Pacific Science (1990), vol. 44, no. 2:135–155

A New and Primitive Barnacle (Cirripedia: Balanomorpha) from the North Fiji Basin Abyssal Hydrothermal Field, and Its Evolutionary Implications[1]

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ABSTRACT: A new sessile barnacle, *Eochionelasmus ohtai*, n. gen., n. sp., has been discovered associated with an abyssal hydrothermal vent at 1990 m depth in the North Fiji Basin, Southwest Pacific. The genus is distinguished from its closest and bathyal relative, *Chionelasmus*, in having distinct, multiple whorls of basal imbricating plates. These and other characters render it the most primitive living member of the suborder Balanomorpha. Knowledge of the organization of its shell, and of the ontogeny of the shell wall in *Chionelasmus*, profoundly alters our understanding of the evolution of balanomorph barnacles, and a new hypothesis is proposed. Two previously described abyssal hydrothermal barnacles also proved to represent the most primitive living members of their suborders: Scalpellomorpha and Verrucomorpha. It may be puzzling why three such antiquated morphologies should have persisted in association with abyssal hydrothermal springs while their antecedents became extinct elsewhere. However, barnacles are noted for their adaptability to a wide range of habitats including rigorous environments such as estuaries, the highest intertidal, and the effluent from power plants. The notable feature here, in contrast to their conservative but distinctly different shell morphologies, is the uniquely convergent adaptation of their setose feeding mechanism to vent-related food sources.

A NEW SESSILE barnacle, *Eochionelasmus ohtai*, n. gen., n. sp. (Figure 1), was discovered associated with a living *Bathymodiolus*-like mussel, the hairy gastropod *Alviniconcha hessleri* (Okutani and Ohta 1988), a galatheid crab (*Munidopsis* sp.), a brachyuran *Bythograea*-like crab, serpulid and polynoid polychaetes, sea anemones, and an unidentified small stalked organism from rocks at ca. 1990 m depth in the North Fiji Basin (Honza et al. 1988, KAIYO 87 Shipboard Party 1988). Observations made with a deep-tow camera and TV indicate that the mussels and the barnacles are abundant elements of the macrofauna associated with this hydrothermal system (S. Ohta, pers. comm.).

This Southwest Pacific vent community is similar to hydrothermal vent communities of the eastern Pacific in having galatheid and brachyuran crabs and mussels in common (Jones 1985, Hessler et al. 1988). It is notable that the brachyuran crab from the Mariana Back-Arc Basin represents a new genus of Bythograeidae (Hessler and Martin 1989). The occurrence of a hairy gastropod and the lack of vestimentiferan worms in the area discussed in this paper are characteristics shared with the Mariana Back-Arc Basin (S. Ohta, pers. comm.).

Each of these three hydrothermal fields is inhabited by a unique barnacle. Each is an endemic genus representing the most primitive living member of its suborder: Scalpellomorpha, Verrucomorpha, and Balanomorpha. The endemic balanomorph *Echionelasmus*, from the North Fiji Basin, is new to science and, following its systematics, we present a new interpretation of the chionelasmatine wall, and, utilizing new ontogenetic informa-

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[1] This is a contribution of the Scripps Institution of Oceanography, New Series. Manuscript accepted 22 June 1989.

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tion derived from a study of juveniles of its closest living descendant, *Chionelasmus*, we present a new hypothesis concerning the evolution of the eight-plated balanomorph wall. The nature and significance of hydrothermal barnacles in general is also considered.

SYSTEMATICS

Subclass CIRRIPEDIA Burmeister, 1834
Superorder THORACICA Darwin, 1854,
?Cambrian, Silurian–Recent
Order SESSILIA Lamarck, 1818,
Upper Mesozoic–Recent
Suborder BALANOMORPHA Pilsbry, 1916,
Upper Cretaceous–Recent
Family PACHYLASMATIDAE Buckeridge, 1983,
Paleocene–Recent
Subfamily CHIONELASMATINAE Utinomi, 1968,
Eocene–Recent

DIAGNOSIS: Symmetrical sessile barnacles having primary wall plates [rostrum (R), carina (C), and two pairs of dedicated latera (RL-CL)] in contact with the substratum and surrounded by several (amend.) distinctly separate whorls of basal imbricating plates, or (as previously known) having such whorls integrated into a single whorl; sheath formed by R, C, and the principal pair of latera [previously considered the median latus (L) but interpreted as the carino-latus (CL) herein; N.B., the rostro-latus (RL) does not enter sheath, a condition known elsewhere only in *Pachylasma* among the balanomorphs]. Basis ?thinly calcareous (Nilsson-Cantell 1928) or membranous. The subfamily includes *Chionelasmus* Pilsbry (1911) and *Eochionelasmus*, n. gen.

