

# A new genus and species of barnacle (Cirripedia, Verrucomorpha) associated with vents of the Lau Back-Arc Basin: its gross morphology, inferred first juvenile stage and affinities

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## ABSTRACT

Two specimens of a remarkable new neoverrucid and a few metamorphosing cyprid larvae containing its inferred first juvenile stage were found among the barnacles collected by the submersible *Nautile* during the BIOLAU Expedition (1989) to the Lau Back-Arc Basin, Tonga. The new form, *Imbricaverruca yamaguchii* n. gen. and n. sp., differs from the only previously known species, *Neoverruca brachylepadiformis* Newman, 1989, in having an operculum with a relatively large, permanent median latus and a reduced primary wall supported by relatively large, close-fitting, imbricating plates, the lowermost of which are apparently not deciduous. On the other hand, it has a superficial facies similarity with verrucids. However, its construction and inferred first juvenile stage are quite different whereby it appears to represent a relatively specialized neoverrucid rather than an evolutionary step leading to proverrucids and/or verrucids. The new form not only provides evidence that a significant diversification took place within the neoverrucids, it constitutes a significant addition to our knowledge of the vent-inhabiting cirriped fauna of the Lau Basin already considered the most diverse known in the world.

## KEY WORDS

Vent fauna,  
thoracican first juveniles,  
systematics,  
evolution,  
biogeography.

## RÉSUMÉ

*Un nouveau genre et une nouvelle espèce de cirripède (Cirripedia, Verrucomorpha) des sources hydrothermales du bassin de Lau : morphologie générale, premier stade juvénile et affinités.*

Deux spécimens d'un nouveau Neoverrucidae remarquable et quelques larves cypris en métamorphose contenant leur premier stade juvénile supposé ont été trouvés parmi les cirripèdes récoltés par le sous-marin *Nautile* pendant la campagne BIOLAU (1989) dans le bassin arrière-arc des îles de Lau, à Tonga. La nouvelle espèce, *Imbricaverruca yamaguchii* n. gen. et n. sp., se différencie de la seule espèce précédemment connue, *Neoverruca brachylepadoformis* Newman, 1989, par son opercule relativement grand, une plaque latérale médiane permanente et une muraille primaire réduite soutenue par des plaques relativement grandes, bien jointes et imbriquées, dont les plus basses sont apparemment permanentes. D'autre part, l'espèce a un aspect superficiel similaire aux Verrucidae. Toutefois, sa construction et son premier stade juvénile sont très différents, ce par quoi l'espèce semble représenter un Neoverrucidae relativement spécialisé plutôt qu'une étape évolutive conduisant aux Proverrucidae et/ou aux Verrucidae. La nouvelle espèce ne prouve pas seulement qu'une diversification est intervenue parmi les Neoverrucidae, elle représente un complément significatif à notre connaissance de la faune des cirripèdes des sites hydrothermaux du bassin de Lau, déjà considérée comme la plus diversifiée du monde.

## MOTS CLÉS

Faune des sources hydrothermales, premiers stades juvéniles de cirripèdes thoraciques, systématique, évolution, biogéographie.

## INTRODUCTION

Explorations of deep-sea hydrothermal vents, which began barely 20 years ago, have revealed a remarkable diversity of unusual invertebrates, many of which are endemic at relatively high taxonomic levels (McLean 1985; Newman 1985; Tunnicliffe 1992; Desbruyères & Segonzac 1997; Tunnicliffe *et al.* 1998). Some of the animals encountered were evidently derived from taxa inhabiting the surrounding deep sea, or from those inhabiting "cognate" environments such as cold and hydrocarbon seeps (Newman 1985), dead whales (Smith *et al.* 1989) and sunken wood (Dando *et al.* 1992). But many have no known living representatives from which they could have been derived and this is particularly true among the barnacles (Newman 1979; Newman & Hessler 1989; Yamaguchi & Newman 1990; Newman & Yamaguchi 1995). The new barnacle (Fig. 1A), from the Lau Back-Arc Basin, Tonga (NAUTILAU 1991), belongs to the Neoverrucidae, suborder

Verrucomorpha. It is a relatively advanced form compared to the only other known neoverrucid, *Neoverruca brachylepadoformis* Newman, 1989 (in Newman & Hessler 1989). The verrucomorphs or asymmetrical sessile barnacles first appear in the Late Cretaceous as the Proverrucidae and Verrucidae (Newman *et al.* 1969; Buckeridge 1996). However, while the neoverrucids presently have no fossil record, they are not only morphologically vastly more primitive than the other two families, they have clearly descended from the most primitive suborder of sessile barnacles, the Brachylepadoromorpha (Newman & Hessler 1989). In fact, the side with the movable operculum in *Neoverruca* is virtually indistinguishable from either side of a brachylepadoromorph, the only notable differences between the movable and fixed sides being the complete loss of the median latus and the marked gap between the rostrum and carina of the latter.

The brachylepadoromorphs were thought to have gone extinct in the Miocene until the recent discovery of a living representative in the Lau Basin

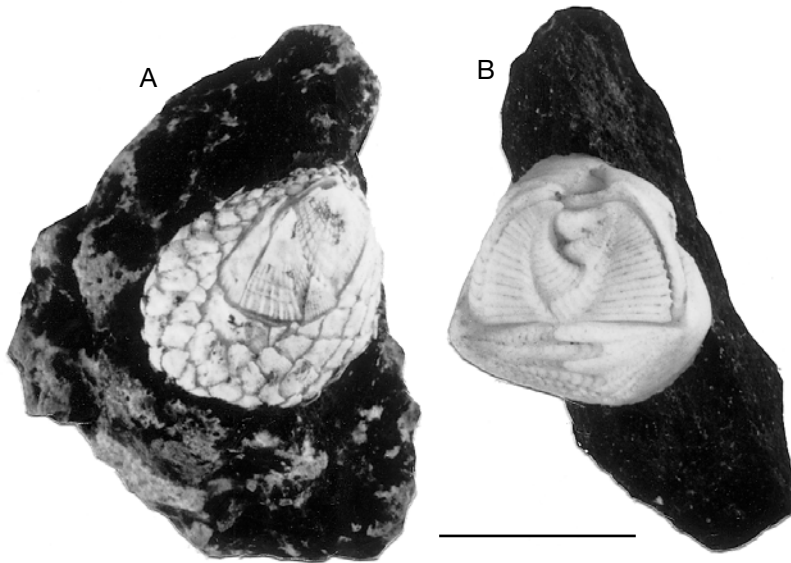


FIG. 1. — **A**, *Imbricaverruca yamaguchii* n. gen. and n. sp. (holotype, MNHN Ci2710); **B**, *Verruca* s.l., both viewed from above with the right scutum and tergum forming the operculum. Note that in the former the four plated wall appears to be covered largely by imbricating plates and the operculum includes a large median latus, characters that readily distinguish it from *Neoverruca*. Scale bar: 5 mm.

