

***Pyrgoma kuri* Hoek, 1913: a case study in morphology and systematics of a symbiotic coral barnacle (Cirripedia: Balanomorpha)**

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"Whoever attempts to make out from external characters alone, without disarticulating the valves ... will almost certainly fall into many errors ..."

Charles Darwin, 1854

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Abstract

The systematics of pyrgomatids, stemming from the early 1800's, has traditionally been based on the number of plates making up the wall (six, four or one) and specializations in the opercular plates. A recent study of the related bryozobiines focused attention on detailed structural modifications of the basis, which we now find also applies to some highly derived pyrgomatids and an archaeobalanine. Reexamination of the Indonesian coral barnacle *Pyrgoma kuri* Hoek, 1913 has revealed previously unknown morphological features, including separable opercular plates, a true tergal spur, and a basis lined with ladder to arch-like calcareous structures covering "atrial passageways". Thus, the present study expands our knowledge of such specializations and our understanding of the evolution and relationships of the derived pyrgomatids as well as the archaeobalanines and bryozobiines. The complex modifications of the basis found in these three groups evidently function as an avenue for chemical mediation of growth between the barnacle and its host. Although monophyly of the archaeobalanines and bryozobiines based on such structures is possible, there is no obvious connection between them and the few derived pyrgomatids in which these features occur. There is apparently a propensity toward such modifications in archaeobalanids resulting in parallel evolution in association with distinctly different hosts (e.g., sponges, corals and bryozoans).

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Introduction

During 1899 and 1900 H.M.S. "Siboga" explored the waters of the Netherlands East Indies, or what is now largely known as Indonesia. The "Siboga", some 50 m in length, takes its name from a town on the west coast of Sumatra. Although originally designed to be a gun-boat it was retrofitted as a research vessel prior to completion. Under the leadership of Max Weber (Pieters & De Visser, 1993), the shipboard party collected samples at 323 stations, from shore to depths of nearly 4400 m. A total of 114 species of barnacles were collected, 75 of which were new to science including an unusual coral-inhabiting pyrgomatid (Hoek, 1913).

The systematics of pyrgomatids traditionally has been based on the number of plates comprising the wall (six, four or one) and on modifications of the opercular plates (Leach, 1817, 1818; Gray, 1825; Darwin, 1854; Hiro, 1931, 1935; Nilsson-Cantell, 1938; Ross & Newman, 1973; Newman & Ladd, 1974; Galkin, 1986; Anderson, 1992). It was not until recently that specializations involving (1) the wall and feeding appendages (Ross & Newman, 1969, 1995), (2) the modified scuto-tergal flaps or apertural frill (Anderson, 1992), and (3) the basis (Ren, 1986; Anderson, 1992) were noted and in part utilized in classification (Anderson, 1992; Ross & Newman, 1995, 1996).

A study of distant relatives of the pyrgomatines, the bryozobiines, focused attention on detailed structural changes to the basis and wall (Ross & Newman, 1996). We now find such changes also apply to some derived pyrgomatines and to an archaeobalanine. The present study not only expands our knowledge of such changes in the basis, it also has a significant impact on our understanding of the evolution of the pyrgomatids and their distant relatives among the archaeobalanids. As in *Bryozobia synaptos* Ross & Newman, 1996, complex modifications of the basis, and to some extent the wall, also likely involve chemical mediation between it and its host. This has profound evolutionary as well as systematic implications because, while monophyly of these structures between the archaeobalanines and bryozobiines is possible, there is no obvious structural continuity between these structures in the foregoing and the pyrgomatines.

Among the specimens collected by the “Siboga”, those taken off Kur Island in the Banda Sea included two pyrgomatid barnacles attached to the same solitary, ahermatypic, caryophyllid coral. These obligate symbionts were described as *Pyrgoma kuri* by Hoek (1913), and none has been found since.

As part of our ongoing studies of pyrgomatids, we decided to reexamine *P. kuri*. Among the features especially in need of reevaluation was the presence of sutures on both surfaces of the opercular plates, which were purportedly “calcified” together and therefore inseparable. We also wanted to evaluate various parameters of the tergum, which is similar to that of *Pyrgoma cancellatum* Leach, 1818 and several related species.

In addition, our dissection of the lectotype revealed previously unappreciated features similar to structures described earlier in bryozobiines (Ross & Newman, 1996), and mentioned briefly in passing by Ren (1986), Anderson (1992) and Ogawa et al. (1998) in other species. Furthermore, it was necessary to restudy the archaeobalanid *Armatobalanus terebratus* (Darwin, 1854) also collected by the “Siboga” off the Kei Islands, because Darwin (1854) and Hoek (1913) had noted that the basis in this species has tissue-covered perforations. This unusual feature could be indicative of monophyly

between archaeobalanines and bryozobiines, but it appears to have evolved independently in pyrgomatines. However, the basis for the structure, chemical mediation between the barnacle and its host, is apparently well established in the archaeobalanines and their allies.

Materials and methods

Armatobalanus terebratus (Darwin, 1854). – “Siboga” station 257, Duroa Strait, Kei Is. (Kepulauan Kai); approx. 5°40’S, 132°44’E, 52 m, Dec. 11, 1899, Zoölogisch Museum Amsterdam (ZMA) Cirr. 2038777.

Pyrgoma kuri Hoek, 1913. – “Siboga” station 251, off Kur I., Moluccas, 5°28.4’S, 132°0.2’E, 204 m, Dec. 8, 1899, ZMA Cirr. 100.324. The wall and opercular plates described and illustrated by Hoek (1913: 259, pl. 27, fig. 1, wall of left specimen, see Fig. 1C (arrow) herein, and Hoek’s fig. 2, opercular plates) could not be located. The remaining complete, but originally undissected specimen, shown in apical view in Hoek is described and illustrated herein, and it is designated the lectotype.

Hoek encountered problems prying off the first specimen, having broken the tip of the steel tool he was using which remains embedded in the coral. Therefore, we used a small hand-held, electric-driven diamond-coated wheel to remove the remaining specimen from the host coral. The cut was placed so as to leave a small portion of the basis intact on the coral (Fig. 3C). The soft parts and opercular plates were then removed from below. The wall and the coral were soaked overnight in a 5.25% solution of sodium hypochlorite (commercial bleach), and the opercular plates were immersed for about 30 minutes to remove adhering tissues. Contrary to expectations the scuta and terga disassociated in the process. They were then transferred to water, the remaining adhering cuticle removed with a fine-tipped artist’s brush, rinsed several times in tap water, and air dried.

The opercular plates, wall with the principal part of the basis, and the coral were mounted on aluminum stubs with double-sided tape, sputter coated with gold-palladium, viewed and then photographed in a Cambridge S360 scanning electron microscope operating at 3 to 10 kV. The specimens of *A. terebratus* were similarly prepared and photographed.

Procedures for the preparation of soft parts are detailed in Newman & Ross (1971: 17). We elected to mount the mouth parts and cirri on a single glass slide using glycerin jelly. The opercular muscles and remaining portion of the prosoma and thorax are stored in 80% ethanol.