Genus *Eochionelasmus* Yamaguchi, n. gen.

DIAGNOSIS: Chionelasmatine with distinctly separate multiple whorls of monomorphic imbricating plates. Type: *Eochionelasmus ohtai*, n. sp.

ETYMOLOGY: An early (*eo*, G.) *Chionelasmus*.

Eochionelasmus ohtai Yamaguchi, n. sp.

Figures 1, 2*A*–*F*, 3, 4, 5, 6, 7 D1, and 8*C*

DIAGNOSIS: As the genus: basal imbricating plates in as many as five distinctly separate whorls followed by as many as four relatively incomplete whorls; imbricating plates uniform in shape (monomorphic), without lateral expansions. Occludent margin of scuta (S) with weak, oblique growth ridges. Mandible with a strong superior spine and three low teeth with very short inferior margins and long superior margins, the latter provided with a more or less single row of fine, sharp spines; branchiae simple, sacklike, without filaments.

ETYMOLOGY: The species has been named for Suguru Ohta, specialist in deep-sea ecology, in appreciation for provision of this and other primitive barnacles.

MATERIAL EXAMINED: Eight adult specimens (hermaphrodites, several damaged) and one juvenile were collected by a rectangular dredge attached to the JAMSTEC (Japan Marine Science and Technology Center) deep-tow camera system from an abyssal hydrothermal field at 1990 m in the North Fiji Basin, Southwest Pacific (16°59.4′ S, 173°54.9′ E) by the Japan-France KAIYO 87 Cruise (site B of station 4) on 28 December 1987. The barnacles were living attached to one another and to the ferro-manganese–coated, glassy crust of pillow basalt, temperature anomaly +0.1 to +0.2°C above an ambience of +2.2°C (Honza et al. 1988, KAIYO 87 Shipboard Party 1988).

DEPOSITION OF TYPES: Holotype: University Museum of the University of Tokyo (UMUT) cat. no. UMUT RA-18631. Paratypes: UMUT RA-18632, RA-18633, RA-18634 (juvenile); U.S. National Museum of Natural History (NMNH) cat. no. 221862; British Museum (Nat. Hist.) reg. no. 1989.47; Mus. Nat. d'Hist. Nat. Paris cat. no. Ci 2110.

DESCRIPTION: The largest individual (paratype RA-18633) of the three complete adult specimens was attached to the ferro-manganese–coated glassy crust of the basalt, while a medium-sized specimen (holotype, RA-18631) and smallest individual (paratype RA-18632) were attached to it (Figure 1). The three specimens, all basically translucent white, have rostro-carinal (R-C) and lateral