(Newman & Yamaguchi 1995). Since fossil brachylepadomorphs, extending back to the Late Jurassic, well before the appearance of the Verrucomorpha (Late Cretaceous), are generally disarticulated, and since even an articulated primitive neoverrucid like *Neoverruca* is not easily distinguished from a brachylepadomorph, distinguishing between their fossil remains would be difficult at best. Therefore it seems likely some fossil material presently attributed to the brachylepadomorphs or related scalpellomorphs may actually represent neoverrucids, just as early workers including Darwin (1854) identified yet to be recognized brachylepadomorphs as scalpellomorphs (Withers 1953).

Contrary to the generalization proposed by Tunnicliffe *et al.* (1998), that the diversity of vent organisms is greater in the eastern than the western Pacific, the greatest diversity of vent barnacles is in the relatively poorly sampled western Pacific, and this trend in diversity is in keeping with that known in deep-sea as well as the shallow-water faunas (Newman & Yamaguchi 1995; Yamaguchi & Newman 1997). Therefore, if the vent barnacles are any indication, the supposed reversal of

the diversity gradient for vent organisms indicated by Tunnicliffe *et al.* (1998) may be in large part a reflection of the vastly different sampling intensities in the two regions.

The new neoverrucid to be described here is relatively advanced compared to *Neoverruca*. Therefore knowledge of it is relevant not only to our understanding of the remarkable radiation of asymmetrical sessile barnacles, of which we presently know of but two, but to an appreciation of the refugial nature, rich diversity and faunal legacy afforded by hydrothermal vents.

#### SYSTEMATICS

Subclass CIRRIPEDIA Burmeister, 1834  
(Cambrian-Recent)

Superorder THORACICA Darwin, 1854  
(Cambrian-Recent)

Order SESSILIA Lamarck, 1818  
(Upper Jurassic-Recent)

Suborder VERRUCOMORPHA Pilsbry, 1916  
(Late Cretaceous-Recent)

Family NEOVERRUCIDAE Newman  
in Newman & Hessler, 1989 (Recent)

DIAGNOSIS. — Distinguished from the extinct Proverrucidae and extant Verrucidae in having a primary wall elevated above the substratum by basal whorls of imbricating plates and an operculum including a median latus at least in juveniles (Newman 1989: 268).

*Imbricaverruca* n. gen.

TYPE SPECIES. — *Imbricaverruca yamaguchii* n. sp.

ETYMOLOGY. — From the Latin *imbric-* (to cover with tiles or scales) and *Verruca*, in reference to its otherwise *Verruca*-like appearance.

DIAGNOSIS. — A neoverrucid differing from *Neoverruca* in numerous ways including having 1) a more verrucid-like operculum despite having the included median latus well developed rather than vestigial or absent, 2) a fixed scutum and tergum much wider than high rather than at least as high as wide, and 3) in retaining a complete set of well developed imbricating plates on the movable side of the wall.

*Imbricaverruca yamaguchii* n. sp.  
(Figs 1A; 2; 3; 4C; 5; 6)

MATERIAL. — Specimens were collected by the French submersible *Nautile*, BIOLAU Cruise of 1989 to the Lau Basin, Tonga (A.-M. Alayse-Danet, chief scientist), and they were received from the Centre national de tri d'Océanographie biologique (CENTOB), IFREMER, Brest. Two adult specimens on round stones partially coated with sulfide deposits, plus several juveniles about to shed their cyprid shells, inferred to belong to this species (Jensen's x-juveniles of Høeg & Newman 1997; see below), all from station 1 (Hine Hina, 22°32'S, 176°43'W, at 1900 m depth). Two of these samples (BL-01 & BL-03) contained other vent barnacles and other vent organisms (Newman & Yamaguchi 1995; Yamaguchi & Newman 1997; Southward & Newman 1998; cf. Desbruyères *et al.* 1994).

ETYMOLOGY. — Named for Toshiyuki Yamaguchi in appreciation of his numerous and exacting works on the systematics and ecology of the living and fossil cirrped, especially the vent barnacles.

DIAGNOSIS. — As for the genus.

Sample	R-C	W	Type designation	Depository
1. BL-01	-7	-6	holotype (intact)	MNHN-Ci2710
2. BL-01	-7	-6	paratype (dissected)	MNHN-Ci2711
3. BL-03	Jensen's x-juveniles, care of J. Høeg, Copenhagen			

R-C rostro-carinal diameter  
W width, both in mm.

COMPARATIVE DESCRIPTION

*Hard parts*

The low-conic profile of the new genus, *Imbricaverruca*, is similar to *Neobrachylepas* Newman & Yamaguchi, 1995, whose representatives were relatively young, and to the juveniles of *Neoverruca* and *Eochionelasmus* Yamaguchi & Newman, 1990. The operculum forms a flat lid, as in the Proverrucidae and Verrucidae, but the hinge line is curved rather than essentially straight as in *Neoverruca*, and in higher verrucomorphs (cf. Figs 1A; 2A). Therefore, in order for the operculum to open, there is likely some flexibility to the wall as well as some freedom in the arthrodial membrane forming the hinge, and it must be able to bend

along the scuto-tergal articulation, an ability likely facilitated by the basal gap protected by the median latus (Fig. 2C). Like *Neoverruca*, the scutal adductor muscle inserts in a pocket below the apex of the movable plate (Fig. 2E), and its origin on the fixed scutum, near the centre of the plate (Figs 2G; 4C), is supported by an adductor ridge or "myophore" as in *Metaverruca* Pilsbry, 1916 and *Verruca* Schumacher, 1817 (cf. Young 1998 for revision) (Fig. 4G-H).

