A REVISION OF THE DEEP-SEA BARNACLES *PACHYLASMA* AND *HEXELASMA* FROM JAPAN, WITH A PROPOSAL OF NEW CLASSIFICATION OF THE CHTHAMALIDAE (CIRRIPEDIA, THORACICA)[1)]

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With 7 Text-figures

SYNOPSIS

The deep-sea barnacles *Pachylasma* and *Hexelasma* are little known and a few species have been sporadically recorded from isolated localities of all oceans.

Of the genus *Pachylasma*, only two species *P. crinoidophilum* PILSBRY and *P. japonicum* HIRO have been known from Japan. A third species *P. scutistriatum* BROCH is newly added to the Japanese fauna.

The other known species, *P. ecaudatum* HIRO formerly referred to *Pachylasma*, is now transferred to the genus *Hexelasma*, of which two species *H. velutinum* HOEK and *H. callistoderma* PILSBRY only have been so far known from Japan.

An attempt to subdivide the family Chthamalidae into three subfamilies (Catophragminae, Chthamalinae and Pachylasminae) is newly presented.

Systematic Account of the Japanese Species (Revised)

Genus *Pachylasma* DARWIN, 1854

Diagnosis. Chthamalidae having a wall of eight compartments, in which the rostrum and rostrolaterals are united by inconspicuous, linear sutures, or are wholly concrescent in the adult stage, the wall thus becoming virtually six-plated. Radii wanting or very narrow and not well differentiated from the parietes. Wall-plates non-porous, not ribbed on the inner surface in adults. Basis essentially membranous but often secondarily calcified in adults. Scutum without an adductor ridge and a pit for lateral depressor muscle. Caudal appendages present. Labrum without a median notch. Mandible with three teeth and a pectinated lower angle. Living in deep-sea.

Type species. *Pachylasma giganteum* (PHILIPPI, 1836) (Original designation by DARWIN, 1854)

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1. *Pachylasma japonicum* HIRO, 1933

(Japanese name: Beni-atuhuzitubo)

(Figs. 1 and 2)

Pachylasma japonicum HIRO, 1933, p. 65, text-figs. 19–20, pl. III figs. 1–1e (Sôyô-maru St. 303, off Toi-saki, Hiuga-nada, 364 m, on broken tests of the cake urchin *Clypeaster japonicus* Död.); HIRO, 1937, p. 430 (off Seto and Tosa Bay, on a volute shell *Fulgoraria*); UTINOMI, 1964, p. 3 (Tosa Bay, on an Emperor's slit shell *Mikadotrochus hirasei* PILS.).

New Material.—Many specimens attached to the Emperor's slit shell *Mikadotrochus hirasei* (PILSBRY) obtained off the south of Island Okino-sima, southwest of Tosa Bay, 150–170 fathoms. Coll. Kichijiro YAO, 1953. Deposited in the museum of the Seto Marine Biological Laboratory.

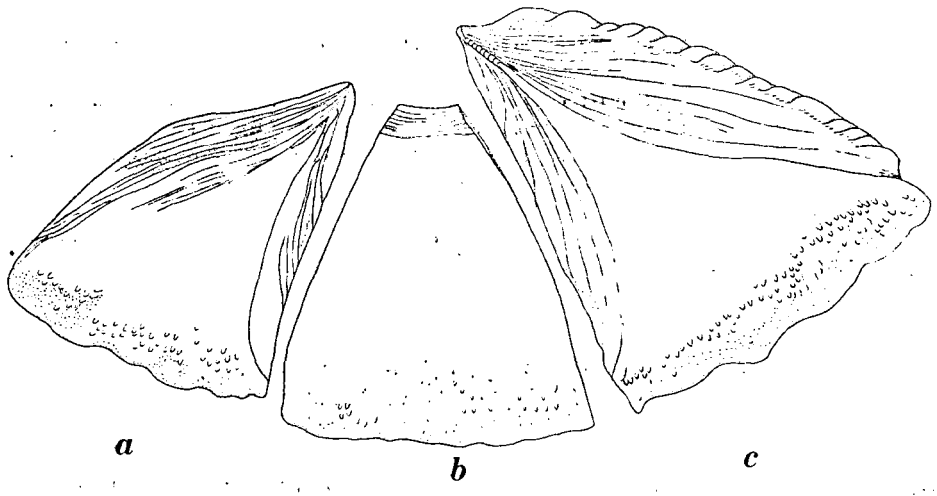

Fig. 1. *Pachylasma japonicum* HIRO.
Inner view of rostrum and 2 rostrolaterals, when separated. *a*, Right rostrolateral; *b*, rostrum; *c*, left rostrolateral. (All ×8)

Supplementary Description.—The shells here examined are generally large, depressed conical and yellowish white, tinged orangish towards the carina. The largest one measures about 23.5 mm in carino-rostral diameter, 22 mm in lateral diameter and 10 mm in height. The largest number of barnacles occurring on a shell of *Mikadotrochus hirasei* (PILSBRY), measuring 97 mm long and 100 mm wide, is eleven, all orientating the carina upwards. I have never found this barnacle on other species of *Mikadotrochus* known in Japanese deep-sea.

The orifice is large, diamond-shaped in upper view and quite horizontal *in situ*, in parallel to the base of the wall. The scuta on both sides in the orifice are slightly convex on the upper surface and located on a slightly higher level than the upper

margins of the wall (at least 2-3 mm *in situ*). In the largest specimen mentioned above, the orifice is 15 mm long and 11 mm wide, approximately a half as large as the basis.

The external surface of the wall is quite smooth, the growth-lines being not prominent. Of the six sparate compartments, the composite rostral plate is the widest and lacks the alae on both sides, the sutural lines between the real rostrum