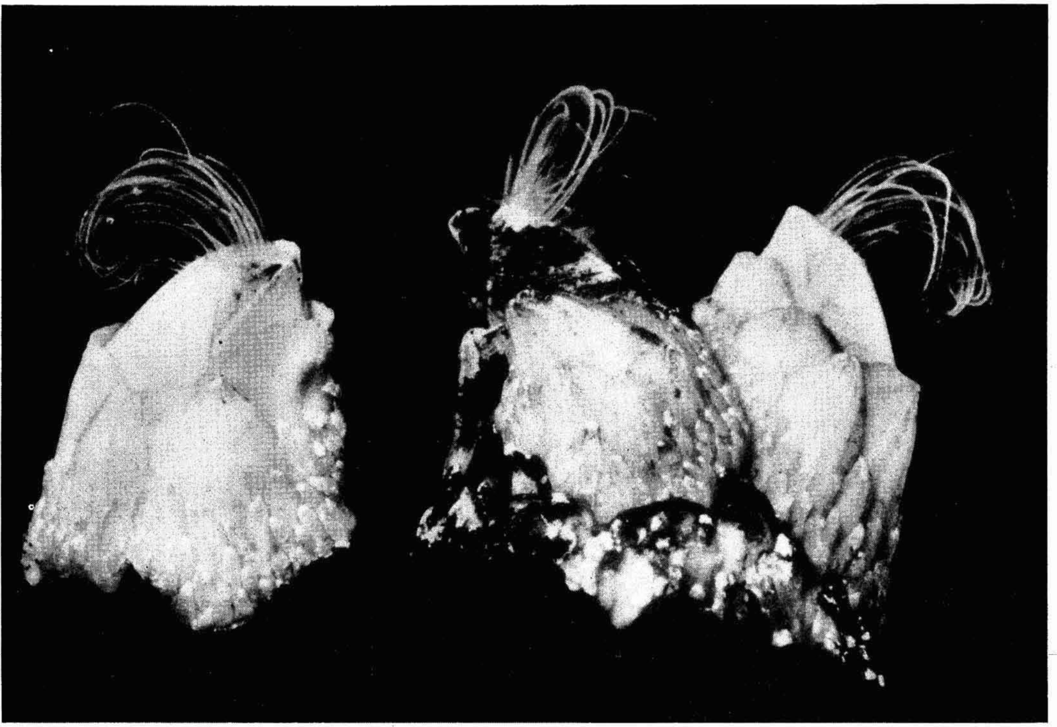

FIGURE 1. *Eochionelasmus ohtai*. *Left*: holotype [UMUT RA-18631; rostro-carinal (R-C) diameter 14.3 mm] viewed from the right side. *Right*: right end, holotype viewed from the left side; central, the white, smallest specimen is a paratype (UMUT RA-18632; R-C diameter 9.5 mm), and the black, largest specimen is a paratype (UMUT RA-18633; R-C diameter 19.5 mm).

basal diameters of 19.5 mm × 16.0 mm, 14.3 mm × 12.7 mm, and 9.5 mm × 8.1 mm, respectively.

The shell is as high as wide, and the orifice is rather large and rhomboidal; the carina (C) stands at approximately right angles to the base, but the rostrum (R) slopes obliquely toward the orifice. The largest specimen has, except for the corroded chalky white apex of each plate, become stained or tinted light to dark brown. Exposed surfaces, where some of the imbricating plates have been partially peeled away, are white. The stains are ferromanganese oxides. In the largest specimen, the lower portion of each wall plate is faintly tinted with brown in comparison to the heavier staining of the upper, older portion of the same plate. The same pattern is observable on the basal imbricating plates, but the tinted portion is narrow in comparison with that of the wall plates. The abrupt change in color apparently reflects either an abrupt increase in growth rate, a change in water quality, or both. In marked contrast with the largest specimen, the color of the other two specimens has remained almost entirely white.

In *Eochionelasmus*, plates of primary wall grow proportionately larger than the imbricating plates; that is, the body chamber enlarges by accretion along the basal and lateral margins of the primary wall plates, as in *Chionelasmus* and *Catophragmus*, rather than as much by accretion to and addition of imbricating plates, as in *Brachylepas* and to a lesser extent in *Neoverruca* (Newman 1987, Newman and Hessler 1989).

Hard parts (Figure 3): The shell is composed of the scuta and terga forming the operculum (S-T), the rostrum, rostro-latera, carino-latera, and carina forming the primary wall