The fixed scutum and tergum are much reduced in height (Fig. 2F-G, J-K) and there is a complex articulation between them. Together with the rostrum and carina, which are also much wider than high, they form a ring-like wall supporting

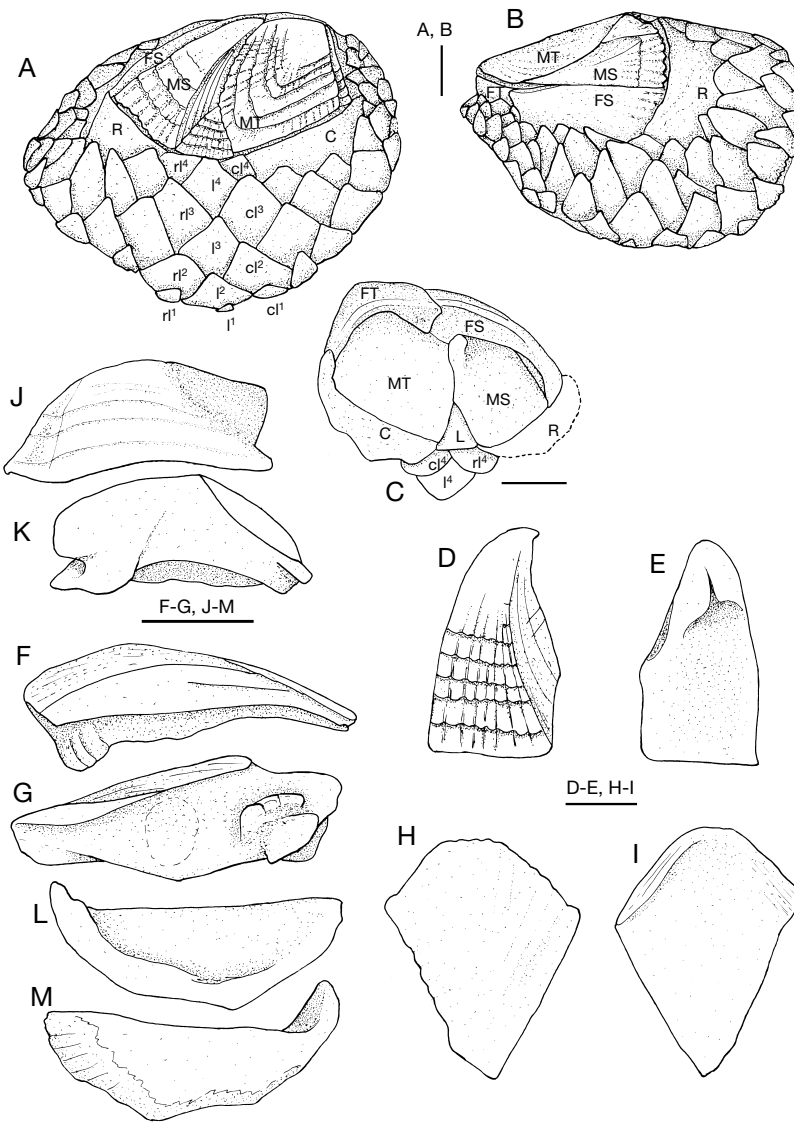


FIG. 2. — Plates of *Imbricaverruca yamaguchii* gen. et n. sp. (paratype, MNHN Ci2711) ; A, B, viewed from above and from the rostral end, respectively; A, note the operculum, comprising the plates of the right side (MS-L-MT), includes a large median latus; B, note the slightly open aperture to the mantle cavity between the occludent margins of the movable (MS & MT) and the fixed (FS & FT) scutum and tergum, respectively; C-M, variously disarticulated hard parts; C, interior view of wall (R-C-FS-FT) and operculum (MS-L-MT) with all of the imbricating plates, except the uppermost of the three principle lateral tiers of the right side ( $r1^1$ - $r1^4$ - $cl^1$ ), stripped away [an approximation of the rostrum (R), which did not survive dissection, is indicated by the dashed line]; D, E, movable scutum (MS); external and internal views respectively; scutal adductor muscle, inserting from just below to up under the apical concavity in Fig. 2E, extends to its origin on the fixed scutum (FS, Fig. 2G; the relationship of MS to FS can be seen in Fig 2C); F, G, fixed scutum (FS); basal and internal views, respectively. Dashed line in G indicates origin of scutal adductor muscle but no scar is evident. The relationship of the two protuberances (best seen near the tergal margin in Fig. 2G) to the fixed tergum (FT, Fig. 2J, K), was not resolved; H, I, movable tergum (MT); external and internal views respectively (external corrosion in bleach and cleaning inadvertently obliterated growth line ornamentation in H); J, K, fixed tergum (FT); external and internal views respectively; L, M, carina from below and above respectively (the rostrum did not survive dissection and cleaning). Abbreviations: C, carina;  $cl^{1-4}$ ,  $r1^{1-4}$ , carino-lateral, lateral and rostrolateral plates forming three tiers each four plates high, respectively; FS, FT, fixed scutum and tergum; L, median latus; MS, MT, movable scutum and tergum; R, rostrum. Scale bars: 1 mm.