Terminology of opercular plates

The terminology employed in the past for describing the relationship of the scutum to the tergum can lead to different interpretations. Therefore, we suggest avoiding the terms “fused”

and “conrescent” when applied to the opercular plates. Instead, the following criteria and terms, to describe their relationships are recommended:

Separate. – Movably articulated together and readily disarticulated manually, but commonly treated with bleach before attempting their separation to avoid breakage.

Cemented. – Immovably bound together by a cement that is partly or wholly destroyed by immersion in bleach before separation occurs.

Calcified. – Secondary deposition of calcareous material on the internal surface thereby obliterating the suture, not separable in bleach.

Fully calcified. – No evidence of an external or internal suture between plates, not separable.

When the opercular plates are articulated they are either separated by the integument, or the suture may simply be filled with organic cement. The absence of a suture line on the interior of the plates indicates they are calcified together. We know of no example where a suture line is visible internally but not externally.

The use of commercial bleach in the above definitions, which has replaced potassium hydroxide (= caustic potash, Darwin, 1854: 3) stems from its common use in removing tissue adhering to the calcareous parts of barnacles (Newman & Ross, 1971; Anderson, 1992; Ross & Newman, 1995; Ogawa et al., 1998). When used with discretion it has little or no obvious effects on the parts themselves.

Systematics

Family Pyrgomatidae Gray, 1825

Subfamily Pyrgomatinae Gray, 1825

(nom. transl. Ross & Newman, 1973 [ex Pyrgomatidae Gray, 1825])

Tribe Pyrgomatini Gray, 1825

(nom. transl. Ross & Newman, 1995 [ex Pyrgomatinae Gray, 1825])

Genus *Pyrgoma* Leach, 1817

Pyrgoma Leach, 1817: 67; Leach, 1818: 171; Darwin, 1854: 354 (synonymy); Ross & Newman, 1973: 156 (synonymy, included species); Newman & Ross, 1976: 58.

Paranobia Galkin, 1986: 1293; Newman, 1996: 503.

Definition (emended). – Wall low conical to flat, solid, fully calcified (no sutures present); sheath adpressed; transverse, calcareous, ladder to arch-like structures internally bridging gap between longitudinal ribs of basis terminating at suture between wall and basis; opercular plates separate or cemented but not calcified together; scutum

transversely elongate, adductor ledge large, extending below true basal margin, rostral tooth present; tergum with true spur.

Type species: *Pyrgoma cancellatum* Leach, 1818, by original monotypy; Recent, Shirahama, Honshu I., Japan, 33°39'N, 135°22'E; on *Turbinaria contorta* Bernard.

Remarks. – *Pyrgoma* is related to *Hiroa* Ross & Newman, 1973, and to a new genus from Taiwan (Ross & Newman, 1999). *Hiroa* has separate wall plates that distinguish it from the new genus, and from *Pyrgoma*, and separate opercular plates similar to those of *Pyrgoma* which distinguish it from the new genus. What allies these genera is the transversely elongate scutum having a large adductor ledge and a prominent rostral tooth (lacking in *Hiroa*), and the tergum having a true spur (“...a projection...on the basal margin” Darwin, 1854: 52).

Pyrgoma kuri Hoek, 1913

(Figs. 1-5)

Pyrgoma kuri Hoek, 1913: 259; Hiro, 1931: 155; Hiro, 1935 25; Nilsson-Cantell, 1938: 70 (relationships).

Nobia kuri; Ross & Newman, 1973: 155 (opercular plates); Newman & Ross, 1976: 58 (references); Ogawa & Matsuzaki, 1992: 95 (host coral).

Paranobia kuri; Galkin, 1986: 1293.

Supplementary description (lectotype). – Wall and opercular plates white in preserved specimen; wall dome-shaped, with periphery growing vertically rather than obliquely from the basis (Fig. 2E); surface ornamented with 24 low, broad radial ridges in various stages of overgrowth by the coral (Fig. 2F); orifice ovate, rostro-carinal diameter less than 1/3 that of wall; internal surface of wall smooth; sheath less than 1/2 height of wall at rostral end, basal margin slightly sinuous, adpressed except for lateral and rostral areas where there are low ridges (Fig. 3A). Basis moderately deep, enlarging to maximum diameter in distinct steps (Figs. 3B: nos. 1-3; C); external ribs corresponding with those on wall (Fig. 2E); internal longitudinal ribs with median sulcus to receive radial septa of wall, adjacent ribs bridged by transverse ladder-like calcareous con-