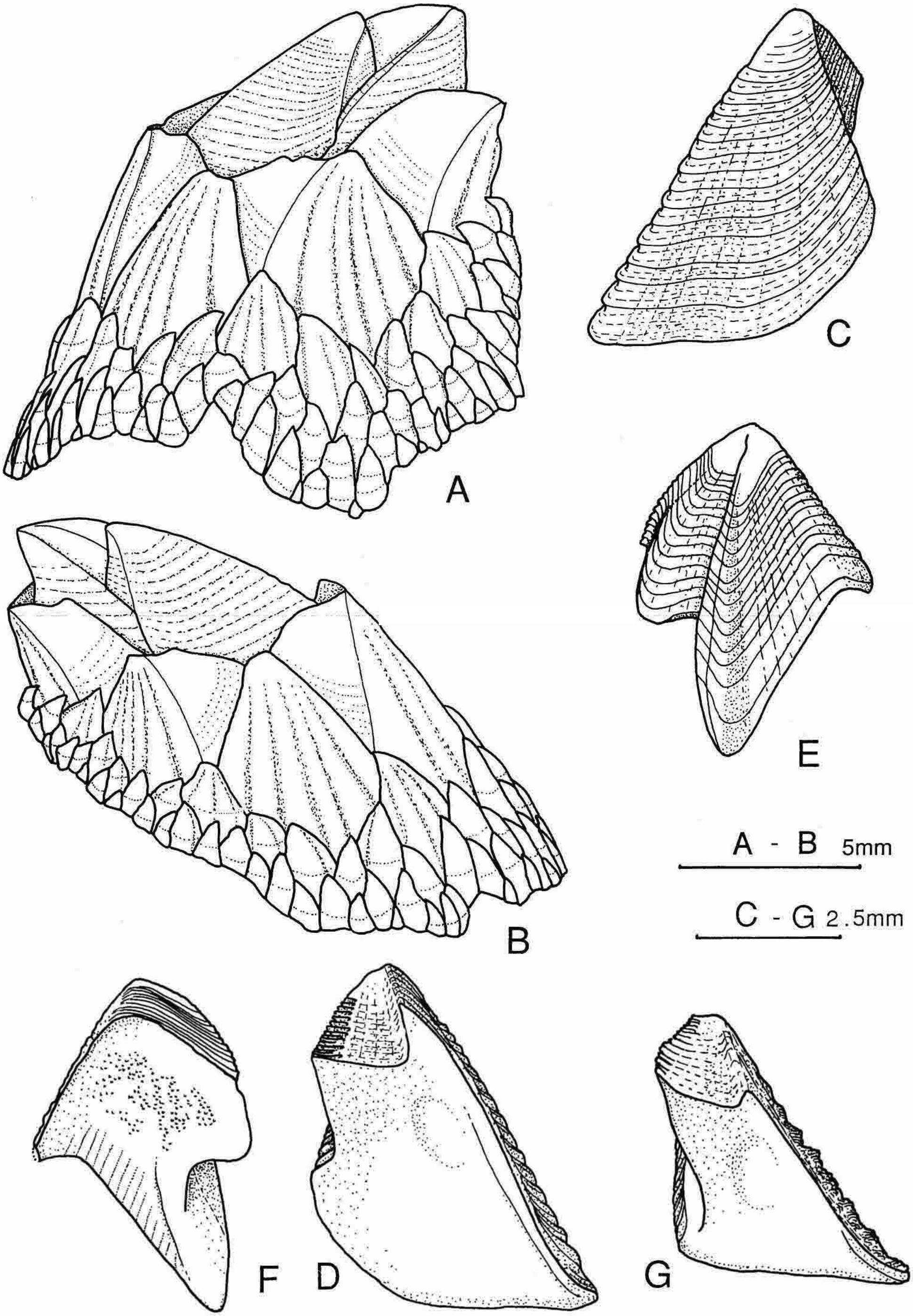

FIGURE 2. *A–F*, *Eochionelasmus ohtai*, holotype (UMUT RA-18631): *A* and *B*, right and left sides, respectively; *C* and *D* and *E* and *F*, exterior and interior views of the scutum (S) and tergum (T), respectively. *G*, *Chionelasmus darwini* (Pilsbry): interior view of scutum [SIO cat. no. C6665, from Makapuu, Oahu, Hawaiian Islands, 420 m depth, on bamboo coral, *Ceratosis grandis* (Nutting), coll. R. Grigg].