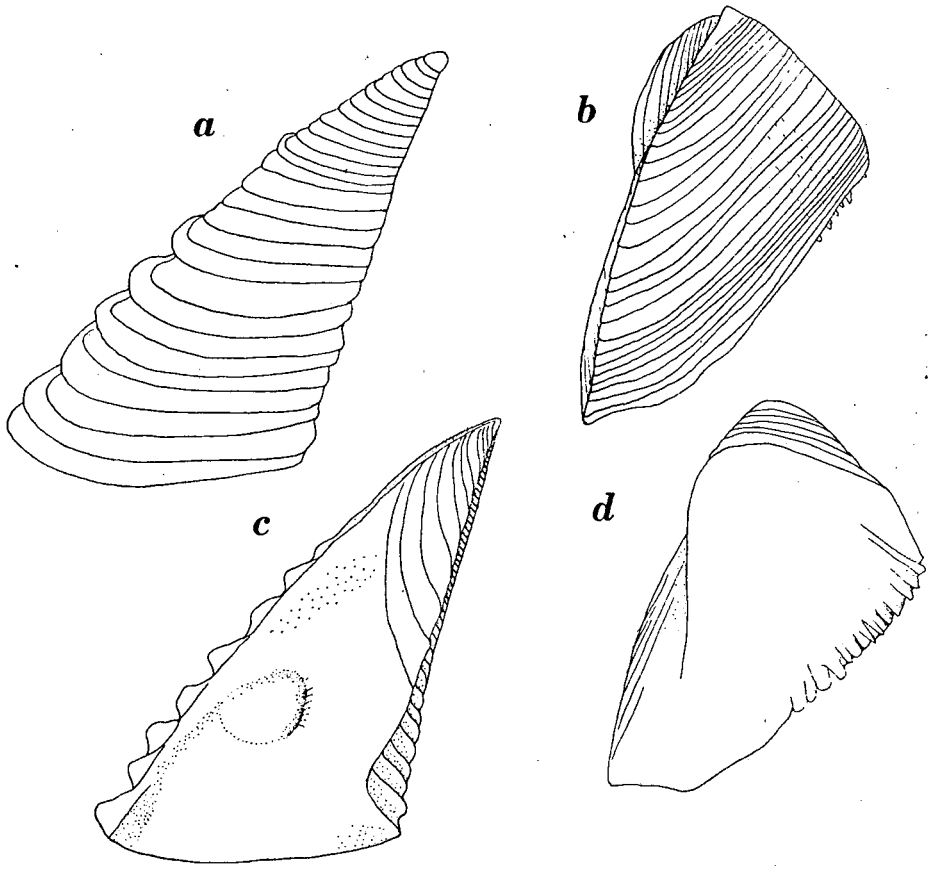

Fig. 2. *Pachylasma japonicum* HIRO.
a, Scutum, outer view; *b*, tergum, outer view; *c*, scutum, inner view; *d*, tergum, inner view. (All ×12)

and rostrolatera being retained both externally and internally. The real rostrum is of an equilateral triangle, truncted at apex and bears a very short sheath, occupying the upper 1/6–1/7 of the height; both the sutural edges are narrow and straight. The rostrolatera has the broad, obliquely striated sutural inner surface, *i. e.* the radii overlapping the lateral and rostral compartments on both sides. Between these inner radii a slight ridge ("shoulder" as DARWIN called) is only retained, not

forming such a sheath as seen in the other separate compartments. In this respect, *Octomeris sulcata* NILSSON-CANTELL presents an intermediate state of development of the sheath between the ordinary forms of the genera *Octomeris* and *Pachylasma* (cf. HIRO, 1939b, p. 256, figs. 5–6).

The lateral and carinolateral compartments are ordinary, as they are completely separated and have a narrow triangular radius on the inner surface only, although the radius is not differentiated from the parietal portion on the outer surface.

The basis in all adults is wholly membranous. The scutum is feebly convex externally, much elongated triangular in outline. The tergal margin is straight and the outer surface is marked with many smooth growth-ridges. The apex is sharply pointed. Internally, the articular ridge is very long and does not protrude beyond the tergal margin of the exterior. The articular furrow is narrow and shallow. The adductor pit is rather shallow and situated in the middle; the rest is smooth.

The tergum is triangular, rather wider than the scutum and flat on the external surface, but often forms a narrow, inflected ledge along the curved scutal margin. The articular ridge is developed and moderately protrudes beyond the scutal margin at the apex. The basal margin is nearly straight, bearing a number of short crests for the depressor muscles and an indistinct spur obscurely coalesced to the obtuse basiscutal angle.

For the mouthparts and internal anatomy refer to the original description (HIRO, 1933).

2. *Pachylasma crinoidophilum* PILSBRY, 1911

(Japanese name: Atuhuzitubo)

(Fig. 3)

Pachylasma crinoidophilum PILSBRY, 1911, p. 81, text-fig. 11, pl. XVII figs. 1–11 (*Albatross* St. 4934, off Kagoshima Gulf, 152 fms., on the stem of a crinoid); PILSBRY, 1916, p. 329 (listed only); NILSSON-CANTELL, 1932, p. 14, text-fig. 5, pl. I figs. 1–2 (Awa and Kanya*, both off Tokyo Bay).

New Material.—9 small specimens, together with *P. scutistriatum* BROCH and *Balanus crenatus* BRUG. 32° 21′ N, 128° 39′ E (south of Goto Islands, western Kyusyu, East China Sea), 200–150 fathoms. Taken by a ship belonging to the "Great Northern Telegraph Company", arrived at Copenhagen on 10 January, 1934. Deposited in the Universitets Zoologiske Museum, Copenhagen.

Supplementary Description.—The shell is white, tinged with light orange towards the apex of the carina, measuring about 5–8 mm in carino-rostral diameter and 4–4.5 mm high.

* 'Kanya' is truly 'Kanaya', Uraga Strait, entrance to Tokyo Bay. 'Awa' is the county name, located south of Kanaya Town.

The rostrum and two rostrolaterals are united by linear sutures distinct both externally and internally; the rostrum has a broad sheath, about two-thirds of the total length; it is about as wide as the rostrolaterals at their bases. The carina rises vertically and recurved at the apex; V-shaped as viewed from above.

The carinolaterals are narrower than the laterals.

The basal margin of these wall-plates are thin and smooth.