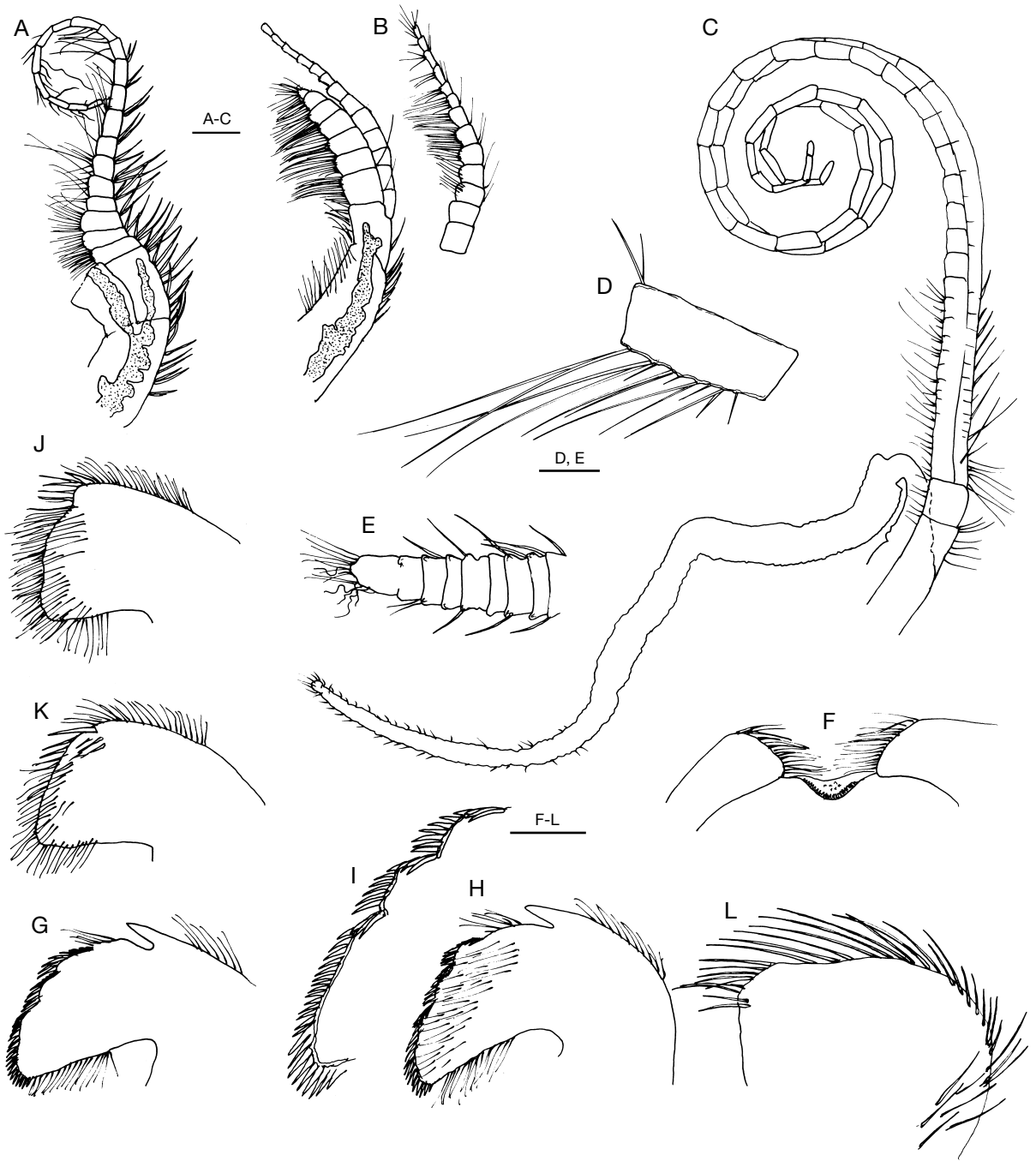


FIG. 3. — Cirri (right side) and the trophi (appendages from the right side viewed from without, those of the left sides from within) of *Imbricaverruca yamaguchii* n. gen. and n. sp. (paratype, MNHN Ci2711); **A**, cirrus I, anterior ramus missing; **B**, cirrus II, setae omitted from the posterior ramus of the intact cirrus (left) are shown on the excised ramus (right); **C**, cirrus VI (setae of distal half omitted) and penis (annulations omitted); **D**, setation of an intermediate segment of outer ramus of cirrus VI (17th article from distal end); **E**, end of penis enlarged; **F**, labrum and mandibular palps; **G**, **H**, right and left mandible; **I**, spinous margin of H enlarged; **J**, **K**, right and left first maxillae; **L**, right second maxilla. Scale bars: A-C, 0.5 mm; D, E, 0.15 mm; F-L, 0.2 mm.

the operculum. Therefore, the imbricating plates between this primary wall and the substratum form a substantially greater proportion of the body chamber than in *Neoverruca*. The principal three tiers of lateral imbricating plates, standing four plates high ( $rl^{1-4}$ ,  $l^{1-4}$  and  $cl^{1-4}$ ), are fully represented in these two apparently adult *Imbricaverruca* (Figs 1A; 2A; 4C), as they are in brachylepadomorphs (Newman 1987: fig. 4A) and in the juveniles of *Neoverruca* (Newman & Hessler 1989; Newman 1989).

#### Soft parts

The trophi and cirri (Fig. 3) are similar to those of other hydrothermal vent barnacles (Scalpellomorpha, Brachylepadomorpha, Verrucomorpha and Balanomorpha), reflecting adaptations to feeding on very fine particles, presumably small, suspended bacterial clumps and filaments (cf. Southward & Newman 1998). The slightly bullate, indented but unnotched labrum of *I. yamaguchii* (Fig. 3F) supports the usual row of fine teeth and relatively large palps provided with relatively fine, stiff setae. The mandible (Fig. 3G, right exterior, H, I, left interior) is comparable to that of other hydrothermal vent forms, especially that of *Neoverruca brachylepadoformis*, in having one superior incisiform tooth above a setose area, followed by two low teeth each supporting a row of numerous, short, sharp spines along their superior curvatures, several of the uppermost of which roll over onto the inner or posterior surface (Fig. 3I), and the upper margin of the inferior angle supports a row of similar spines.