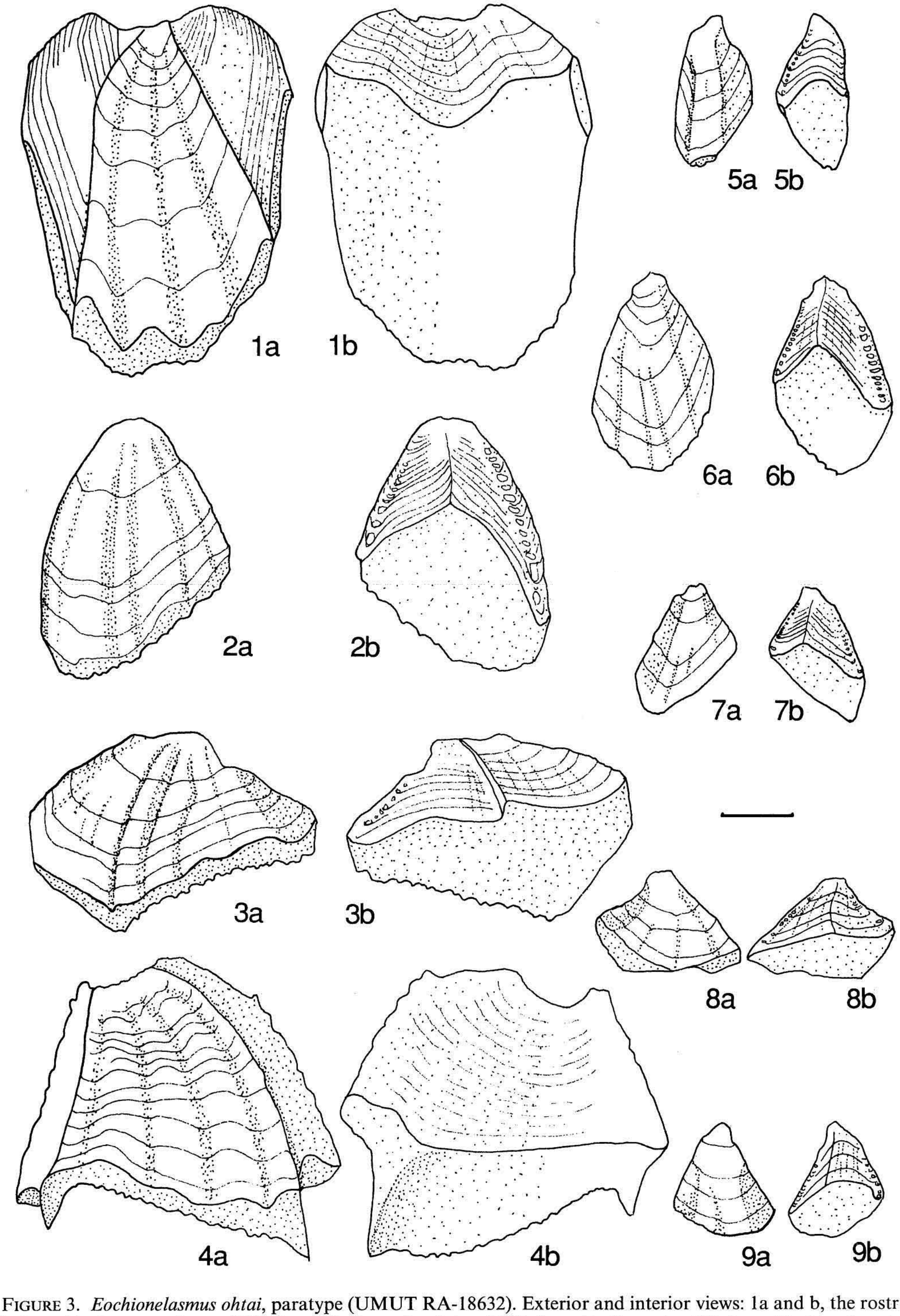

FIGURE 3. *Eochionelasmus ohtai*, paratype (UMUT RA-18632). Exterior and interior views: 1a and b, the rostrum (R); 2a and b, the rostro-latera (RL); 3a and b, the carino-latera (CL); 4a and b, the carina (C); 5a and b, the subrostrum (sr); 6a and b, r^1; 7a and b, l^1; 8a and b, c^1; 9a and b, the subcarina (sc). Scale bar = 1 mm.

