth, composed of numerous calcareous rods contained in a chitinous envelope continuous with basis; basis elongate and membranous; opercular plates separate, well calcified, scutum transversely elongated; tergum triangular with short irregular spur; living in sponges.

Species assigned to genus:

Pyrgopsella annandalei (Gruvel), 1907: 8; Andaman Islands; host unknown.

Remarks.—The remarkable feature in *Pyrgopsella* is the membranous basis that Gruvel (1907: 9) thought served as a peduncle. Rosell (pers. comm.) recently discovered a new species of *Pyrgopsella* living in a sponge in the Philippines, and from this it is clear that the function of the elongate membranous basis is comparable to that of the elongate calcareous basis of the other pyrgomatines, and that being membranous is simply a secondary adaptation to living in sponges as opposed to corals.

Utinomi (1943: 16) studied the post larval settlement stages in *Creusia indicum*, and found the basis to be initially cup-like and wholly membranous. It is evident that calcification of the basis is delayed, at least in *C. indicum*, and hence it is not difficult to envisage that in *Pyrgopsella* ontogenetic suppression of calcium deposition would result in a membranous basis.

The general shape of the shell and the opercular plates of *Pyrgopsella* are similar to those found in *Savignium dentatum*. From the morphology of the hard parts it is apparent that *Pyrgopsella* was derived from *Savignium*.

Genus *Boscia* Ferussac

Boscia Ferussac, 1822: 145. Type species: *Balanus madreporarum* Bosc, 1812 [= *Boscia madreporarum* (Bosc)], Recent, Caribbean-western Atlantic, by monotypy.

Megatrema Leach, 1825 (not Sowerby, 1823, *nomen nudum*): 210. Genus without originally included nominal species; first species assigned to genus: *M. [egatrema] stokesii* Gray, 1825 [= *Boscia madreporarum* (Bosc), 1812], Recent, Caribbean-western Atlantic; *ipso facto* type species by subsequent monotypy (Gray, 1825: 102), and subsequent designation of Philippi (1853: 424).

Adna Leach, 1825 (not Sowerby, 1823, *nomen nudum*): 210. Genus without originally included nominal spe-