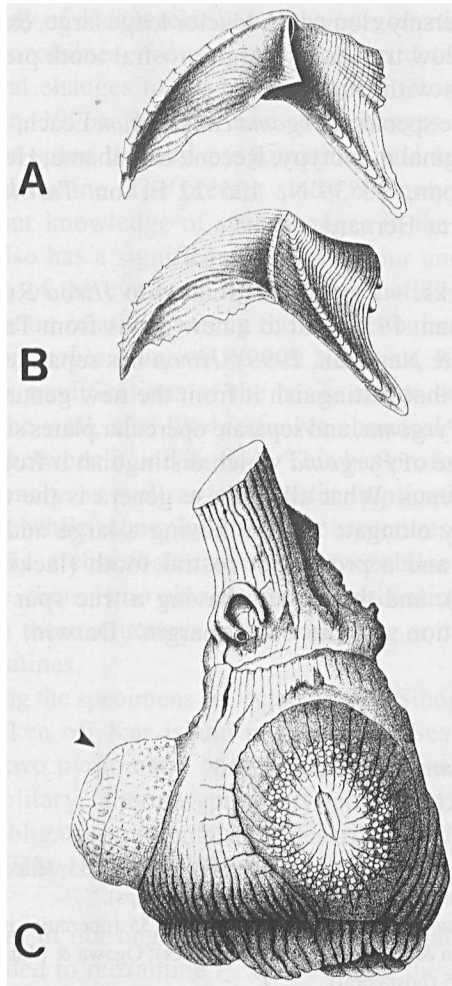


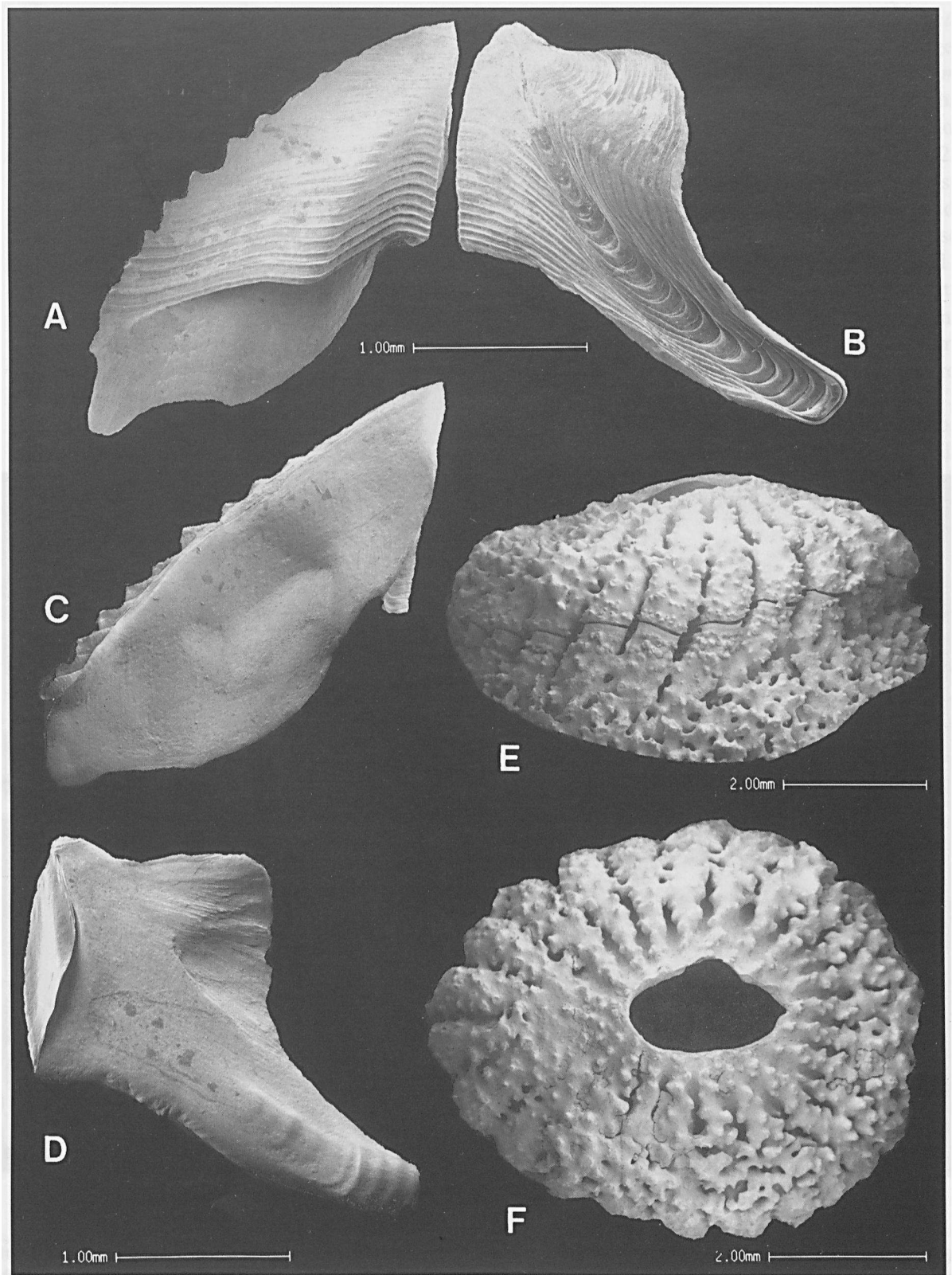
Fig. 1. *Pyrgoma kuri* Hoek, from Hoek, 1913, pl. 27, figs. 1-2 (slightly reduced). A, internal view of left opercular plates. The serrate basal margin of the adductor ledge is likely due to breakage (cf. Fig. 2A). B, external view of right opercular plates. C, barnacles in situ. Apparently due to space constraints and artistic license, Hoek oriented the coral upside down, as shown here. The rostro-carinal axis of both barnacles is aligned with the long axis of the coral, with the carina in the lectotype orientated towards the expanding calyx. The specimen on the left (arrow), in side view, is the one dissected by Hoek, but it apparently has been lost. The other, the lectotype (ZMA Cirr. 100.324), is shown in Figs. 2-5.

nections (Fig. 3B, C), becoming arches as basis develops (Fig. 4B).

Scutum transversely elongate (Fig. 2A), with large, depending adductor ledge; apical angle 58° ; growth ridges simple; occludent margin toothed, slightly convex; tergal margin straight, less than $1/2$ length of occludent margin, ratio of occludent to tergal margin 2.29 : 1; basal margin sinuous, longer than tergal margin; articular furrow narrow, shallow; adductor ledge depending, basal margin not paralleling true basal margin; rostral tooth long, bluntly rounded, slight irregular ridges on upper surface for insertion of lateral depressor muscle; adductor muscle depression large, ovate, deep, medial (Fig. 2C). Tergum higher than wide (Fig. 2B), height to width ratio 1.78 : 1, apical angle 90° ; external longitudinal furrow open; growth ridges of furrow reflected on internal surface (Fig. 2D); distal end of spur truncated; articular ridge cuneiform; muscle crests with subsidiary ridges, separated from spur by shallow depression (Fig. 2D).

Labrum with one tooth on each side of notch; a single row of numerous stiff setae along apical margin (Fig. 5A). Palps ovate, medially proximate; apical margin with short slender setae; setae of distal margin longer, slender; posterior face and basal margin covered by exceedingly long, slender setae. Mandible with 4 teeth and straight molariform lower angle (Fig. 5B); teeth 2-3 bicuspid; apical margin with slender widely spaced setae; basal margin with closely spaced long, slender setae; short, stout spines covering lateral face; left mandible with malformed apical tooth, tooth 4 simple or bicuspid (Fig. 5C). Maxilla I with single, long, stout, bifid spine above subapical notch (Figs. 5E, F); 4-5 short slender spines in notch; medial cluster bearing 6 long, stout spines; basal cluster with 7 shorter, slender spines; apical and basal margins clothed with slender setae; lateral face armed with

Fig. 2. Scanning electron micrographs of *Pyrgoma kuri* Hoek (lectotype, ZMA Cirr. 100.324). A, external view of right scutum. Note the continuous smooth margin of the adductor ledge. B, external view of right tergum showing the open spur furrow. C, internal view of left scutum. D, internal view of left tergum. Note the crests do not extend beyond the basal margin (cf. Fig. 1A, B). E, lateral view of right side of wall and apical portion of the basis, carinal end at right. Note narrow seam between wall and basis and the continuity of the atrial passages with the spaces between septa of the wall. Both wall and basis are covered by coral overgrowths. F, apical view of wall. Note partial to complete roofing over of spaces between ribs by the coral. The perpendicular surface of the orifice appears uniformly worn resulting from cirral rasping, which also produced the notch in the carinal end of the wall.