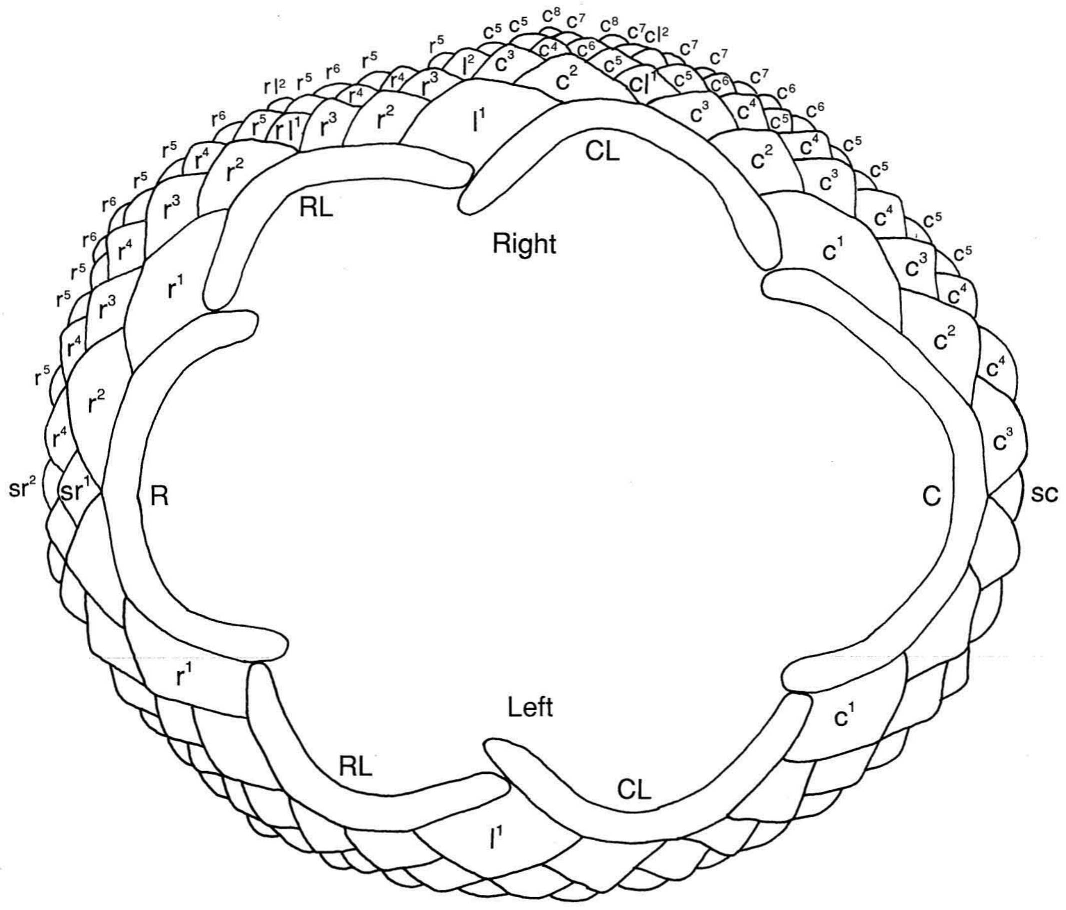

FIGURE 4. Plan view of the wall of *Eochionelasmus ohtai* viewed from below, identifying the principal wall plates and whorls of imbricating plates in the holotype (UMUT RA-18631): S, scutum; T, tergum; R, rostrum; RL, rostro-latus; CL, carino-latus; C, carina; r, imbricating plates added between R and l^1, the last belonging to the "L" tier, "L" having gone with the operculum in brachylepadomorphs and neoverrucids and subsequently lost in higher sessile barnacles; c, imbricating plates added between l^1 and C; sr and sc, imbricating plates added below R and C.

(R-RL-CL-C), plus 5 to 9 whorls of monomorphic, imbricating basal plates (justification for considering the latus nearest the carina CL rather than L is taken up under the section on *Chionelasmus* below). All primary wall plates, while relatively smooth, bear external shallow and narrow grooves that radiate from the apex to the base. Alae are also smooth and bear faint external growth lines. The sheath on the interior of the orifice is indicated by faint growth lines. Growth lines on both sides of the rostro-latus (RL) and on the carinal side of the carino-latus (CL) form a row of numerous small knobs where they overlap adjacent plates.

As in *Chionelasmus darwini*, C is the highest and RL is the lowest plate in the primary wall. However, C becomes externally concave rather than convex with growth. C and R bear wide alae and have nearly the same form and ornamentation. CL has the same external ornamentation as the other plates, but in addition to a wide ala on the lateral margin the opposite margin forms an internal articulation where it receives the alar margin of C. RL has internal articular surfaces that overlap the

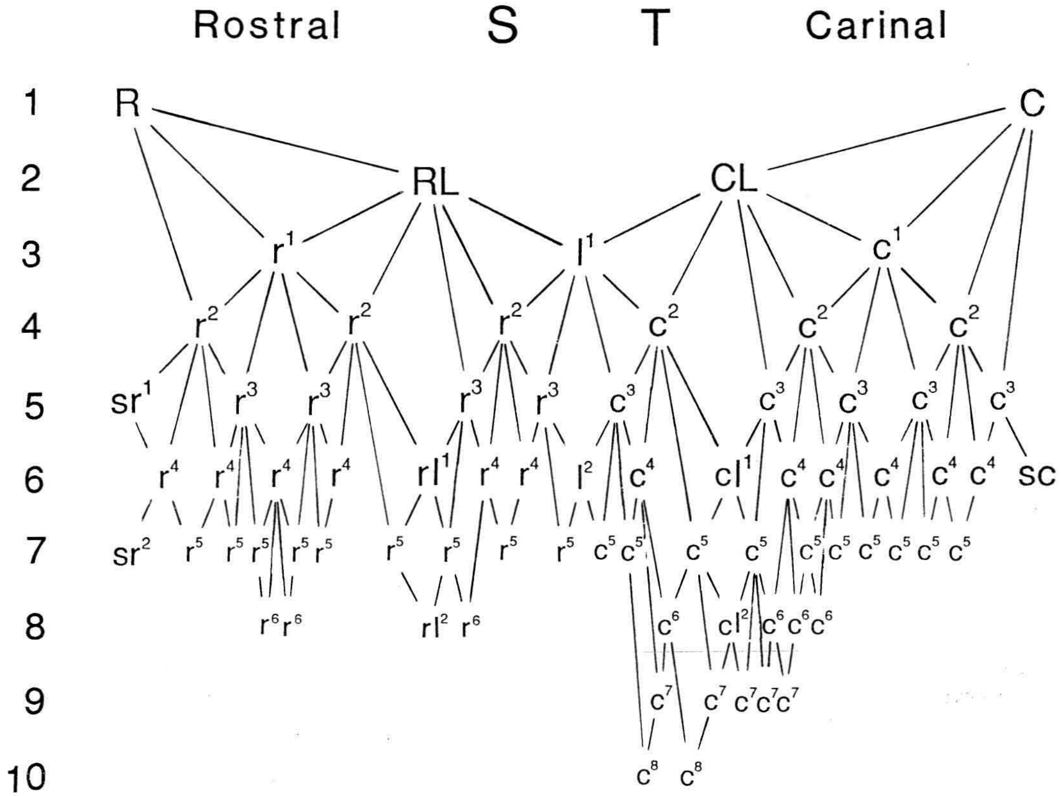

FIGURE 5. The ontogenetic addition of parietal plates in *Eochionelasmus ohtai* as deduced from some knowledge of early ontogeny and the ultimate arrangement in the adult (holotype UMUT RA-18631). Symbols as in Figure 4.

alae of R and CL, respectively. However, the alar margins of R and CL meet so that RL cannot enter the sheath. Although RL does not enter the sheath in *Pachylasma* either, it forms a distinct part of the sheath in the rest of the eight-plated balanomorphs and in six-plated forms derived from them retaining RL.