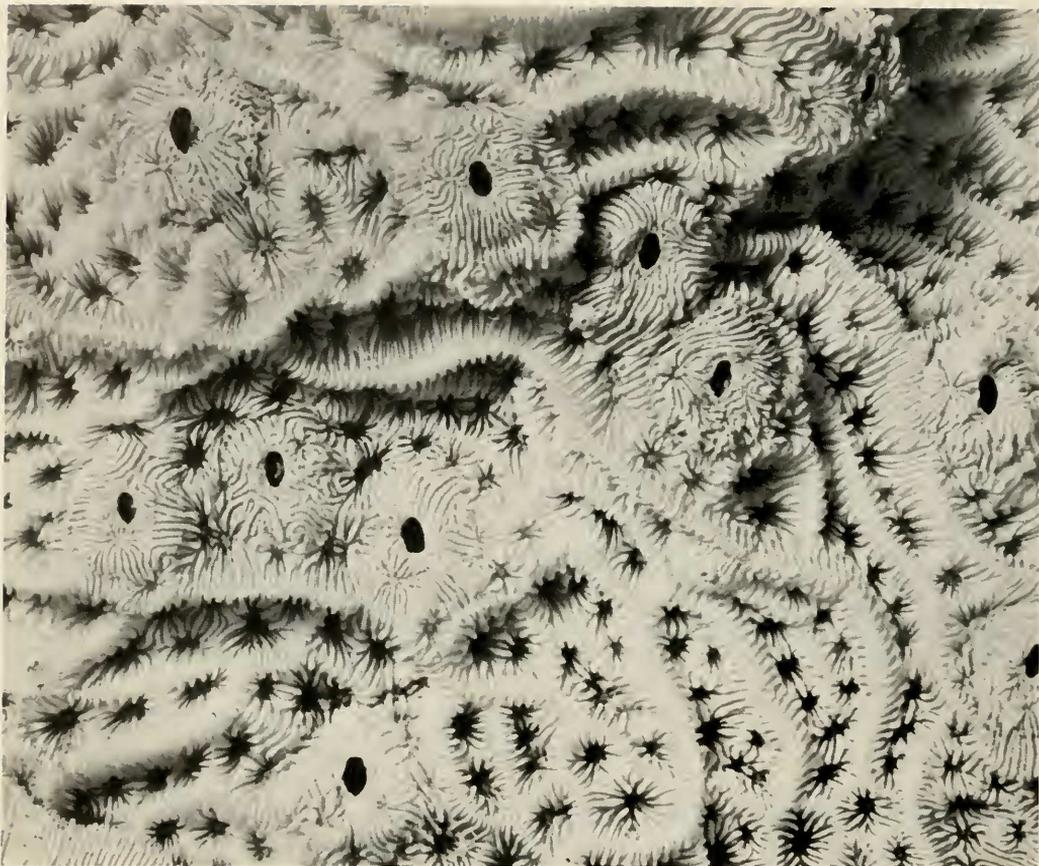


Figure 21. *Boscia madreporarum* on *Agaricia agaricites* (Linnaeus); Dry Rocks, off Key West, Florida.

cies; first species assigned to genus: *M. [egatrema] (A. [dna]) anglica* Gray, 1825 [= *Boscia anglicum* Sowerby, 1823]. Recent, coast of Devonshire, England; *ipso facto* type species by subsequent designation of Philippi (1853: 424).

Pyrgominia Baluk and Radwański, 1967b: 691. Type species: *Pyrgominia seguenzai* Baluk and Radwański, 1967 [= *Boscia seguenzai* Baluk and Radwański], by original designation, Pliocene, Island of Crete, Greece.

Definition.—Shell conical in juveniles and commonly flat or low conical in later stages; shell plates totally fused externally; pseudo-alae may be present; sheath adpressed and covering $\frac{2}{3}$ to entire inner wall; opercular valves typically balanoid; terga lacking depressor muscle crests; basis cup-shaped or sub-cylindrical, exserted or flush with corallum.

Species assigned to genus:

Boscia anglicum Sowerby, 1823 [no pagination] (syn.: *Pyrgoma sulcatum* Philippi, 1836, pl. 12, fig. 24; *Pyrgoma undatum* Michelotti, 1839: 140-141); coast of Devonshire, England; on *Caryophyllia smithii*.

Boscia madreporarum (Bosc), 1812: 66 (syn.: *Creusia boscii* DeBlainville, 1824: 378; *Pyrgoma stokesii* Gray, 1825: 103; *Creusia decorata* Chenu, 1843 [no pagination]; *Pyrgoma stockesi* [sic]; Kruger, 1940: 382); "Amérique" [= Caribbean western-Atlantic]; on *Agaricia agaricites*.

Boscia oulastreae (Utinomi), 1962: 83; Nomosaki, Kyushu Island, Japan; on *Oulastrea crispata*.

Boscia seguenzai (Baluk and Radwański), 1967b: 691; Gournes, Island of Crete, Greece; Pliocene.

Remarks.—Ferussac's (1822: 14) original description of *Boscia* follows: "Test univalve en cones tres-surbaisse, a parois tubuleuses; articule avec la base. Celle-ci, plus grande, en forme de godet ou de cupule."

In the year following the publication of *Boscia*, Sowerby (1823) published two manuscript names of Leach: *Megatrema* and *Adna*. When Sowerby described *Megatrema* he failed to mention any nominal species. Subsequently, *stokesii* was assigned to the genus (Gray, 1825: 103). However, it appears that *Megatrema stokesii* is a junior subjective syn-



Figure 22. *Boscia madreporarum* (= *Pyrgoma stokesii*). Top, slab with several shells and opercular valves mounted and identified by Darwin; bottom right, external view of shell shown at top center of slab; bottom left, internal view of shell shown at top left of slab. British Museum (Nat. Hist.) 1962. 12.7.1.

onym of *Boscia madreporarum*, because there are no differentiating morphological features, and because it occurs on the same host coral, *Agaricia agaricites* (Linnaeus), in the same geographical region.

Adna was described by Sowerby (1823) as a subjective synonym of *Pyrgoma*. However, Sowerby is regarded as the author only of the specific name *anglica* (see Article 11(d), ICZN). Leach, who originally proposed *Adna*, did not publish the name until 1825. At that time no nominal species was assigned to the genus. Gray (1825: 103) included only one species, *Adna anglica*.