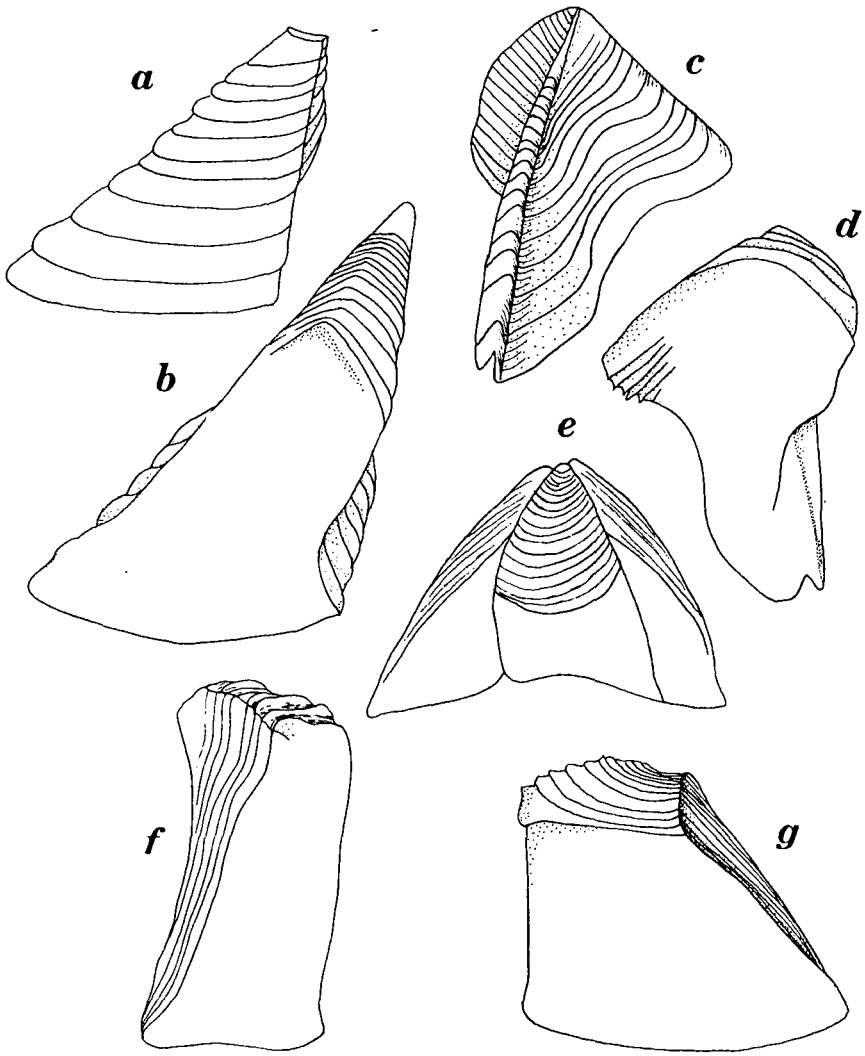

Fig. 3. *Pachylasma crinoidophilum* PILSBRY.

a, Scutum, outer view; *b*, scutum, inner view; *c*, tergum, outer view; *d*, tergum, inner view; *e*, rostrum and rostrolaterals united together by linear sutures, inner view; *f*, carinolateral compartment, inner view; *g*, lateral compartment, inner view.

(All ×12)

The basis is a thin, transparent film which is itself very resistant against treatment with hydrochloric acid, thus it is virtually membranous in nature.

The scutum is marked externally with widely-spaced smooth growth-lines; internally the inflected apical part of the articular ridge is very broad and marked with transverse striae continued from the broad articular furrow; this striated apical part occupies the upper half of the articular ridge to receive the prominently protruding articular ridge of the tergum. The articular ridge is slightly convex and projects beyond the tergal border of the exterior. The inner surface below the striated apex is quite smooth and devoid of any depression for muscle attachment.

The tergum has a short, truncated spur distinctly separated from the basi-scutal angle by a notch which is formed by a strong ridge along the scutal border running from the apex; the basal margin is concave and provided with only 5–6 short crests for the depressor muscles. The articular ridge is well developed and prominently projects beyond the scutal border of the exterior.

The mouthparts and internal anatomy agree well with the former descriptions gvien by PILSBRY (1911) and NILSSON-CANTELL (1932).

3. *Pachylasma scutistriatum* BROCH, 1922

(Japanese name: Yasuri-atuhuzitubo, nov.)

(Figs. 4–5)

Pachylasma scutistriata BROCH, 1922, p. 301, figs. 48–50 (38°12′S, 149°40′E, Bass Strait, SE of Australia), 100–160 fms. Taken by "Endeavour" during Dr. Th. MORTENSEN's Pacific Exped. on 16/IX, 1914. —Types originally designated); NILSSON-CANTELL, 1927, p. 781, text-fig. 17, pl. I fig. 14 (6°15′N, 114°44′E, South China Sea, 400 fms. Pres. by Eastern Telegraph Company and 6°15′N, 93°35′E, SE of Great Nicobar, Indian Ocean, 1120 fms. Pres. by Eastern Extension Telegraph Company).

New Material.—One specimen, together with *P. crinoidophilum* and *Balanus crenatus* BRUG. 32° 21′ N, 128° 39′ E (south of Goto Islands, western Kyusyu, East China Sea, 200–150 fms. Presented by the "Great Northern Telegraph Company" on 10/I, 1934. Deposited in the Universitets Zoologiske Museum, Copenhagen.

Supplementary Description.—A single adult specimen, measuring 20 mm in carino-rostral diameter, 15 mm in lateral diameter, 18 mm in height and 12 mm in orificial diameter, agrees well with the type specimens of *Pachylasma scutistriatum* BROCH now deposited in the Copenhagen Museum and were re-examined by myself through the kindness of Dr. Torben WOLFF of the Museum.

The wall is steeply conical and dirty white all over. The six compartments forming the wall are well separated, thickly solid and apparently smooth on the exterior of parietes, the growth-lines being obsolete. The alae, on the other hand, are very broad, perpendicularly striated in parallel with the margin of the adjoining parietes. Internally, the sheath is very broad, occupying the upper half; the inner

surface below the sheath is almost smooth, but their basal part is roughened with irregular tubercles.

The composite rostral compartment is the widest of all the compartments, about 18 mm wide and 16 mm high. It is composed of the real rostrum fused with two rostrolaterals by linear sutures retained only internally. The rostrolaterals are about 2/3 as wide as the real rostrum at base and bear only the obliquely striated narrow sutural inner surface, in contact with the sheath of the real rostrum; this sutural area is in reality the radius which is not differentiated from the parietal area on the exterior of the compartment.

The laterals are about as wide as the carinolaterals; the right one is 9 mm wide, 15 mm high, while the left one 8 mm wide, 16 mm high. Their sheath is short, 6 mm long, occupying the upper third of the plate. They have the well-developed alae like the carina. The basis remains membranous in the central part, but calcareous in the marginal part towards the base of the wall and ca. 0.8 mm in thickness; its inner and outer surfaces are irregularly rugged (Fig. 5*i*).

The carina is narrower than the composite rostral compartment, and forms a pointed angle (ca. 60°) at the apex by the broad alae on both sides. The sheath inside is very broad and occupies the upper half of the plate, measuring about 11 mm wide at the base of the sheath and 10 mm wide at the base of the wall.