Maxillae I and II (Fig. 3 J, K and L, respectively) each support a relatively uniform comb of slender setae along the cutting edge, but maxillae I of *I. yamaguchii* differs from *Neoverruca* in having a single strong spine among the ordinary setae inside and just below the superior angle (Fig. 3K). What could be seen of the cirri (Fig. 3A-D) suggested they were typical of most vent barnacles, but unfortunately those of the paratype were badly damaged or missing. The right side was in the best condition and the cirral counts are as follows (a, anterior ramus; p, posterior ramus; -, ramus absent; +, terminal articles missing):

Cirrus	I	II	III	IV	V	VI
a	-	7	-	-	-	37+
p	20	13	-	39+	-	41+

As can be observed (Fig. 3A, B), the first two pairs of cirri are modified as maxillipeds and at least the posterior ramus of the first as well as of the second are antenniform. The posterior four pairs of cirri are normal (ctenopod), but the lesser curvature of the intermediate articles of cirrus VI each have as many as five pairs of moderately long setae, fewer than *Neoverruca*, and their s/a ratios are markedly different, that for *Imbricaverruca* falling within the range for other vent barnacles while that for *Neoverruca* is the lowest known (Table 1).

TABLE 1. — Seta/article ratios for four neolepadines compared to four sessile barnacles also from vents: the ratio (the width of the article of an intermediate segment of cirrus VI as the denominator and the length of longest seta of that article as the numerator), while highest in the bacteria-farming neolepadine (*Lau* sp. A), is lowest in *Neoverruca*. That for *Imbricaverruca* as well as for *Neobrachylepas* are not only similar to each other but fall in the low end of the range for vent barnacles.

	Measurement in mm		Ratio s/a	Reference
	article width	setal length		
<i>Lau</i> sp. A	0.33	4.60	14.0	Southward & Newman 1998
<i>Lau</i> sp. B	0.10	0.67	6.7	<i>idem</i>
South-East Indian Ridge	0.18	1.70	9.4	<i>idem</i>
Lihir volcano	0.30	1.85	6.2	<i>idem</i>
<i>Neobrachylepas</i>	0.07	0.31	4.4	Newman & Yamaguchi 1995
<i>Neoverruca</i>	0.25	0.70	2.8	Newman & Hessler 1989
<i>Imbricaverruca</i>	0.15	0.68	4.5	This paper
<i>Eochionelasmus</i> (NFB)	0.25	1.65	6.6	Yamaguchi & Newman 1990