The manner in which Gray (1825: 103) cited the taxon *Adna* suggests that it was to be recognized as a subgenus of *Megatrema*. He did not state why this, rather than a generic assignment was made, nor did Darwin (1854: 360) who also cited *Adna* as a subgenus.

Leach's original definition of *Megatrema* is "Testa indivisa: basis immersa, valvae Balani," while that of *Adna* is: "Testa indivisa: basis exserta, valvae Balani" (1825: 210). The only difference between the two, as proposed by Leach, is in the basis, which in *Adna* is not flush with the surface of the corallum.

Of the pyrgomatids known to Darwin (1854a: 355), only *Pyrgoma stokesii* (= *Boscia madreporarum*) and *P. anglicum* (= *B. anglicum*), "... have some claims to be generically separated from the other species of *Pyrgoma* ..." This opinion was based on the similarity of the operculum, and the conical shells which internally exhibit carinal pseudodeltae. The authors have adopted Darwin's suggestion and maintain these two species, in addition to *Boscia oulastreae* and *B. seguenzai* in a distinct genus.

What has been interpreted as carinal sutures are a pair of lines where the arthrodival

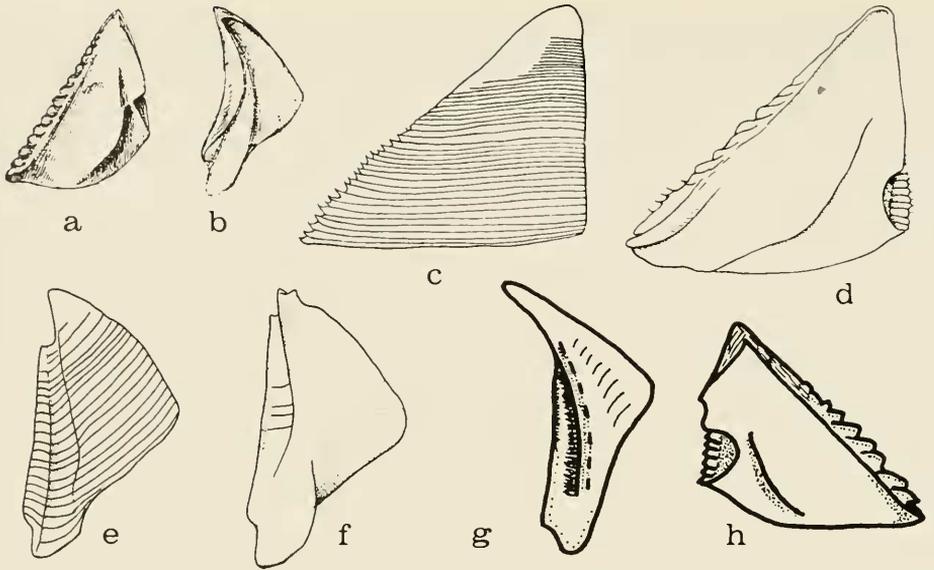


Figure 23. Opercular plates of *Boscia*. a, b, *B. anglicum*, after Darwin, 1854; c-f, *B. oulastrae*, after Utinomi, 1962; g, h, *B. madreporarum*.

membranes of the scuta and terga attach to the sheath. As the operculum is carried basally with growth of the sheath, the lines remain marking the points of earlier attachment. These lines could represent vestiges of the suture, but they appear only in the sheath and not the wall. When the shell is ground transversely, the area beneath the lines has a folded appearance; the overlapping portion being termed a pseudoala.

Genus *Ceratoconcha* Kramberger-Gorjanovic

Ceratoconcha Kramberger-Gorjanovic, 1889: 50. Type species: *Ceratoconcha costata* Kramberger-Gorjanovic [= *Creusia krambergeri* nom. nov. = *Ceratoconcha krambergi* (Baluk and Radwański, 1967: 145)], Miocene, Yugoslavia, by monotypy.

Paracreusia Abel, 1927: 101. Type species: *Paracreusia trolli* Abel [= *Ceratoconcha trolli* (Abel)], Miocene, Italy, by monotypy.