The scutum is triangular with straight margins and externally marked with prominent growth-ridges which are slightly sinuous due to the fine riblets running longitudinally. The apex projects freely and bears internally a distinct longitudinal furrow to receive the articular ridge of the tergum. The articular ridge is moderately developed and protrudes slightly beyond the tergal border of the exterior. The inner surface is almost smooth.

The tergum is roughly triangular and almost flat on the outer surface, although a shallow, broad depression where the growth-lines are prominent can be traced, running from the apex to the spur, bordering by a narrow ridge along the scutal margin. The basal margin is almost straight, the spur being broad, about a half of the basal width and nearly confluent with the basi-scutal angle. The crests for depressor muscles are very numerous, becoming longer towards the basi-carinal angle. The articular ridge is high, quadrangular in inner view and prominently protrudes beyond the scutal border of the exterior.

Mouthparts. The labrum has no notch nor teeth, though hairy all along the cutting edge. The palpus is conical, with setae in the frontal part and along the upper margin.

The mandible has three teeth, not pectinated along their upper edge, and a short pectinated lower angle.

The maxilla I has three-stepped frontal edge bearing spines of different size.

The maxilla II is bilobed, with an inward curvature in the middle, lacking setae.

The *cirri* show the number of segments in their rami as follows:

I	II	III	IV	V	VI	C.A.
14 9	18 19	20 20	26 25	24 26	26 28	12

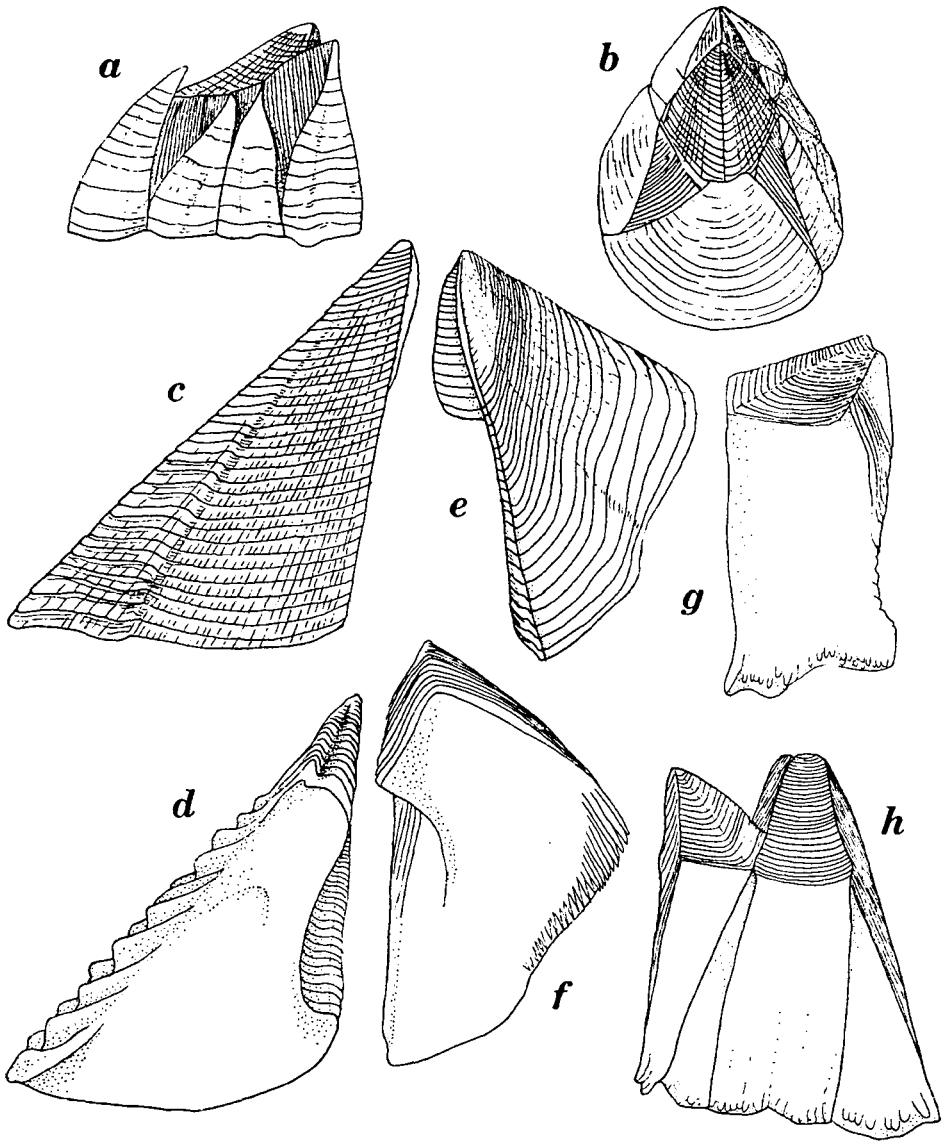

Fig. 4. *Pachylasma scutistriatum* BROCH.

a, Shell, side view; *b*, shell, upper view; *c*, scutum, outer view; *d*, scutum, inner view; *e*, tergum, outer view; *f*, tergum, inner view; *g*, lateral compartment, inner view; *h*, rostrum and rostrolaterals united together by linear sutures, with which a lateral compartment is articulated on the left side. (*a-b* ×1.5, *c-f* ×4; *g-h* ×2)

In the posterior longer cirri IV-VI, the intermediate segments have three pairs of long, stout setae, accompanying a tuft of much smaller setae between the larger pairs on the frontal curved margin.