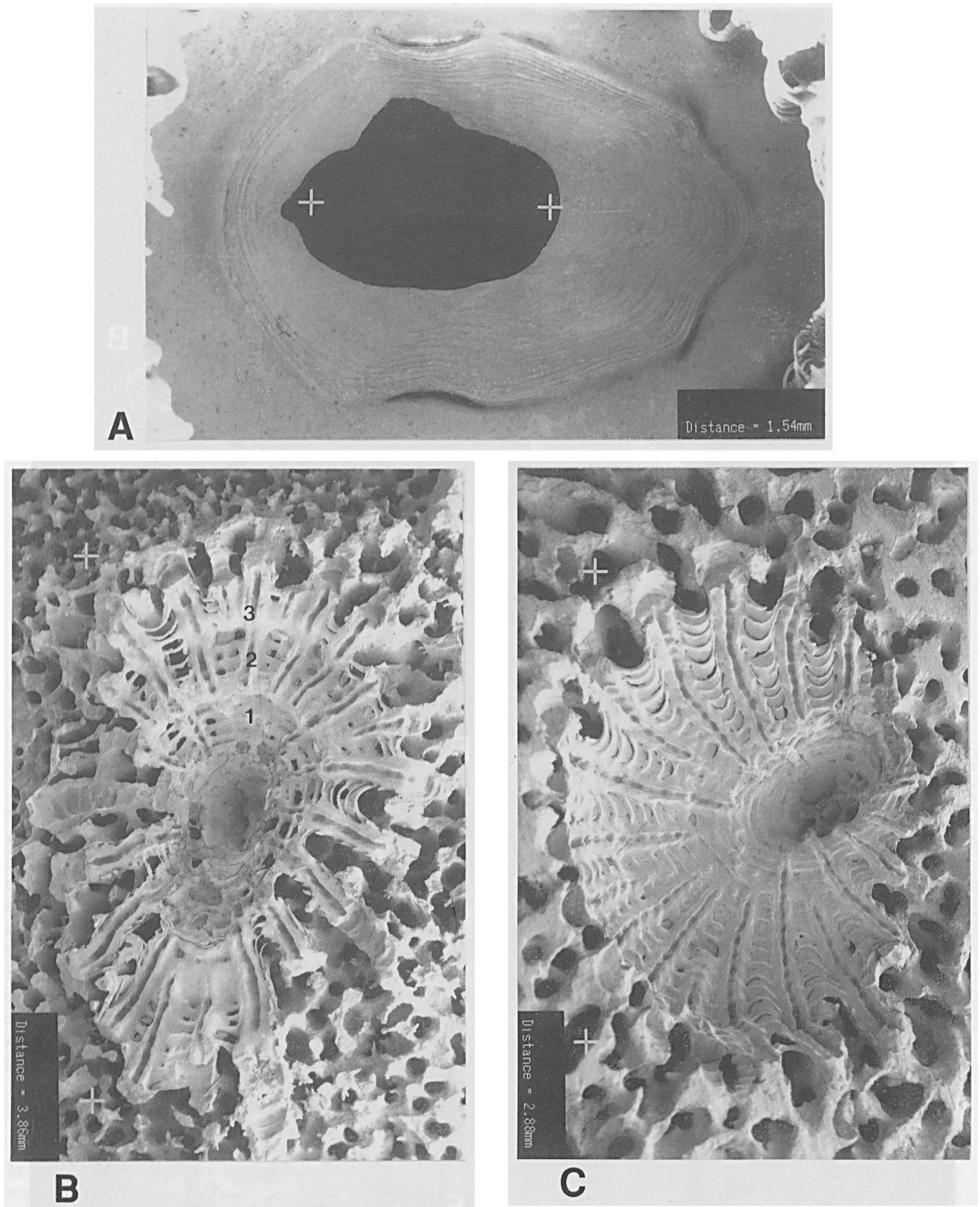


Fig. 3. Scanning electron micrographs of *Pyrgoma kuri* Hoek (lectotype, ZMA Cirr. 100.324). A, internal view of wall and sheath, carinal end at left. At the rostral end (right), there are diverging raised areas between which there is a sulcus to accommodate the curvature of the scuta. The raised lateral areas, slightly to the left of the mid point of the orifice accommodate the inflected portion of

slender spines. Maxilla II tall, bilobed (Fig. 5D); basal lobe shorter and with fewer setae than apical lobe; anterior border of apical lobe bearing moderately long setae.

Posterior ramus of cirrus I less than 1/2 length of anterior ramus (Fig. 5G); basal segments of anterior ramus wider than high, rapidly tapering to higher than wide. Cirrus II about 2/3 length of cirrus I and 3/4 length of cirrus III (Fig. 5H); rami subequal, articles slightly wider than high. Rami of cirrus III subequal; anterodistal margins bearing a few ctenoid scales and short, acicular spines. Cirrus IV with subequal rami; somewhat shorter and with fewer articles than cirri V and VI. Cirrus VI having equal rami; setation ctenopod, 4 pairs (Fig. 5J); 1 or 2 short slender setae at base of 3 apical pairs of setae; 2-3 short to long setae at posterodistal angle, longest seta about 2/3 length of article; ratio of anterodistal setae to width of article 5.1 : 1. Basi-dorsal point of intromittant organ large, triangular, apex acute (Fig. 5K). Intromittant organ about 3 times length of cirrus VI; setae in 4 longitudinal rows; setae at distal end in clusters. Cirral counts follow (a = anterior ramus; p = posterior ramus; xx = damaged ramus):

	I	II	III	IV	V	VI
right (a/p)	15/7	8/7	9/7	17/19	21/xx	xx/23
left (a/p)	14/5	7/6	10/8	16/19	21/23	23/23

Lectotype not brooding eggs.

Remarks. – Cirral counts for the first three cirri in the specimen that Hoek dissected (11/6, 8/7 and 9/8) are similar to those above, but those of the last three (16-17, 18-19 and 20-21) have fewer segments than those of the lectotype. Hoek stated there were two teeth on each side of the labral cleft in the specimen he dissected, but we found only one in the lectotype.

Ross & Newman (1973) and subsequent workers considered *P. cancellatum* to be the sole representative of *Pyrgoma*. Our evaluation herein of *P. kuri*, as well as *P. cancellatum* var. *japonica*

Weltner, here assigned species rank, *P. projectum* Nilsson-Cantell, and *Nobia sinica* Ren, suggests all of these also should be included in *Pyrgoma*.