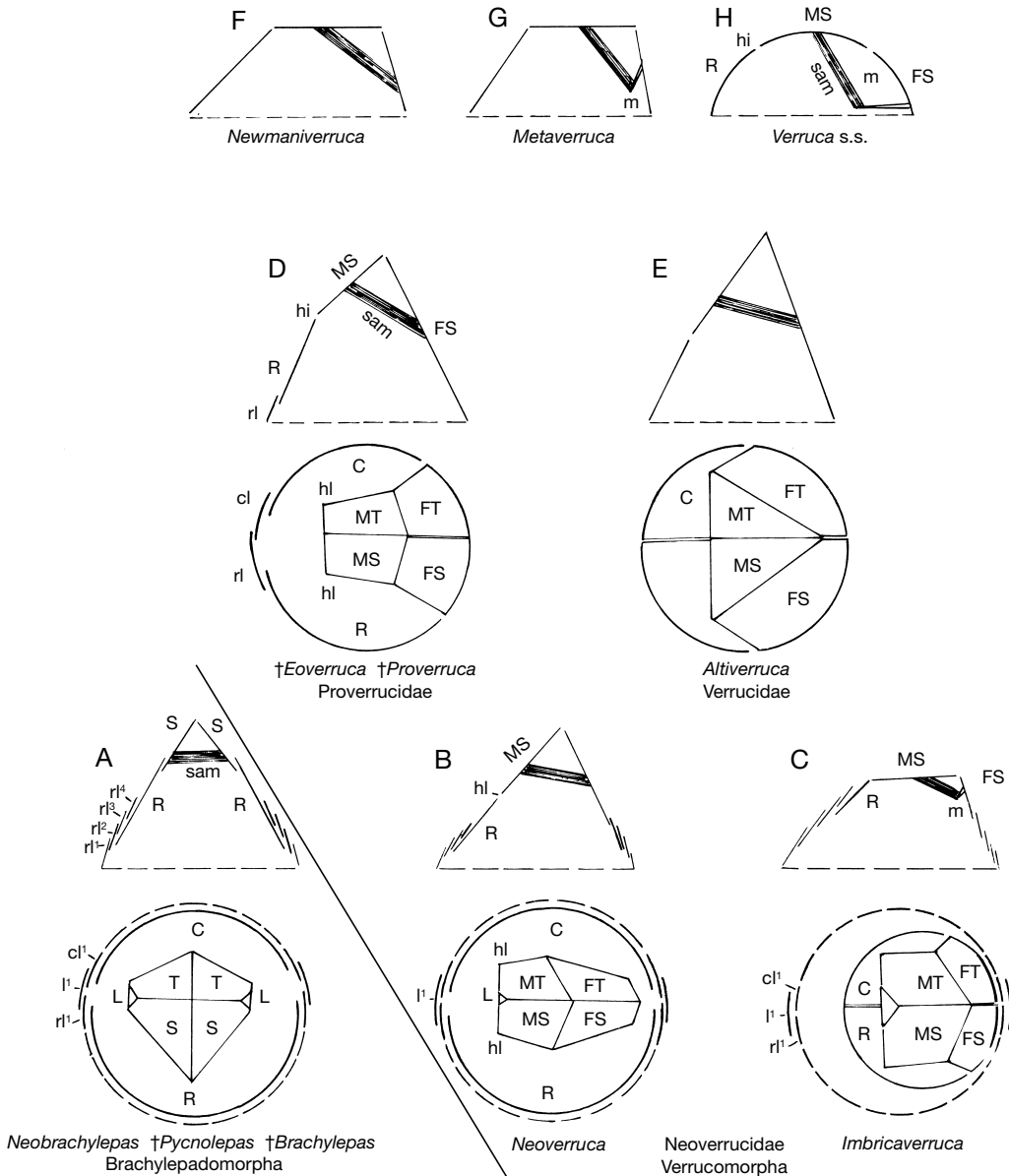


Fig. 4. — Schematic plan views and transverse sections of grades of skeletal organization from the most primitive sessile barnacles (A, Brachylepadomorpha) through the asymmetrical sessile barnacles (B-H, Verrucomorpha). Of the eight verrucid genera currently recognized (Young 1998) only the four most representative ones (*Altiveruca*, *Newmaniveruca*, *Metaveruca* and *Verruca* s.s.) are depicted here. Right sides are to the viewers right and rostral ends are downward in plan views or coming out of the page in transverse sections. The transverse sections are slightly rostral of the rostro-carinal gap or suture. While there are numerous whorls of imbricating plates standing in tiers four plates high in brachylepadomorphs, and on the movable side of neoverruccids, only those of the R-C gap are labeled. Abbreviations: **C**, **R**, carina and rostrum; **cl**<sup>1-4</sup>, **l**<sup>1-4</sup>, **r**<sup>1-4</sup>, carinolateral, lateral and rostrolateral tiers of imbricating plates respectively; **cl**, **rl**, the pair of imbricating plates in proverruccids; **FS**, **FT**, fixed scutum and tergum; **hl**, hinge line; **L**, median latus (completely lost in proverruccids and verrucids); **m**, myophore; **MS**, **MT**, movable scutum and tergum; **sam**, scutal adductor muscle; **S**, **T**, normal terga and scuta in brachylepadomorphs; dashed horizontal lines: membranous basis (transverse sections F-H after Young 1998).



The caudal appendages, while multiarticulate in *Eochionelasmus* and minute and uniaarticulate in *Neolepas* Newman, 1979 and *Neobrachylepas*, are absent in *Imbricaverruca* as well as *Neoverruca* (Fig. 3C). Both adults were hermaphroditic; penis long, conspicuously annulated, and sparsely clothed with short, stiff setae (Fig. 3C, E). While the generally well-developed penes of vent barnacles have a well-developed pedicel, there is no basiodorsal point (Fig. 3C). Well-developed testes extend into the pedicels of cirrus I & II (Fig. 3A, B), and to a lesser degree into at least those of cirrus III & IV. Ovigerous frena were not seen, but no ovigerous lamellae were being incubated and in their absence frena may be easily overlooked.

#### *The x-juvenile*

A number of attached cyprids found on sulfide deposits associated with hydrothermal activity were included with the collection from the Lau Basin sent by CENTOB. Some were sent to Peter G. Jensen for the study of lattice organs (cf. Jensen *et al.* 1994) who removed the cyprid shell covering the first juvenile stage inside, when preparing them for SEM. Some of these were neolepadines but two were the first juvenile stage of an unusual thoracic cirriped. It was studied and dubbed "Jensen's x-juvenile" by Høeg & Newman (1997) (Fig. 5). Its capitulum, supported by a peduncle of comparable length, is armored by the five primordial valves commonly found in juvenile thoracicans, except iblomorphs.

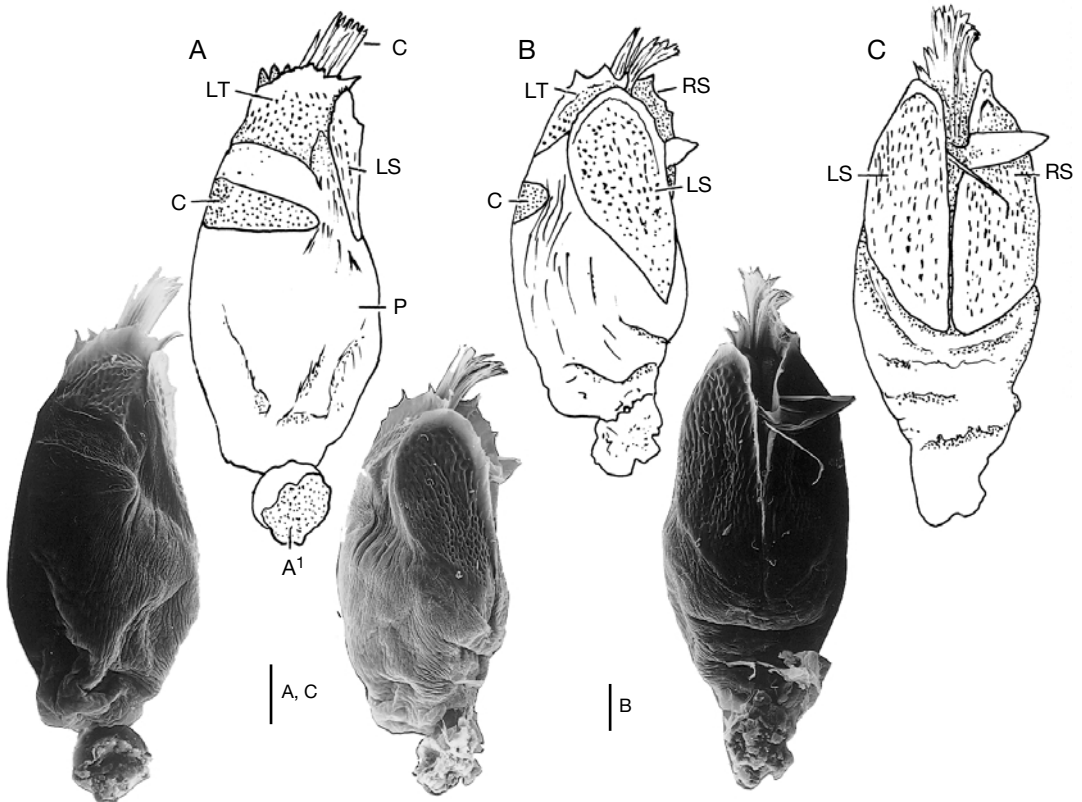


FIG. 5. — Jensen's x-juvenile from the Lau Basin, Tonga (Høeg & Newman 1997); **A**, viewed from the left dorso-lateral; **B**, left lateral; **C**, ventral sides, respectively (the shard of chitin extending from the aperture in B and C apparently left over from the last molt). It is a first juvenile of a thoracic cirriped and likely that of *Imbricaverruca yamaguchii* n. gen. and n. sp.; see Fig. 6 and text for explanation. Abbreviations: **A**<sup>1</sup>, first antenna; **C**, carina; "**C**", incipient cirri; **LS**, left scutum; **LT**, left tergum; **RS**, right scutum; **P**, peduncle. Scale bars: 100  $\mu$ m.