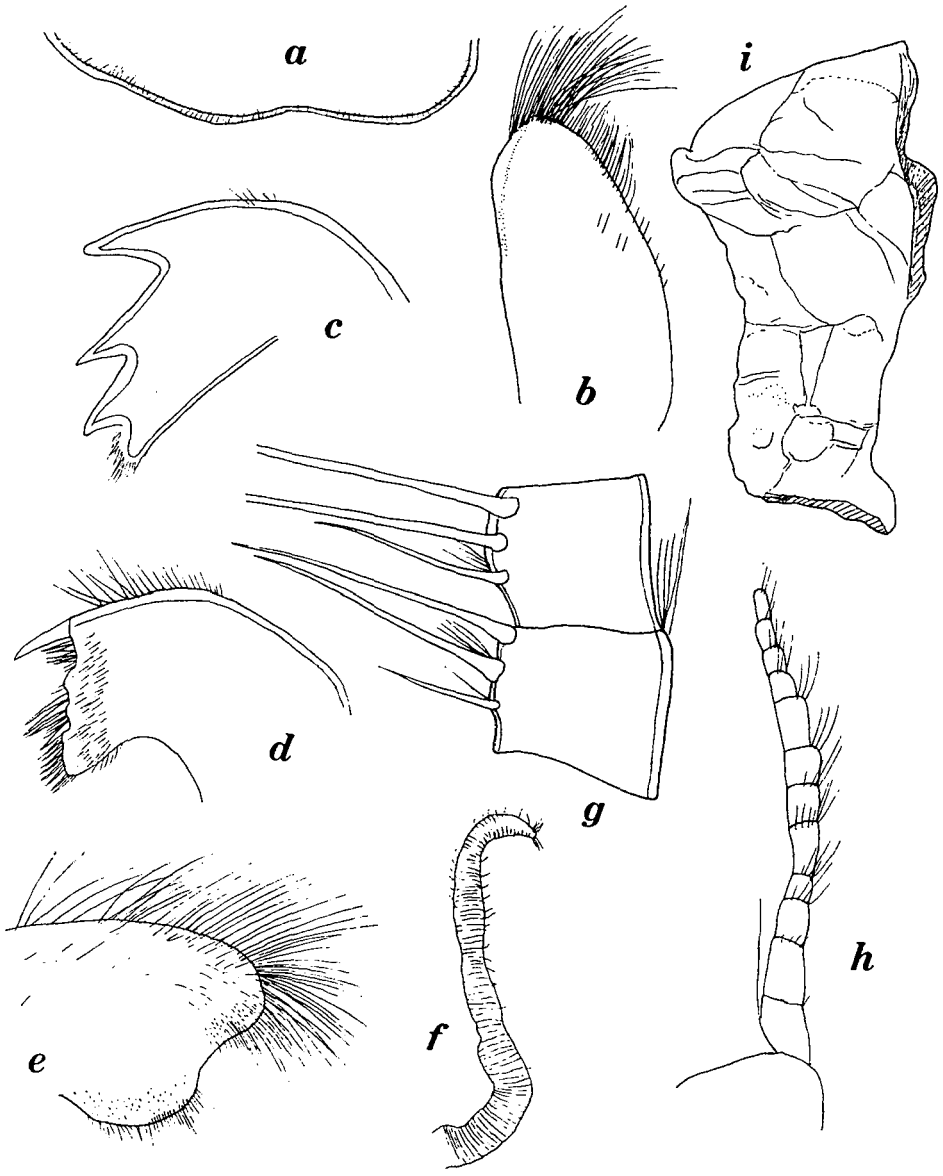

Fig. 5. *Pachylasma scutistriatum* BROCH.
a, Labrum; *b*, palpus; *c*, mandible; *d*, maxilla I; *e*, maxilla II; *f*, penis; *g*, intermediate segments of last cirri; *h*, caudal appendage; *i*, part of strongly calcified basis, inner view.
(*a-e*, *g* ×33; *f*, *i* ×12; *h* ×18)

The caudal appendage is small, 4 mm long and 12-segmented, slightly longer than the protopodite of the last cirri.

The penis is very short, slender and coarsely annulated.

Remarks.—This species was first recorded from Bass Strait, southeast of Australia in the southern hemisphere (BROCH, 1922), and later from the southeast of Great Nicobar, Indian Ocean and South China Sea in the northern hemisphere (NILSSON-CANTELL, 1927). Therefore, this species extends its known range further northward to Japan.

Genus ***Hexelasma*** HOEK, 1913

Diagnosis. Chthamalidae having a wall of six compartments, in which the carina, carinolateral and lateral compartments with alae, but without radii externally differentiated; the rostrum completely fused with rostrolaterals not indicating any suture; parietes not porous and not ribbed inside; basis membranous or partially calcified; scutum often marked internally with a pit or crests for lateral depressor muscles; mouth with the labrum not notched in the middle; mandibles with 3 to 5 sharply pointed teeth; maxillae I with numerous spines beneath the notch; caudal appendages absent; living in deep-sea (HOEK 1913, emend.)

Type Species. *Hexelasma velutinum* HOEK, 1913 (Subsequent designation by UTINOMI, 1965).

4. *Hexelasma velutinum* HOEK, 1913

(Japanese name: Mutuhuzitubo, nov.)

Hexelasma velutinum HOEK, 1913, p. 246, text-figs. 1–2, pl. XXVI figs. 1–16 (Malay Archipilago, 204 to 390 m); BROCH, 1931, p. 53 (Malay Archipilago, 245–290 m); HIRO, 1933, p. 70, pl. III figs. 2 (near Muroto-zaki, Kôti Pref, Japan, 269 m).

No new material is represented here.

5. *Hexelasma callistoderma* (PILSBRY, 1911)

(Japanese name: Suruga-mutuhuzitubo, nov.)

Balanus callistoderma PILSBRY, 1911, p. 78, text-fig. 10, pl. XII fig. 5, pl. XV figs. 3–7 (Suruga Gulf, Japan, 77 fms.).

Hexelasma callistoderma (PILSBRY), PILSBRY, 1916, p. 332, fig. 99 (Suruga Gulf, 77 fms. and off Ose Zaki, 63–68 fms.).

Balanus corolliformis HOEK, KRÜGER, 1911, p. 55, text-figs. 112–114, pl. I fig. 1 and pl. IV fig. 38 (off Misaki, Sagami Bay, Japan, depth unrecorded) Not *Hexelasma corolliforme* (HOEK, 1883 from Antarctic deep-sea).

No new material is represented here.

6. *Hexelasma ecaudatum* (HIRO, 1939) comb. nov.

(Japanese name: Ogasawara-mutuhuzitubo, nov.)

(Fig. 6)

Pachylasma ecaudatum HIRO, 1939a, p. 52, figs. 3–4.

Material Re-examined.—Holotype and paratype specimens attached to the shell of *Malleus regulus* FORSKAAL (SMBL Type 30). Collected by the late Dr. Hayato IKEDA at the north of Muko-zima (28°N, 142°E) in the Ogasawara Islands, 200 m, on July 21, 1938. Deposited in the museum of the Seto Marine Biological Laboratory.