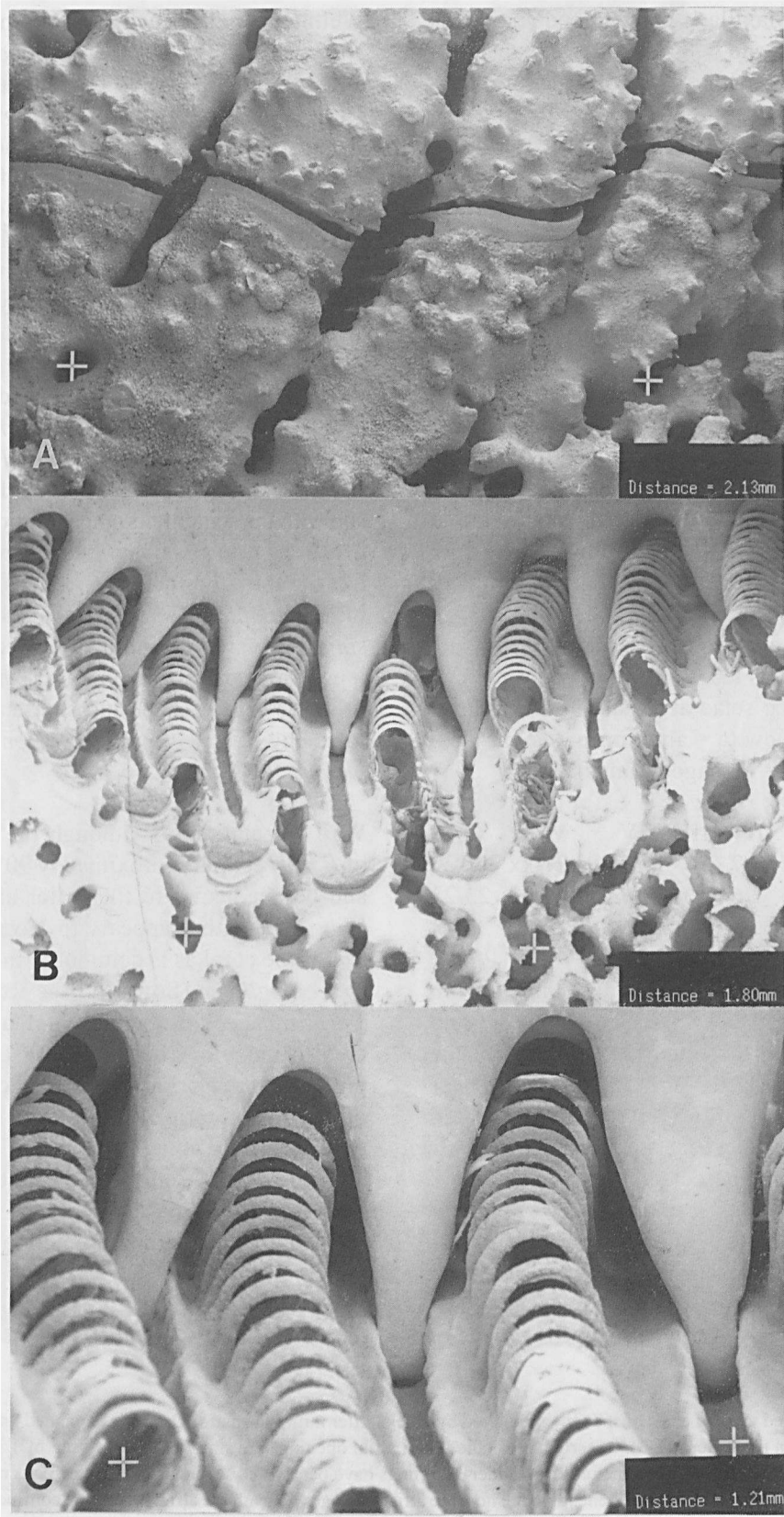
Pyrgoma kuri differs from *P. projectum* in having only a few tergal crests and these extend to or barely beyond the basal margin (cf. Figs. 1B, 2B). The counts for cirri I-III are identical in these species, but there are differences in the others and in the opercular plates and trophi. Although Nilsson-Cantell (1938: 71) stated they may be one and the same species, we consider them to be distinct.

The tergal muscle crests of *P. sinica* are more numerous and extend well beyond the basal margin, more so than in *P. projectum*. These crests are lacking in *P. cancellatum* and *P. japonica*. The tergum in *P. cancellatum* is dwarfed by comparison with the scutum; its apical portion is the smallest of the species, and it has the narrowest spur which, like the apical portion, becomes progressively wider in *P. japonica*, *P. kuri*, *P. projectum*, and lastly *P. sinica*. The rostral tooth of the scutum is by far longer and more slender in *P. sinica*, becoming progressively broader and shorter in *P. kuri*, followed by *P. cancellatum*, *P. japonica*, and *P. projectum*.

Wall orientation. – Although the two specimens of *P. kuri* settled approximately 90° apart (Fig. 1C) and perpendicular to the major axis of the coral (Fig. 1C) neither appears to have settled on the rim of the coral as is commonly the case in *Megatrema anglicum* (Sowerby; see Ross & Newman, 1973: fig. 1). The original orientation of the host coral is unknown, but both barnacles likely had a preferred orientation on its surface. The polarity of the rostro-carinal axis of the specimen Hoek removed could not be determined, although it was aligned with the long axis of the coral. However, it was likely as in the lectotype, which similarly aligned, had the carina oriented toward the rim of the coral.

Parasites. – Between the setae at the juncture of

the scutum. B, enlarged view of basis of specimen removed by Hoek. After initial formation the basis expanded laterally to essentially maximum diameter in three steps (1-3). In certain areas the initial atrial openings are simply ovate (cf. Fig. 6C). C, enlarged view of basis of lectotype. The spaces between the uniform ladder-like rungs have been filled secondarily by calcareous material presumably upon withdrawal of the coral tissue from beneath. Note how the atrial passages beneath the atrial arches are confluent with comparable passages in the skeleton of the coral (cf. Fig. 4B).