Andromacheia Kolosváry, 1949: 4. Type species: *Andromacheia noszkyi* Kolosváry [= *Ceratoconcha noszkyi* (Kolosváry)], Upper Miocene, southern Hungary, by monotypy.

Withersia Baluk and Radwański, 1967c: 485. Type species: *Creusia barbadensis* Withers, Pleistocene, Barbados by original designation.

Definition.—Shell of four compartments separated by radii and alae, the latter trending toward reduction in size; shell ribbed, ranging from conical to nearly flat; sheath approximately $\frac{1}{2}$ height of wall, with basal margin depending freely; well developed ribs may occur on inner surface of shell and extend from base to sheath; opercular valves typically balanoid; rostral tooth of scutum either inconspicuous or wanting; well developed lateral depressor muscle pit present; tergum commonly bears a prominent ridge or plate on carinal segment, rather than depressor muscle crests; basis commonly deep and cylindrical.

Species assigned to genus:

†*Ceratoconcha barbadensis* (Withers), 1926: 2 (syn.: *Creusia barndensis* [sic]; Nilsson-Cantell, 1938: 63); Barbados, West Indies; Pleistocene.

†*Ceratoconcha costata* (Sequenza), 1876, p. 316 (syn: *Creusia costata elargata* (Sequenza), 1876: 317; *Creusia moravica* Prochazka, 1893: 20; *Creusia spinulosa* forma *praespinulosa* Kolosváry, 1949: 1, fig. 5 only; *Creusia spinulosa* forma *kojumidgievae* Kolosváry, 1962: 86); Messina, Italy; Pliocene (Astian).

†*Ceratoconcha darwiniana* (Prochazka), 1893: 23; Leibnitz, Australia; Miocene.

†*Ceratoconcha diploconus* (Sequenza), 1876: 322; Messina, Italy; Pliocene (Astian).

Ceratoconcha domingensis (Des Moulins), 1867: 307; Port-au-Prince, Haiti; on *Porites astreoides*.

Ceratoconcha floridanum (Pilsbry), 1931: 81; Gulf of Mexico; on *Maeandra* sp. cf. *M. areolata*.

†*Ceratoconcha krambergeri* (Baluk and Radwański), 1967a: 145 (see Kramberger-Gorjanovic, 1889: 50); Podsused, Yugoslavia; Miocene.

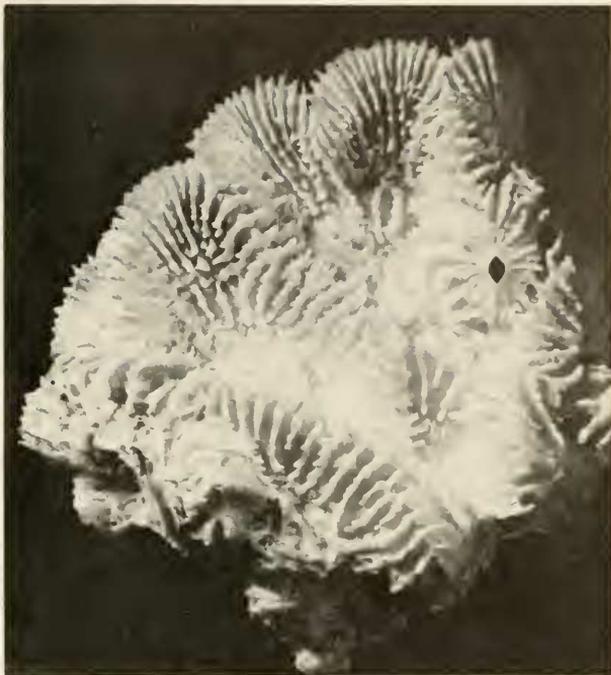


Figure 24. *Ceratoconcha floridanum* on *Mycetophyllia lamarekana* Milne-Edwards and Haime; Recent, Florida Keys.

†*Ceratoconcha miocaenica* (Prochazka), 1893: 22; Wollersdorf, Austria; Miocene.

†*Ceratoconcha noszkyi* (Kolosváry), 1949: 4; Magyarszek, Hungary; Miocene.

†*Ceratoconcha prefloridana* (Brooks and Ross), 1960: 355 (syn.: *Creusia neogenica* weisbord, 1972: 60); Florida, U.S.A.; Pliocene; on *Manicina mayori*.