Supplementary Description.—This species has already been described in detail,

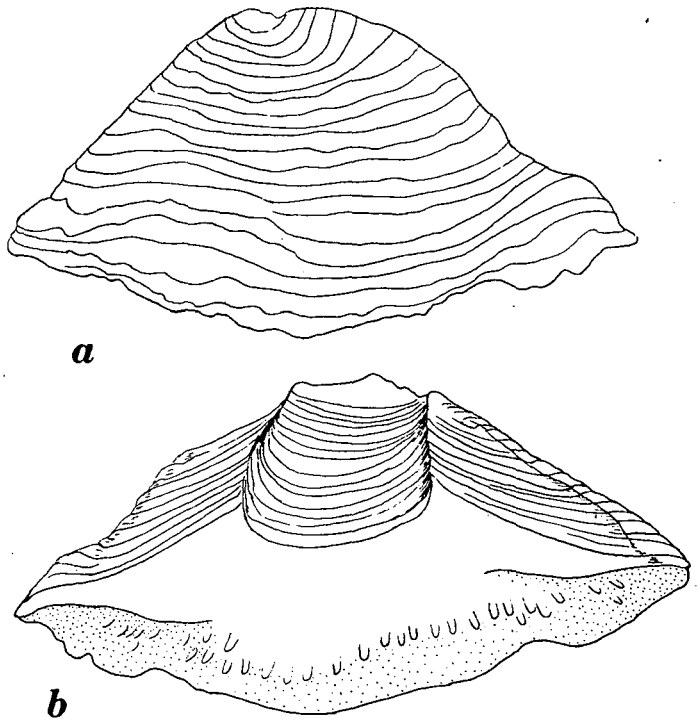

Fig. 6. *Hexelasma ecaudatum* (HIRO).
a, Composite rostral compartment, outer view; *b*, the same, inner view.
(All ×12)

accompanying many illustrations (HIRO, 1939a, pp. 52–56), so that it may be superfluous to reiterate here. However, some important morphological characters are here mentioned as a supplement, in reconsideration on its taxonomical status, comparing with the other larger species such as *Hexelasma corolliforme* (HOEK), *H. hirsutum* (HOEK) and *H. antarcticum* BORRADAILE all of which could be examined actually through

the courtesies of Drs. William A. NEWMAN and A.J. SOUTHWARD.

The wall is thick, 6-plated, and their parietes are whitish, mottled with pink network patterns and their alae are evenly rosy. The growth-lines on the parietes are faint in comparison with *H. corolliforme* and *H. hirsutum.*

The composite rostral compartment (Fig. 6) is wider than high *in situ*, being 3.2 mm high and 7 mm wide; the apex is rounded and the base is slightly flared. Internally, the transversely striated apical part, occupying the upper half of the plate, is tripartite, although perfectly fused; its median area is considered to be the sheath of the real rostrum and the triangular lateral areas are in reality the radii of the rostrolaterals, if they are separated, to overlap the alae of the adjoining laterals.

The lateral and carinolateral compartments are about of the same width (3 mm at base) and bear a broad ala on the rostral side.

The carina is the highest of all compartments, with pointed apex, V-shaped as viewed from above, measuring 4 mm wide at base and 6 mm high; the sheath is about a half of the height.

The basis is thinly calcareous, though remains membranous in the center.

The scutum is feebly convex outsides, elongate-triangular, and coloured pink on the upper half. The outer surface is marked with strongly sinuous growth-ridges. Internally, the adductor muscle depression is broad, but the pit for the lateral depressor muscles cannot be traced. The articular ridge is long and its inflected apical part is elongate but does not protrude beyond the tergal border of the exterior.

The tergum is wider than the scutum, with a broad, short spur followed from a number of projecting crests for the carinal depressor muscles; the spur is distinctly separated from the pointed basiscutal angle; the articular ridge is broad but does not protrude beyond the articular furrow.

Mouthparts. The labrum with a slight concavity is hairy in the middle and provided with a few denticles on both sides.

The mandible has only three teeth, of which the second and third are pectinated along the upper edge, and a pectinated lower angle.

The maxilla I has a wide notch below the upper spine, followed by two series of spines of different size along the frontal edge.

The maxilla II is distinctly bilobed.

In the cirri III to VI, each segment of their rami supports four pairs of long, stout setae on the frontal edge.

The caudal appendge is apparently absent.

Remarks.—In describing this species, I originally referred it to the genus *Pachylasma.* At present, however, I consider it should be referred to the genus *Hexelasma* on account of the complete concrescence of the rostrum and rostrolaterals and the absence of the caudal appendages, although it is closely allied to the type of *Pachylasma, P. giganteum* (PHILIPPI) DARWIN and *P. integrirostratum* BROCH, both having the multiarticulate caudal appendages.

In the chthamalid group the calcification of the basis seems to be a secondary product in growth, so that the character whether the basis is membranous or calcareous, is not an essential character differentiating the genera *Pachylasma* and *Hexelasma*, as is also the case of *Chthamalus*.

Phylogeny of the Deep-sea Chthamalids

(Fig. 7)

The phylogeny of the Chthamalidae has been repeatedly discussed by PILSBRY (1916), NILSSON-CANTELL (1921, 1928), WITHERS (1928, 1935), KRÜGER (1940) and ZULLO (1963).

The Balanomorpha comprise two large groups of sessile barnacles which are generally accepted as the families Chthamalidae and Balanidae. The Chthamalidae in the solid walls and the structure of the compartments and opercular valves, and in certain details of the animal's body, are considered more primitive than the Balanidae, and in many of the characters which differentiate them from the Balanidae they approach the Verrucomorpha on one hand and the Lepadomorpha on the other. The paleontological evidence supports the assumption that the two groups arose independently from the Lepadomorph stock.

The Chthamalidae are represented in the Miocene by *Pachylasma* (*P. giganteum* PHILIPPI) and *Hexelasma* (*H. aucklandicum* HECTOR) and in the Pliocene by *Chthamalus* (*C. ligusticus* DE ALESSANDRI). Of the existing forms of chthamalid group the most primitive and the most generalized form is undoubtedly *Catophragmus* with 8 main compartments and several whorls of imbricating plates at the base, somewhat like the extinct *Pyconolepas* of the Brachylepadomorpha. *Octomeris* also has 8 separate compartments, but it has lost the outer whorls of supplementary plates.

From *Octomeris*-like stock supposedly there are two steps of derivation in the reduction of wall-compartments. One is the *Pachylasma-Hexelasma* series with 6 compartments and the other series is *Chthamalus* with 6 compartments and further *Chamaesipho* with 4 compartments. The former step is supposed to be arisen through the incomplete or complete fusion of the rostrolateral compartments with the rostrum. The latter step is also supposed to be arisen through the total elimination or the complete fusion of the carinolateral compartment with the lateral compartment.