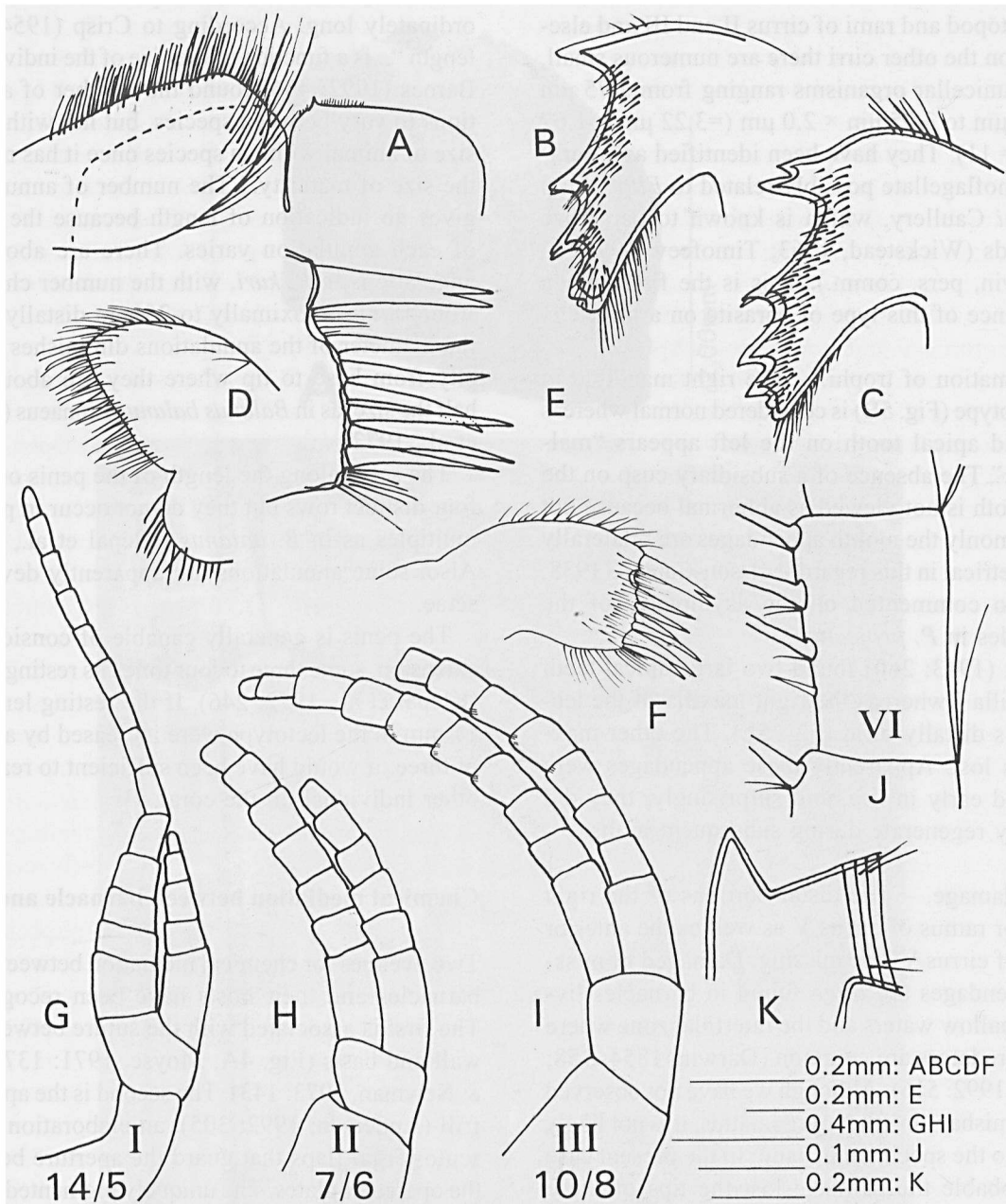


Fig. 5. Trophi and cirral appendages of *Pyrgoma kuri* Hoek (lectotype, ZMA Cirr. 100.324). A, labrum and right palp. There is only one tooth on the left side. B, right mandible. C, left mandible with “abnormal” bicuspid apical tooth. D, maxilla II. E, enlarged view of cutting edge of maxilla I. F, maxilla I. G, cirrus I. H, cirrus II. I, cirrus III. J, intermediate article of cirrus VI. K, basidorsal point of intromittent organ. Fractions below cirri I-III are the cirral counts, with the anterior ramus preceding the posterior.

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 Fig. 4. Scanning electron micrographs of *Pyrgoma kuri* Hoek (lectotype, ZMA Cirr. 100.324). A, external view of seam between wall and basis. Note the open suture and the narrow horizontal zone of vertical growth of the basis that will likely be overgrown by the coral. B, internal view, lower portion of the basis removed, showing the arch-like roof of the atrial passages as well as their relationship to passages in the wall and coral skeleton. C, enlarged view of the left side shown in B. Both margins of the sulcus between the arches are dentate, and a depression above the uppermost denticle prevents the wall from being driven downward.

the protopod and rami of cirrus II and III and elsewhere on the other cirri there are numerous small, ovate, unicellular organisms ranging from $2.75 \mu\text{m} \times 1.63 \mu\text{m}$ to $3.75 \mu\text{m} \times 2.0 \mu\text{m}$ ($=3.22 \mu\text{m} \times 1.67 \mu\text{m}$, $n = 11$). They have been identified as a parasitic dinoflagellate possibly related to *Ellobiopsis chattoni* Caullery, which is known to parasitize copepods (Wickstead, 1963; Timofeev, 1997; R. A. Lewin, pers. comm.). This is the first known occurrence of this type of parasite on a barnacle.

Malformation of trophi. – The right mandible in the lectotype (Fig. 5B) is considered normal whereas the bifid apical tooth on the left appears “malformed.” The absence of a subsidiary cusp on the third tooth is not viewed as abnormal because not uncommonly the mouth appendages are bilaterally asymmetrical in this regard. Nilsson-Cantell (1938: 72) also commented on the asymmetry of the mandibles in *P. projectum*.

Hoek (1913: 260) found two large apical teeth on maxilla I whereas the right maxilla of the lectotype is distally bifid (Fig. 5E). The other maxilla was lost. Apparently these appendages were damaged early in life, and surprisingly, they did not fully regenerate during subsequent molts.

Cirral damage. – The distal portions of the right posterior ramus of cirrus V as well as the anterior ramus of cirrus VI are missing. Damaged or missing appendages are often found in barnacles living in shallow waters and the intertidal zone where visual predators are common (Darwin, 1854: 158; Barnes, 1992: 516). Although we have not observed similar mishaps in other pyrgomatids, it is not likely unique to the specimen in hand. In the present case it is probable the barnacle lost the tips of these appendages to a predator rather than to the coral.

Intromittent organ. – The intromittent organ is in-

ordinately long. According to Crisp (1954: 476) length “...is a function of the size of the individual.” Barnes (1992: 486) found the number of annulations to vary between species, but not with “...the size of animal within a species once it has reached the size of maturity.” The number of annulations gives no indication of length because the length of each annulation varies. There are about 232 annulations in *P. kuri*, with the number changing from 18/mm proximally to 25/mm distally. Also, the diameter of the annulations diminishes gradually from base to tip where they are about one-half the size, as in *Balanus balanus* Linnaeus (Klepal et al., 1972).

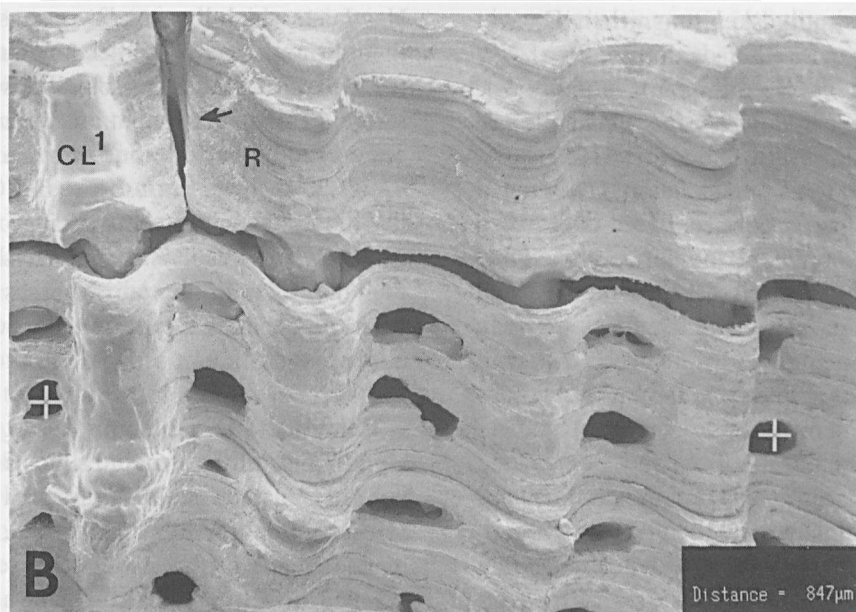
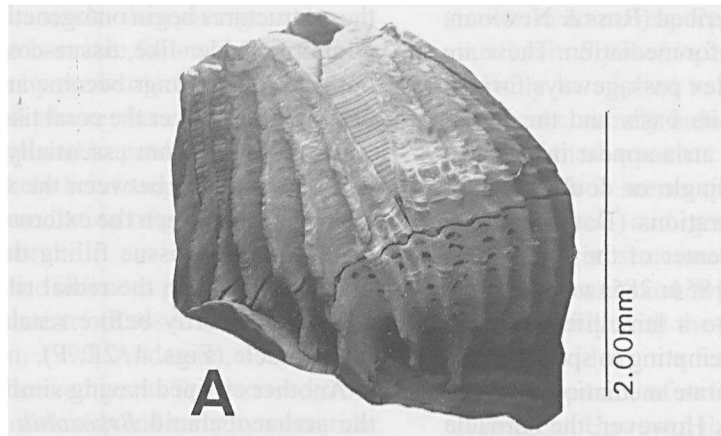
The setae along the length of the penis occur in four distinct rows but they do not occur in pairs or multiples as in *B. balanus* (Klepal et al., 1972). Also, some annulations are apparently devoid of setae.