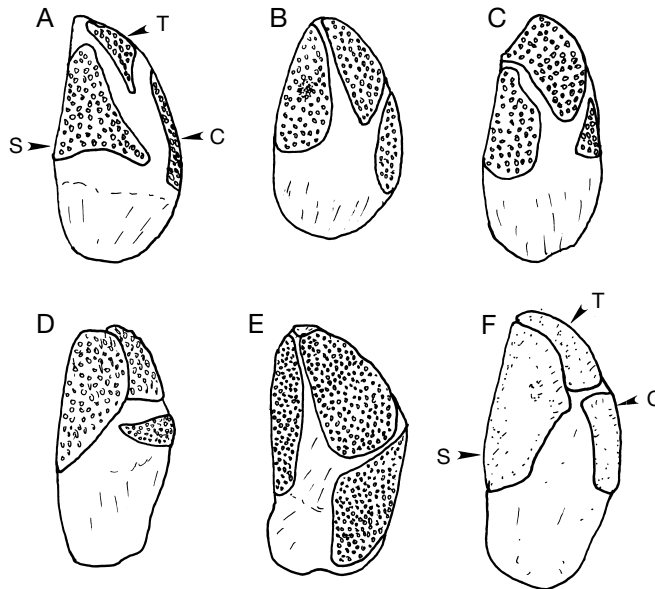


FIG. 6. — Comparison between the primordial plates of the earliest juvenile stages of the principal suborders of thoracic Cirripedia; **A**, Lepadomorpha, *Lepas* (from Newman *et al.* 1979: fig. 87); **B**, Scalpellomorpha, composite of *Neolepas* and *Pollicipes* (respectively from Newman, in prep. and Broch 1922); **C**, *Neoverruca* (reconstructed from Newman 1989); **D**, x-juvenile (Høeg & Newman 1997 & herein); **E**, *Verruca* and *Semibalanus* (respectively from Runnström, 1925, 1927). Abbreviations: **S**, scutum; **T**, tergum; **C**, carina).

TABLE 2. — Comparison between the primordial plates of the earliest juvenile stages of the principal suborders of thoracic Cirripedia (See Fig. 6 for corresponding figures and text for a full explanation).

Taxon/Character	Carinal proportions	Carinal of position	Terga and scuta of each side
Lepadomorpha (Fig. 6A)	Higher than wide and longer than terga	Extending up between terga	Symmetrical
Scalpellomorpha (Fig. 6B)	Higher than wide and nearly as long as terga	Extending up between terga	Symmetrical
Verrucomorpha			
Neoverrucidae (Fig. 6C)	Higher than wide and shorter than terga	Extending up between terga	Initially symmetrical
X-juvenile (Fig. 6D)	Wider than high, shorter than terga and perhaps displaced to one side	Not extending up between terga	Scuta if not terga initially symmetrical
Verrucidae (Fig. 6E)	About as wide as high, shorter than terga and displaced to one side	Not extending up between terga	Distinctly asymmetrical
Balanomorpha (Fig. 6F)	Higher than wide	Not extending up between terga	Symmetrical

The position and shape of the carinal primordium and a slight asymmetry between the scuta suggested the juvenile was a verrucomorph (Høeg & Newman 1997).

The early juveniles of *Neoverruca* (Newman, 1989) can be distinguished from the x-juvenile in being more generalized; e.g. in having a carinal primordium that is higher than wide extending up between the terga (Fig. 6; cf. Table 2). The only first juvenile of a verrucid known is that of *Verruca stroemia* Müller, 1776 described by Runnström (1927) and it differs from the x-juvenile in the scutal primordia being grossly unequal rather than nearly equal in size. Therefore it was concluded the x-juvenile could represent 1) a verrucid more primitive than *V. stroemia* such as an *Altiverruca*, 2) an advanced neoverrucid such as the one described from Lau herein, or 3) a yet-to-be discovered population of the presumably extinct proverrucid, and it was thought that, because of these uncertainties, determining the affinities of Jensen's x-juvenile would require further sampling of the Lau Basin fauna (Høeg & Newman 1997). However, the Lau neoverrucid, now known as *Imbricaverruca*, turned out not only to be more highly evolved than *Neoverruca*, but the adult has an autapomorphy, a carina that is much wider than high, which is the most notable characteristic of the x-juvenile. Therefore it seems highly likely that Jensen's x-juvenile is the first juvenile of *Imbricaverruca*.

#### *Origin and diversification of the Verrucomorpha*

Until recently, the affinities of the verrucomorphs have been puzzling. This was in good part due to the fact that while sessile, they appeared to share as many characters with the scalpellomorphs as with the balanomorphs. Darwin was the first to study their anatomy in detail and work out the homologies of their plates, and in his first volume on the fossil barnacles he notes (1851: 5), *Verruca* "[...] though hitherto included amongst the Sessile Cirripedes, must, when its whole organization is taken into consideration, be ranked in a distinct family of equal value with the Balanidae [balanomorphs] and Lepadidae [scalpellomorphs], but perhaps more nearly related to the latter than to the Sessile Cirripedes." In his second volume on the fossil barnacles [1855

(1854): 41], he again notes that "Upon the whole, the Verrucidae are nearly equally related to the Lepadidae and Balanidae; but certainly nearer to the Lepadidae, than to the sub-family Balaninae or typical sessile cirripedes..." But he then goes on to write, "[...] if compelled to place *Verruca* in one of these two families, I should place it amongst the Chthamalinae, the other sub-family of the Balaninae", and on the same page he notes this was written after his Ray Society monograph on the living sessile barnacles (1854: 495) where he gives a more detailed version of the same thing. So, while the verrucomorphs shared characters more or less equally between the scalpellomorphs and balanomorphs, Darwin considered them not just early sessile barnacles but, if compelled to place them within the existing classification, he would include them with the primitive balanomorphs. However, when it came to his classification, Darwin abandoned the Pedunculata and Sessilia as formal taxa, and subsequent workers (Pilsbry 1916; Withers 1928; Krüger 1940) followed suit. Consequently the sessile barnacles, Verrucomorpha and Balanomorpha, were considered to have sprung independently from the scalpellomorphs (Newman *et al.* 1969: R266, fig. 133; Ghiselin & Jaffe 1973: fig. 1; Newman & Ross 1976: fig. 2).