More interesting is the speciation in connection with their habitation. As far as the existing forms are concerned, *Catophragmus* (including *Catophragmus* s. str. and *Catomerus*), which is the most primitive in the wall architecture, lives in the intertidal area, while the related *Chionelasmus* lives in deep-sea (228–288 fathoms), although they have some primitive bodial characters such as the tridentoid mandible, multiarticulated caudal appendages and branchiae. Eight-plated *Octomeris* and the commonest *Chthamalus* and *Chamaesipho* occur on intertidal rocks only. Most of these

genera, however, lack the caudal appendages and branchiae, probably because the wave-beaten habitat most favourable for food-capturing and respiration arose the reduction of such apparatuses, as is also the case of the pedunculate barnacle *Pollicipes* (=*Mitella*) in comparison with the other intertidal hypobiotic forms *Lithotrya*

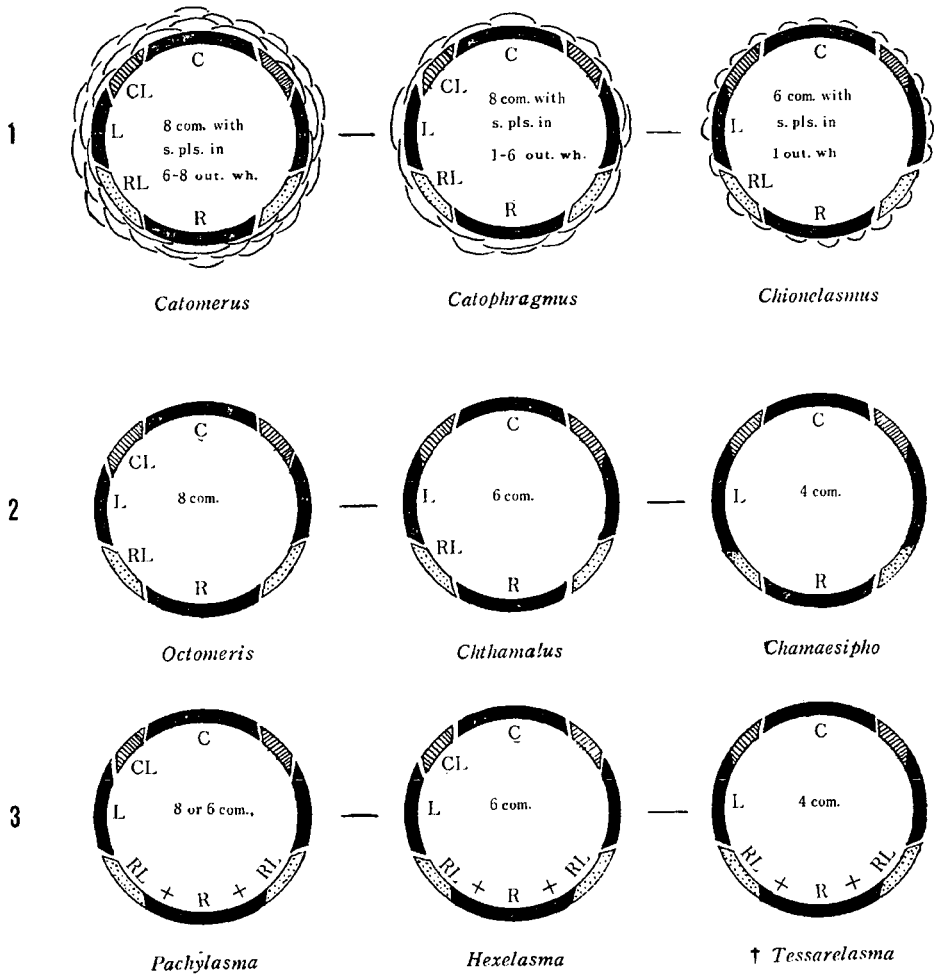

Fig. 7. Diagrams showing the modes of imbrication and the homologies of compartments in the Chthamalidae after a new system of classification.
1, Catophragminae; 2, Chthamalinae; 3, Pachylasminae. C, carina; CL, carinolateral; L, lateral; R, rostrum; RL, rostrolateral. *com*, compartment; *s. pls.*, supplementary plates; *out. wh.*, outer whorl.

and *Ibla*, in which the caudal appendages still remain. In these intertidal chthamalids, the mandibles are either tridentoid or quadridentoid.

Of the deep-sea living genera, *Pachylasma* has exclusively tridentoid mandibles, while *Hexelasma* and *Bathybalanus* have mostly quadri- or quinquedentoid mandibles.

ZULLO (1963), emphasizing the mandibular structure in connection with the feeding adaptations, pointed out the *Pachylasma*-group as highly evolved Chthamalidae and proposed that "Balanidae were derived from the *Pachylasma*-group stock." His opinion is, however, against my view about their phylogenetical trend.

The *Pachylasma*-group is presumably a special derivative survival in deep waters from the ancestral stock and may be comparable with the *Scalpellum*-group in the Lepadomorpha. Many palentological and morphological evidences seem to me to speak for the old Darwinian opinion of the Recent barnacles that the genera with a great number of plates are the most ancient and those with a smaller number of plates have generally been arisen from the former through elimination or fusion of the plates. Indeed, WITHERS (1928, p. 46) says that "the evidence seems overwhelmingly clear that there has been a reduction from eight compartments to virtually a single shell in the two families of the Balanomorpha."

Octomeris sulcata NILSSON-CANTELL among the primitive chthamalid group has the rostrolatera in a state of transition between ordinary 8-plated *Octomeris* (*O. brunnea* and *O. angulosa*) having a narrow sheath on the inside and ordinary 6–plated *Pachylasma* (*P. japonicum*, etc.) lacking a sheath. The reduction of the sheath was arisen through fusion of the original compartments (cf. HIRO, 1939b, pp. 256–257, figs. 5–6). The fusion of wall-compartments is occasionally met with in the field, for *Chamaesipho* rather usually (MOORE, 1944; POPE, 1965) and for *Chthamalus* rather unusually (PILSBRY, 1916; UTINOMI, 1954).

The diversity in the occurrence of the caudal appendages in the Chthamalidae seems to be phylogenetically significant, in view of their total reduction in the evolved Balanidae.