Ceratoconcha quarta (Kolosváry), 1947: 426 (syn.: *Creusia spinulosa* var. 4 Darwin, 1854: 378); West Indies; West Indies; on *Colpophyllia natans*.

†*Ceratoconcha rangi rangi* (Des Moulins), 1867: 302 (syn.: *Pyrgoma multicostatum* Seguenza, 1873: 319; *Creusia fuchsi* Prochazka, 1893: 18; *Creusia spinulosa* forma *caldangiae* Kolosváry, 1949: 1; *Creusia spinulosa* forma *praespinulosa* Kolosváry, 1949: 1, figs. 2-3 only); Bazas, France; Miocene (Aquitanian).

†*Ceratoconcha rangi latum* (Seguenza), 1876: 321; Rometta, Italy; Miocene (Tortonian).

†*Ceratoconcha sanctacrucensis* Baluk and Radwański, 1967c: 468; Korytnica, Poland; Miocene (Tortonian); on *Tarbellastraea reussiana*.

†*Ceratoconcha sturi* (Prochazka), 1893: 15; Sudic, Czechoslovakia; Miocene.

†*Ceratoconcha trolli* (Abel), 1927: 101; Voslau, Austria; Miocene; on *Siderastraea crenulata*.

Remarks.—In view of the allocation of the coral-inhabiting barnacles to different genera, the specific name *Ceratoconcha costata*, proposed by Kramberger-Gorjanovic (1889: 50), becomes a junior homonym of *Creusia costatum* (Seguenza, 1876: 316). As a replacement for this preoccupied name, Baluk and Radwański (1967a: 145) proposed *Creusia krambergeri*.

The validity of *Paracreusia* has long been questioned (Withers, 1929: 565; Hiro, 1938: 414; Krüger, 1940: 452), because no apparent differences allowing separation from *Ceratoconcha* were noted by Abel (1927, 1928), or subsequent workers. Baluk and Radwański (1967c: 482) suggested merging *Paracreusia*, a proposal we have adopted here.

Kolosváry (1949: 4) proposed *Andromacheia* on the basis of one poorly preserved specimen with visible and irregularly developed squamate compartments. The shell surface was said to bear three rows of scales. These are probably the result of weathering inasmuch as the same feature was noted in *Ceratoconcha cladangiae* (Kolosváry, 1949: 2); therefore they are not considered to be of major taxonomic significance. The poor demarcation of the parietal plates and poor development of radii and alae, as noted by Kolosváry, is often encountered in fossil material. Baluk and Radwański (1967c: 476) questioned whether *Andromacheia* was even a barnacle.

Many fossil Pyrgomatines have been described from specimens lacking morphologically important details (Baluk and Radwański, 1967c: 482). Many of these are based on unique specimens, and many of them have not been reported or described since their in-

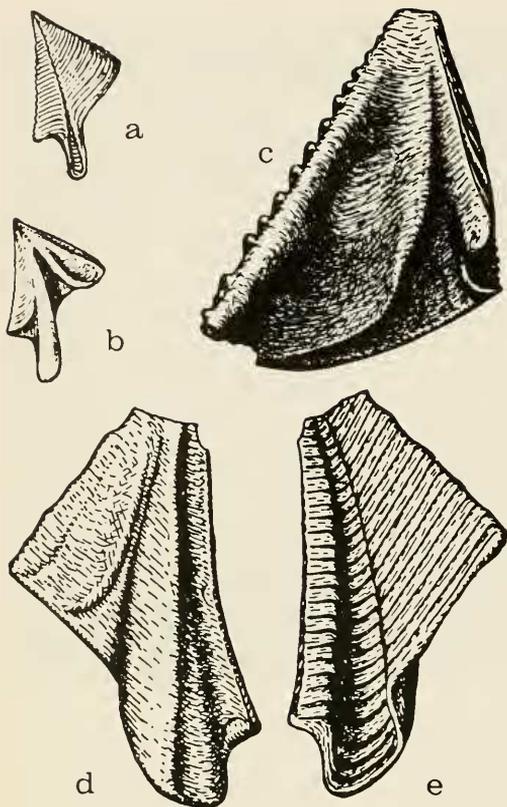


Figure 25. Opercular plates of *Ceratoconcha*. a, b, *C. quarta*, after Darwin, 1854; c-e, *C. prefloridanum*, after Brooks and Ross, 1960.

itial publication. Over half of the species assigned to *Ceratoconcha* were originally based on incomplete specimens and still are known to us solely on the basis of an abbreviated, incomplete description. Invariably these descriptions omit the morphology of the operculum, which is perhaps the most diagnostic feature of this genus. Therefore, the assignment of many of the species must remain tentative until well preserved and more complete material becomes available.