The first basal whorl of imbricating plates, the third whorl of the wall (Figures 4 and 5), consists of r^1, l^1, and c^1; the fourth and fifth, a series of r^2 and c^2 and of r^3 and c^3 (and in some cases sr, rl, cl, and sc), respectively; and the sixth, r^4, c^4, sr, rl, l^2, cl, and sc. The number of whorls on opposite sides of the smallest specimen is 5/6, the intermediate (holotype) 6/8, and the largest complete specimen 8/9.

The first three pairs of basal imbricating plates (r^1, l^1, c^1) are invariably found over the three pairs of sutures between the six primary plates R-RL-CL-C. However, additional basal plates do not always develop over the suture between two adjacent plates of the preceding whorl; variations due to age or adjustments to irregularities in the substrate sometimes occur and then most commonly after the third whorl. For example, the largest specimen lacks a plate in the fourth whorl, and the holotype and the largest specimen lack three in the fifth whorl. Similar small variations occur on both sides of a single specimen, and between different specimens, in the seventh and lower whorls. In general, however, new plates are added in a regular manner over the sutures between adjacent plates of the preceding whorl.

The shape and ornamentation of individual basal imbricating plates of *Eochionelasmus* is uniform (monomorphic), in contrast to those of *Chionelasmus darwini* in which there are three different types depending on presence or absence of lateral (alar) extensions. The former are generally equilateral triangles with faint growth lines running parallel to the base, and with shallow and narrow radial grooves on the surface of the relatively large ones. The characteristic monomorphic form of the imbricating plates in *Eochionelasmus* is similar to that of RL in *Eochionelasmus*, *Chionelasmus*, and *Pachylasma* because RL does not enter the sheath in these genera.

Although S and T of *Eochionelasmus* resemble those of *Chionelasmus darwini*, there are a few notable differences. S is triangular, relatively smooth, but marked externally by weak growth ridges running parallel to the base and faint striations radiating from the apex. Occludent and tergal margins are straight, but the carinal half of the basal margin forms the gently rounded basi-tergal corner, unlike that of *Chionelasmus darwini*, which is straight. The adductor muscle pit is faint, and there is no adductor ridge or pit for the lateral depressor muscles. The articular ridge, marked by weak growth lines, is very high, and the articular furrow is deep. A second distinct furrow occurs on the interior surface of the apex. The occludent margin has weak, oblique growth ridges without ornamentation, unlike *Chionelasmus darwini* in which the ridges are broken into closely spaced small denticles or knobs (cf. Figures 2*D* and *G*).

The tergum is triangular, smooth externally, with a longitudinal shallow external furrow along the scutal margin. The scutal margin is slightly convex, the carinal margin straight, and the basal margin concave near the basi-carinal angle, unlike the basal margin in *Chionelasmus darwini*, which is slightly concave throughout its length. The articular ridge and furrow are the counterparts to those of S. Numerous small tubercles are found on the interior surface and faint markings ("crests") are visible where the tergal depressor muscles insert along the basal margin except near its basi-scutal angle (Figure 2*F*).

Soft parts: The trophi and cirri more closely resemble those of the hydrothermal barnacles, *Neolepas* and *Neoverruca* (Newman 1979, Newman and Hessler 1989), than those of *Chionelasmus darwini*. The mouthparts are relatively small, and the crest of the labrum is concave, without a notch, and supports a single row of minute sharp teeth behind a row of bristle (Figures 6*A* and *B*). Oval mandibular palps are clothed with soft simple and pinnate spines (Figure 6*A*). The superior and inferior margins of the mandible support soft spines and a cutting edge provided with a strong superior spine and three low teeth, the broad superior margins of which support a single row of fine, sharp comblike spines (Figures 6*C* and *D*). The first maxilla, with superior and inferior margins clothed with soft spines and a straight cutting edge, is unlike that of *Neolepas* and *Neoverruca* in having a small shallow notch near the superior angle; the superior angle has two large spines followed by several small spines in the notch and many fine to median spines below it (Figure 6*E*). The second maxilla is clothed with soft simple and pinnate spines; a spineless notch occurs near the middle part of the cutting edge.