In the most primitive genus *Catophragmus*, the surf-loving *C.* (*Catomerus*) *polymerus* DARW. has no caudal appendage, while *C.* (*Catophragmus*) *imbricatus* SOWERB. living in sheltered habitat has 3- to 6-segmented short caudal appendges (HENRY, 1958). *Chionelasmus darwini* (PILSBRY) living in deep-sea has multi-segmented long caudal appendages and a number of filamentous branchiae (NILSSON-CANTELL, 1928). Deep-sea living *Pachylasma* has multi-segmented caudal appendages, while *Hexelasma*-spp. and *Bathybalanus pentacrini* (HOEK) lack caudal appendages. The more evolved genera *Chthamalus* and *Chamaesipho*, both occurring on littoral rocks, lack caudal appendages, with an only exception (*Ch. caudatus* PILS.) as do *Balanus* and *Tetraclita* of the Balanidae.

The caudal appendages found in the Cirripedia, as I think, represent very conservative formation of the animal's body, although their actual function still remains obscure, because with extremely few exceptions, they occur in all Lepadomorpha and Verrucomorpha, whereas amongst the Balanomorpha they occur only in a few species most of which genera are closely allied to the ancestral pedunculate group. In general it is probable that the caudal appendages as well as the filamentary appendages on the prosoma or thorax are degenerative, but when present, they may act as a subsidiary aid to produce water current within the mantle cavity that is very weak in

barnacles living in sheltered habitats or in deeper waters (cf. BATHAM, 1945; CANNON, 1947; CRISP and SOUTHWARD, 1961).

The mouthparts and setation of the cirri are apt to feeding adaptations according to their different habitation.

Indeed, so early DARWIN (1854, p. 470) says that "*Chamaesipho* bears nearly the same relation to *Chthamalus*, as *Tetraclita* and *Eliminius* do to *Balanus*." in view of their phylogenetical trends shown in the simplification of the wall by reduction of the compartmental number.

New Classification of the Chthamalidae

Family **Chthamalidae** (DARWIN, 1854) emend. PILSBRY, 1916

Subfam. Chthamalinae DARWIN, 1854, p. 446.

Fam. Octomeridae (*Catophragmus, Octomeris, Pachylasma*) +Subfam. Chthamalinae (*Chthamalus*) +Subfam. Chamaesiphonae (*Chamaesipho*) GRUVEL, 1905.

Fam. Chthamalidae PILSBRY, 1916, p. 290; NILSSON-CANTELL, 1921, p. 274; WITHERS, 1935, p. 387; KRÜGER, 1940, p. 450; POPE, 1965, p. 10.

Diagnosis. Balanomorpha having four, six, or eight compartments in solid walls, in which the rostrum has alae, but when coalescent with the rostrolaterals the composite plate either has radii or seemingly not, but overlaps the lateral compartments. Rostrolateral compartments, when not coalescent with the rostrum, do not possess alae on either side. Labrum has a concave, not notched edge. Mandible with 3–5 teeth and a pectinated lower angle. Third cirri like the fourth and later pairs, or intermediate between the second and fourth. Caudal appendages often present (never in Balanidae).

1. Subfamily Catophragminae, subfam. nov.

Diagnosis. Wall 8- or 6-plated, encircled with outer whorls of supplementary smaller plates at base; rostrolaterals separated, carinolaterals separated or presumably fused with laterals; basis either membranous or calcareous; caudal appendages and branchiae either present or absent; living in littoral or in deep-sea.

Genera (and subgenera) included. Catophragmus G.B. SOWERBY Jr. 1826 (4 spp.). *C. (Catophragmus)* SOWERBY Jr., 1826 (2 spp.). *C. (Catomerus)* PILSBRY, 1916 (1 sp.). †*C. (Pachydiadema)* WITHERS, 1935 (1 sp.). *Chionelasmus* (PILSBRY, 1911 as subgen.) NILSSON-CANTELL, 1928 (1 sp.).

2. Subfamily Chthamalinae, stat. nov. (not DARWIN)

Diagnosis. Wall 8-, 6- or 4-plated, lacking any outer whorls of supplementary plates; carina and rostrum separated, both with alae on both sides; carinolaterals

either distinct or wanting (or presumably concrescent with laterals); rostrolaterals having no alae persistent as separate compartments (for *Octomeris* and *Chthamalus*) or concrescent with laterals and all sutures ultimately much obliterated (for *Chamaesipho*); basis mostly membranous, rarely calcareous; mandible tridentoid or quadridentoid; caudal appendages and branchiae mostly absent, rarely present; living in littoral.

Genera included. *Octomeris* SOWERBY, 1825 (3 spp.). *Chthamalus* RANZANI, 1818 (at least 23 spp.). *Chamaesipho* DARWIN, 1854 (3 spp.).

3. Subfamily Pachylasminae, subfam. nov.

Diagnosis. Wall 8-, 6- or 4-plated, lacking any outer whorls of supplementary plates; carina with alae separated; carinolaterals either distinct or wanting (or presumably concrescent with laterals); rostrolaterals lacking sheath inside either separably united by linear sutures or completely concrescent with rostrum having sheath inside, overlapping laterals; basis permanently membranous or secondarily calcified; mandible tri-, quadri- or quinquedentoid; caudal appendages either present or absent; living in deep-sea.

Genera included[1]. *Pachylasma* DARWIN, 1854 (8 spp.). *Hexelasma* HOEK, 1913 (9 spp.). †*Tessarelasma* WITHERS, 1936 (1 sp. from Lower Miocene, East Pakistan). *Bathybalanus* HOEK, 1913 (1 sp. on a *Pentacrinus* from 204–304 m depth).

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1) According to NEWMAN (personal communication dated October 24, 1966, accompanying photographs), a living tetramerous chthamalid which resembles the fossil genus *Tessarelasma* but obviously different from the type species *T. pilsbryi* was taken by the *Eltanin*-Expedition to the Antarctic at 1260–1273 fathoms.

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POSTSCRIPT

After I had finished this paper I read two interesting papers ("NEWMAN: A new genus of Chthamalidae (Cirripedia, Balanomorpha) from the Red Sea and Indian Ocean" and "SOUTHWARD: On the ecology and cirral behaviour of a new barnacle from the Red Sea and Indian Ocean" published in Journal of Zoology, London, vol. 153, part 4 (December 1967). In the former paper NEWMAN described an intertidal tetramerous barnacle *Tetrachthamalus oblitteratus* gen. et sp. nov.

Apparently this new chthamalid is much ribbed as in *Chthamalus* and similar to *Chamaesipho* in having the 4-plated wall, but different from the latter by having a composite rather than a simple rostrum like the extinct *Tessarelasma*, details of which are unknown. Probably the intertidal group and the deep-sea group may represent independent offshoots from an *Octomeris*-like stock, and the newly found *Tetrachthamalus* may be placed systematically between the subfamilies Chthamalinae and Pachylasminae here I proposed.