Baluk and Radwański (1967c: 485) proposed the subgenus *Withersia* for two species, one of which, *Creusia barbadensis*, is here referred to *Ceratoconcha*, and the other, *C. oulastreae*, to *Boscia*. The reason for proposing *Withersia* was that the radial sutures are "indistinct or even disappearing." In *barbadensis* sutures are present, but poorly discernible or obscure largely due to secondary calcification, whereas in *oulastreae* radial sutures are never present in the adult stage.

Incertae Sedis

The following taxa cannot be assigned to any of the genera defined herein: *Creusia childreni* Gray, 1825; *Balanus duploconus* Lamarck, 1818; *Megatrema semicostata* Sowerby, 1839; *Pyrgoma stellata* Chenu, 1843; *Pyrgoma spongiorum* Chenu, 1843; *Pyrgoma corymbosa* "Valenciennes" Chenu, 1843; *Creusia radiata* Chenu, 1843; *Creusia multi-striata* Chenu, 1843; *Creusia madreporarum* "Leach?," Chenu, 1843; *Creusia striata* Chenu, 1843; *Pyrgoma undata* Michelotti, 1839.

Darwin (1854: 365, footnote) noted that *Balanus duploconus* Lamarck may be synonymous with *Nobia grandis* Sowerby. Lamarck's (1818: 394) description, "*B. testae parte suprema univalvi, indivisa, convexa; inferiore turbinata, non clausa; apertura elliptica,*" may also apply to other species here included in the genera *Nobia*, *Pyrgoma*, or *Boscia*. The uncertainty that surrounds the nature of *B. duploconus*, which Lamy and Andre (1932) failed to clarify, stems from the lack of a more complete description.

Schluter (1838: 38) considered Lamarck's *Balanus duploconus* to represent a distinct

genus, for which he proposed *Duplocona*, with *D. laevigata* Schluter (= *Balanus duploconus* Lamarck, 1818) as the sole nominal species. Although *D. laevigata* is accompanied by a reference to Lamarck's work, no description or illustrations are given, the section on barnacles being for the most part a list of names. Pilsbry (1916: 261), without any comment, placed Schluter's taxon in the synonymy of *Pyrgoma* as then recognized. Because of the dubious nature of *Balanus duploconus*, *Duplocona* cannot be defined.

Both *Creusia childreni* and *Megatrema semicostata* are presented without description or locality. Sowerby's illustration of the external surface of *M. semicostata* is too small and generalized to be of any taxonomic value. *Creusia childreni* was not figured.

In his "Illustrations Conchyliologiques" Chenu (1843) figured seven species of *Creusia* and five species of *Pyrgoma*. Of these, only *Creusia grandis*, *C. decorata*, *C. madreporarum*, *Pyrgoma cancellatum*, and *P. crenatum* can be identified with any certainty. The lack of text, figure explanations, or locality data, precludes identification of the remaining seven species.

The illustration of *Creusia striata* presented by Chenu shows only the internal surface of the shell *in situ*. Close inspection reveals six lines marking the interior surface of the sheath, indicating that the wall is composed of six plates. Therefore, Chenu's form is either a species of *Balanus* or *Hexacreusia*.

Darwin (1854: 364 footnote) stated that J. E. Gray thought *Pyrgoma stellata* Chenu was a synonym of *P. conjugatum* Darwin. However, Darwin commented that, "... it may be so; but the figure given of the shell will do equally well or rather better for the *Pyrgomum* [sic] *dentatum* of this work, and for some varieties of *P. crenatum*." The uncertainty regarding the identity of *P. stellata* stems from the lack of illustrations of the opercular plates.

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