The penis is generally capable of considerable extension, some three to four times its resting length (Klepal et al., 1972: 246). If the resting length of 11 mm in the lectotype were increased by a factor of three, it would have been sufficient to reach the other individual on the coral.

Chemical mediation between barnacle and host

Two avenues for chemical mediation between coral barnacles and their hosts have been recognized. The first is associated with the suture between the wall and basis (Fig. 4A; Moyse, 1971: 137; Ross & Newman, 1973: 143). The second is the apertural frill (Anderson, 1992: 305), an elaboration of the scuto-tergal flaps that guard the aperture between the opercular plates. The uniquely pigmented scuto-tergal flaps in pyrgomatines (Anderson, 1992) may also contain structures believed to have a chemosensory function (Foster & Nott, 1969).

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 Fig. 6. Scanning electron micrographs of the gregarious “coral”-dwelling *Armatobalanus terebratus* (Darwin), “Siboga” station 257, Kei Is. (ZMA Cirr. 2038777). A, lateral view of wall and basis. Note the projecting buttresses or “holdfasts” on the basis that anchor the barnacle to the substratum or to adjacent barnacles, the shell of one of which can be seen in the lower left. B, enlarged view of external surface of seam between wall and basis and the perforations or atrial passageways in the basis. Note the slight gap in the base of the radius (arrow) between the rostrum (R) and the carinal latus (CL¹) reminiscent of the first whorl of atrial openings found in the archaeobalanid *Bryozobia* (Ross & Newman, 1996). C, enlarged view of internal surface of wall and basis. Note the sulci, into which the radial septa of the wall fit, have been filled secondarily by the barnacle (cf. Fig. 3B, C, in which the sulci have been filled in older parts of the basis, and Fig. 4B, in which the sulci are still open).



Atria, only recently described (Ross & Newman, 1996), are another avenue for mediation. These are relatively simple to complex passageways formed by the barnacle between its basis and the host's skeleton. In *A. terebratus* atria appear in the simplest form known, as a single or double row of membrane-covered perforations (Darwin, 1854: 286) radiating from the center of the cup-shaped basis (Fig. 6C). Darwin (1854: 285) noted that *A. terebratus* was attached to a lamelliferous coral and therefore it might be tempting to speculate the perforations were to facilitate mediation between the barnacle and the coral. However, the barnacle and coral were simply skeletons when Darwin described them, so whether or not the coral was living when the barnacle grew on it is unknown.

Living specimens of *A. terebratus* were collected by the "Siboga" and described by Hoek (1913: 207). Although attached to a coral skeleton, Hoek noted that these gregarious specimens were overgrown by a "sponge-like organism." We have studied this material, and it is definitely a yellow sponge that invades the atrial passages and the space between the calcareous substrate and the barnacle as well as between barnacles when one has partially overgrown another. Therefore, it appears, if chemical mediation occurs, it is between the sponge and barnacle rather than the coral upon which it happens to be growing. Parenthetically, had Darwin seen this material he may have been "...compelled to have ranked [*terebratus*] in ...*Acasta*." However, true *Acasta* not only settle directly on sponges, rather than on solid calcareous substrates, but also individuals are not known to attach to each other. Thus *terebratus* is retained in *Armatobalanus*.

What about barnacles that are obligate symbionts of corals? Ren (1986: 157) noted one of the features characterizing *P. sinica* was the presence of an unusual basis having "...narrow radial grooves between thick ribs, which are imperfectly calcified and sculptured with rows of slightly curved transverse ridges, and covered with brownish membrane." Anderson (1992: 305) commented on a similar structure in specimens referred to *P. cancellatum*, noting the presence of passages that are "...tubular, thin-walled and uncalcified except for transverse ring thickenings. Narrow calcified gutters separate the tubular ribs." We have found

these structures begin ontogenetically, as in *P. kuri*, as simple ladder-like, tissue-covered perforations, but subsequent rungs become arches (Figs. 3B, C, 4B, C). These cover the coral tissue-filled passageways radiating from essentially the center of the basis to the seam between the wall and basis and terminating between the external radial ribs on the wall. The coral tissue filling these passages continues up between the radial ribs on the wall and terminates shortly before reaching the orifice of the barnacle (Figs. 4, 2E, F).

Another cirriped having similar passageways is the archaeobalanid *Bryozobia synaptos* Ross & Newman, which lives on bryozoans. Openings for their atrial passageways become incorporated into the wall during ontogeny, but otherwise their structure is comparable to that of *Pyrgoma*. They start out as simple perforations through the calcareous basis, as in *A. terebratus* (Fig. 6B, C), but the ladder-like rungs subsequently change to similar arch-like structures, as in *P. kuri* (Fig. 4B, C). Some of the latter open in the radii whereas others open in the parietes where they ultimately become elevated above the substratum with growth (Ross & Newman, 1996).

Ren (1986) did not comment on the function or significance of the structures he briefly mentioned nor did Ogawa et al. (1998). However, Anderson's (1992: 337) study of *P. cancellata*, a species having a reduced orifice and a relatively small cirral net, led him to suggest these structures "...raise the possibility that a reduced external feeding mechanism is compensated in some species by uptake of dissolved nutrients from the coral host", but no evidence of nutrient transfer was found in a distantly related form (Cook et al., 1990). In the Hoekiini there is not only an extreme reduction of the thoracopods, but also an elaboration of potential absorptive surfaces and therefore nutrient transfer in these seems likely (Ross & Newman, 1969, 1995). However, at the same time there are other interactions between barnacle and host related to coordinating rates of growth.

Pyrgomatids only settle on and penetrate the soft tissue of actively growing surfaces of the host coral. Once attached to their skeleton, they may live for several years (Ross & Newman, 1973: 142; Newman & Ladd, 1974). Should the rate of growth of the

host exceed the barnacle then overgrowth and entombment of the barnacle follows. Conversely, more rapid growth by the barnacle would result in its protruding well above the corallum, thereby becoming more exposed to predation and fouling. Thus, there has likely been ample selection pressure for chemical mediation of growth rates in the barnacle and the coral.

Available evidence indicates pyrgomatines have an armatobalanid ancestry (Ross & Newman, 1973; Healy & Anderson, 1990; Anderson, 1992). *Pyrgoma* is clearly a derived genus far removed from the ancestral armatobalanids and early pyrgomatids. The decided absence of perforations or atrial passageways in early pyrgomatids was initially puzzling to us. Why these atrial passages should reappear as a parallel innovation may relate to the growth habits of the host corals, i. e., slow growing and/or rapidly spreading corals that do not substantially thicken their skeleton tend to leave the barnacle behind, or do not thicken enough to keep the basis of the barnacle covered. Therefore, these passageways may be an avenue for mediating the localized growth of the coral skeleton.