In the meantime, however, a third group of sessile barnacles, the presumably extinct Brachylepadomorpha, was discovered (Woodward 1901, 1906), which Woodward considered central to the origin of the sessile barnacles. However, largely due to the authority of Pilsbry (1916: 14), who considered the brachylepadomorphs at least pedunculate barnacles if not simply scalpellomorphs, they came generally accepted as an independent sessile group whereby the sessile barnacles were at least triphyletic (cf. Withers 1928; Krüger 1940; Newman *et al.* 1969; Newman & Ross 1976; Newman 1982). However, some authors argued that the brachylepadomorphs were better candidates than the scalpellomorphs for the ancestors of the balanomorphs (Withers 1912; Newman 1987), and if so the sessile barnacles would be diphyletic rather than triphyletic. Furthermore, it was noted the brachylepadomorphs were also better candidates for the origin

of the verrucomorphs, and if so, the sessile barnacles would be monophyletic (Newman 1987: 8, 19 & 33).

Compelling evidence for a brachylepadomorph origin of the verrucomorphs appeared with the astonishing discovery of *Neoverruca* (Newman & Hessler 1989), whereby monophyly for the sessile barnacles became the favored hypothesis (Newman & Hessler 1989; Yamaguchi & Newman 1990; Buckeridge & Newman 1992; Glenner *et al.* 1995; Newman 1996). When viewed from one side, this barnacle has the same arrangement of opercular, wall and imbricating plates as a brachylepadomorph. The opposite side was peculiar and if there had been but one specimen available it easily could have been considered an imperfectly developed brachylepadomorph, due to crowding, predation damage or the like. But there were numerous specimens each with an "anomalous" right or left side. The basis for the

anomaly was the tergum and scutum of that side being immovably integrated into the wall, as in verrucomorphs. Thus, a better "missing link" between the brachylepadomorphs and verrucomorphs could hardly have been imagined.

*Imbricaverruca*, while wholly a neoverrucid in organization, differs from *Neoverruca* in outwardly looking more like a verrucid than a brachylepadomorph (Fig. 1). Thus the question arises as to whether it represents a grade between *Neoverruca* and the proverrucids. The evidence from both juvenile and adult morphology suggests not. In short, *Imbricaverruca* has capitalized on the neoverrucid plan rather than making the reductions and acquiring proportions in the direction of those found in modern forms (Fig. 4). Thus the *Neoverruca* and *Imbricaverruca* plans are markedly divergent, the former's being better suited to the derivation of the proverrucid/verrucid plan (Table 3).

TABLE 3. — Comparison of two juvenile and four adult characters in two neoverrucid and one verrucid genus.

	<i>Neoverruca</i>	<i>Imbricaverruca</i>	<i>Verruca</i>
1) Juvenile pedunculate stages	Several stages pedunculate	Likely several stages	Peduncle vestigial
2) Juvenile carina	Higher than wide	Wider than high	Higher than wide
3) Adult median latus	Vestigial	Well-developed	Lost
4) Imbricating plates	Reduced in number, deciduous	Complete, well-developed	Lost
5) Fixed scutum & tergum	Normal, higher than wide	Reduced wider than high	As wide as high
6) Rostrum & carina	Normal, higher than wide*	Reduced, wider high	As wide as high

\*R-C gap less on movable side, as in all three genera.

In Table 3, character 1 concerns the existence of fully pedunculate juveniles during the ontogeny of *Neoverruca* missing in the ontogeny of verrucids, possibly in proverrucids, and in balanomorphs (Newman 1989). Considering the retention of well-developed imbricating plates and the median latus in *Imbricaverruca*, it too likely has several pedunculate stages in its ontogeny. If so, like *Neoverruca*, it is not becoming specialized like verrucids as far as elimination of its pedunculate stages is concerned. Furthermore, it will be noted (character 2), the carina is much wider than high in the presumed juvenile as well as the adult of *Imbricaverruca*, and together with

the reduced rostrum and fixed scutum and tergum, it forms a ring reinforcing the uppermost imbricating plates rather than forming a major part of the wall. A reduction in the extent of the primary wall in *Imbricaverruca* is an autapomorphy leading away from rather than towards verrucids. Character 3 concerns the median latus, on the verge of being lost in *Neoverruca* but very well developed in *Imbricaverruca*. It is apparently completely lost in proverrucids, as in verrucids, so *Neoverruca* rather than *Imbricaverruca* is also closer to them in this regard. Character 4 involves the relative importance of the imbricating plates; their reduction and deciduous nature in

*Neoverruca* in contrast to their further development and importance in *Imbricaverruca*. Character 5 pertains to the relative proportions of the fixed terga and scuta (also note their degree of integration with the rostra and scuta in forming the wall under character 6. In being wider than high, and in their reduced contribution to the wall, those of *Imbricaverruca* differ conspicuously from the relatively unmodified ones of *Neoverruca* and the squarely proportioned ones of *Verruca*. Character 6 pertains to the concomitant changes in the rostrum and carina seen in character 5; e.g. reduction in height and relative importance to the wall which distinguishes *Imbricaverruca* from *Neoverruca* and *Verruca*. It follows, despite *Imbricaverruca* facies similarity with higher verrucomorphs, that *Neoverruca* comes much closer to their ancestral organization plan than does *Imbricaverruca*.

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