The foundation for this hypothesis follows: *Pyrgoma kuri* grows on a solitary horn coral. The corallite of such corals enlarges disproportionately with growth, whereby little if any skeleton is added to the older portions. Furthermore, soft tissue of the coral tends to withdraw from the oldest parts. Consequently, when *P. kuri* settles on the column of such a coral, it may not only lose the protection of the coral skeleton as it grows, but coral tissue may withdraw from it as well. It apparently overcomes these problems, without giving up this otherwise open niche, by inducing the coral to treat its exoskeleton as coral rather than barnacle. Thus, we see a thick layer of coral skeleton surrounding *P. kuri* as it grows above the general surface of the coral. How might this be accomplished? Most likely by chemical mediation between barnacle and coral tissues through the membranes associated with the openings in the atrial passageways in the basis of the barnacle. This would be the reverse of the process taking place at the suture between the wall and the basis of such barnacles where coral skeleton production is inhibited from sealing the suture with skeletal material (Fig. 4A). This scenario is

similar in some respects to that in explaining the situation in *Bryozobia*, and a similar scenario could probably be applied to the situation involving *A. terebratus*, namely inducing the host to satisfy the needs of the barnacle.

Although it seems quite likely there has been morphological and genetic continuity between complex atrial structures in archaeobalanids, such as *A. terebratus* and *Bryozobia*, there is no obvious continuity with the pyrgomatids because atria are only evident in a few derived forms, and thus the development of atria in pyrgomatids could be convergent. However, there is a less complex structure anticipating atria in both archaeobalanids and early pyrgomatids that effectively bridge this gap. To fully understand the situation, we first need to look at examples where chemical mediation between the barnacle and its host is either negligible or absent.

In conopeans, among the 6-plated archaeobalanids, the relationship with the gorgonian hosts is apparently largely physical. Species such as *Conopea galeata* (Linnaeus) generally become established by settling where the axial skeleton of the host has been exposed by damage (Gomez, 1973). As the barnacle grows it can force its way between the axial skeleton and undamaged spicule-bearing tissues of the host. The host also overgrows the enlarging shell of the barnacle commonly forming functional polyps on its surface, and therefore the gorgonian is treating the shell of the barnacle as self. Apparently the tissue of the gorgonian is stretched rather than broken along the wall-basis and radial sutures of the barnacle during diametric growth. Furthermore, host tissue is prevented from interfering with the orifice and aperture largely by the mechanical activities of the opercular plates and the cirri, which are armed with hooks as in armatobalanids in general. If there is any chemical mediation at all, where it occurs is not obvious because the radial sutures as well as that between the wall and boat-shaped basis are among the tightest fitting seen in balanomorphs.

Megabalanines are 6-plated, generally free-living, albeit opportunistic balanids, but *M. stultus* (Darwin, 1854: SIO C-9722) and *M. ajax* (Darwin, 1854: SIO C-9944) of the tropical West Atlantic and Indo-West Pacific, respectively, are

associated with the fire coral *Millepora* (cf. Ross, 1999). These are quickly overgrown by the coral, but continue to grow diametrically by breaking rather than inhibiting growth of the coral skeleton covering the wall-basis and radial sutures. In both species, skeletal tissue is deposited within the orifice and on the scuta, yet these barnacles are able to maintain an operable operculum also likely entirely by mechanical means.

Similarly, the 6-plated *Hexacreusia durhami* (Zullo, 1961), living on *Porites* in the Gulf of California (Ross, 1962), repeatedly breaks its way as it grows diametrically and upward in keeping pace with growth of the host (SIO C-5885). However, in contrast to the megabalanines, the rim of the orifice and opercular plates are devoid of coral. In fact, the coral simply extends to the orifice where it ends in a clean line, suggestive of cirral rasping rather than mediation via an apertural frill or the chemical erosion by the latter. Evidence that *Hexacreusia* apparently relies on mechanical breakage rather than chemical mediation at the wall-basis suture is a situation we have not observed in pyrgomatids, and thus there is no justification for the assumption (Zullo, in litt. in Newman, 1996) *Hexacreusia* is more appropriately placed in the pyrgomatids than in the armatobalanines.

A better model of the ancestral armatobalanine leading to the pyrgomatids is *Armatobalanus circe* (Kolosváry) dwelling on the branching coral *Stylophora danae* Milne-Edwards & Haime from the East Indies (SIO C-6013). It settles on the side of a branch, and develops a largely free-standing, deeply cup-shaped basis capped by a diametrically growing, 6-plated, conical wall. The whole barnacle extends outward at an angle from the coral, and during its growth soft coral tissue covers it, subsequently secreting a thin layer of prickly coral skeleton. The side of the barnacle closest to the coral acquires a thicker layer of skeletal material than elsewhere, especially the portion of the wall where the coral establishes corallites encircling the orifice. The generally thin skeletal covering on the rest of the wall forms curiously elevated ridges associated with the breakage plane along the carinal side of each suture, and these ridges may divide corallites that straddle them. However, until the skeleton on the wall has thickened sufficiently to

come into broad contact with the coral, there seems to be no breakage of coral skeleton along the open wall-basis suture. This suggests a lack of calcification there and hence chemical mediation. When growth of the barnacle apparently slows, this suture becomes a mere thin line similar to that seen in conopeans, and we have observed similar senescent conditions in pyrgomatids. Therefore, the system of growth seen in this species is essentially the same as that found in early 4-plated pyrgomatids (Ross & Newman, 1973).

From the foregoing, while evidence for chemical mediation is not universal in symbiotic barnacles, where it occurs it is involved in preventing overgrowth of the wall-basis suture by host skeleton, and it is apparently developed to varying degrees in a number of armatobalanids associated with corals. Chemical mediation also takes place at the orifice, where it prevents interference by the coral with the activities of the operculum and hence with feeding and other activities of the barnacle (Anderson, 1992). However, the primary site remains the suture between the wall and basis where, while preventing deposition of skeletal material, soft tissue of the coral is free to deposit skeletal material on either side of the suture (Fig. 2E).

In most moderately fast-growing corals tissue is relatively superficial, so the open wall-basis suture apparently provides ample surface area through which to chemically inhibit coral skeleton while allowing soft tissue to overgrow the suture. But what about when on slowly growing corals? The barnacle can outpace its hosts growth and thus become exposed. Or conversely, on corals that tend to withdraw tissue from the older parts of the skeleton, the barnacle can be left without the advantages of having living coral tissue depositing skeletal material around it. In such cases it would be advantageous to induce the host into favoring the barnacle as though it were an actively growing area of the coral, and this could require a more extensive contact zone for chemical mediation such as that provided by an atrial system. The same can be said for barnacles like *A. terebratus* stimulating sponge growth around it through the extensive surfaces in the basis and comparable scenarios apply to bryozoobines as well as certain pyrgo-

matids. In fact, derived forms of *Pyrgoma*, including *P. kuri* and *P. cancellatum* are associated with either slower-growing corals, or the slower growing portions of them.

It is important to note that atria in the basis are simply built as periodic replications of the gap along the wall-basis suture, i. e., there is in essence a continuity of atrial structures between all three groups of symbiotic barnacles. Therefore, we suggest the appearance of the complex manifestations of this junction in pyrgomatids remained latent until need arose in derived forms, rather than that atria were either lost or nonexistent in early forms.

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