The cirri are delicate, with long, slender, multiarticulate rami clothed with fine setae, all adaptations for feeding on extremely fine particles (Newman 1979, Anderson 1980, Anderson and Southward 1987, Newman and Hessler 1989). The first pair of cirri are separated from and, along with the second and third, are shorter and wider than the posterior three pairs. The first pair are broadly inflated and have profusely setose proximal segments; the rami are unequal, the anterior the longest and antenniform. Proximal segments of the second pair, and the anterior ramus of the third pair, are heavily setose. The second and the following pairs have long, slender, subequal rami and ctenopod setation; proximal articles are wider than high and support one or two pairs of setae, while the distal articles are three times as high as wide and each supports eight pairs of setae on the lesser curvature (Figure 6*F*). Setae of the first to third cirrus are mixed simple and pinnate, but those of the fourth to sixth cirrus are simple. The number of articles of the cirri and caudal appendages are given in Table 1.

The probosciform penis is as long, and the multiarticulate caudal appendages are 1/3 as long, as the posterior cirrus (caudal appendages are lacking in *Neolepas* and *Neoverruca*).

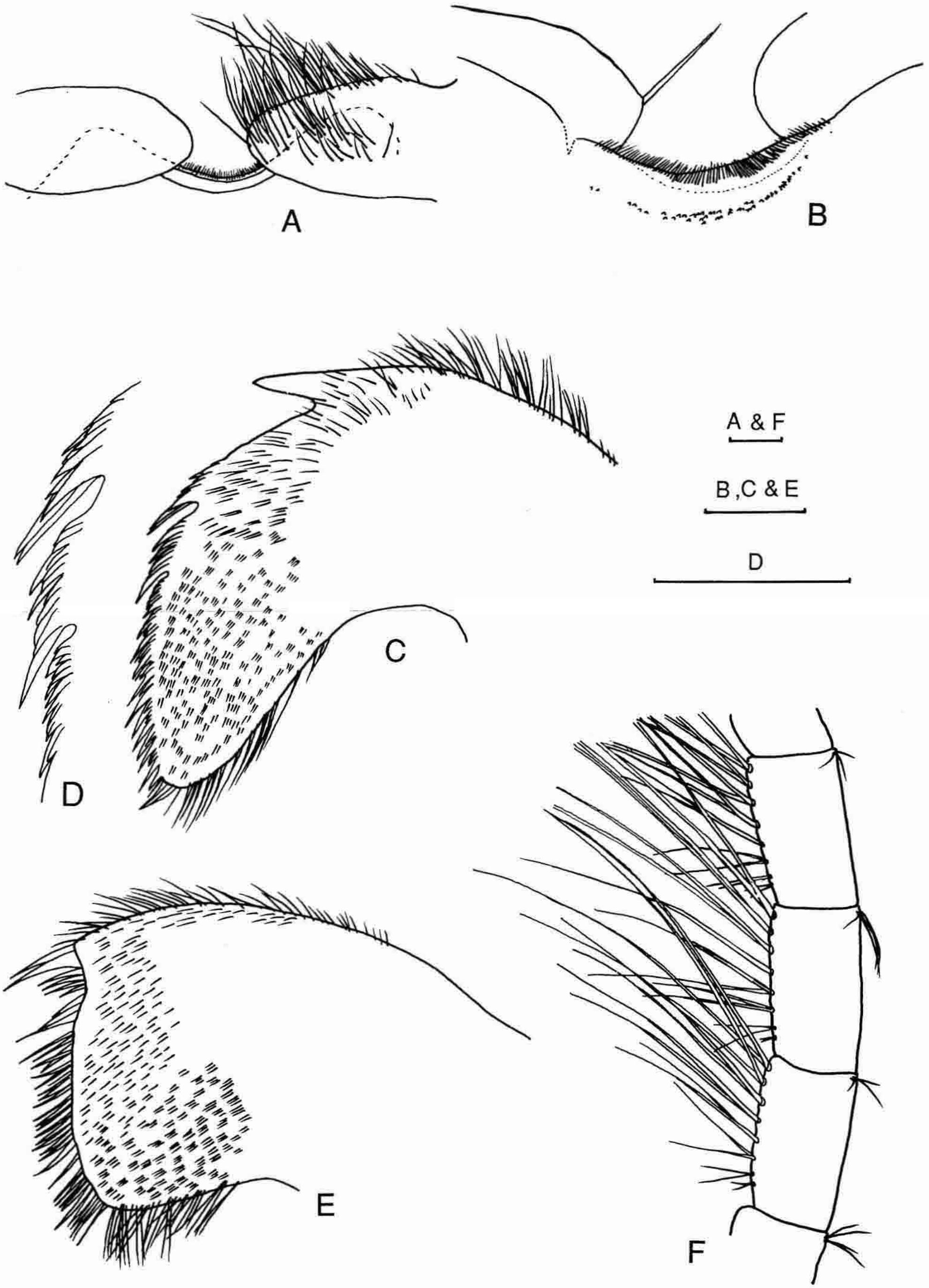

FIGURE 6. *Eochionelasmus ohtai*, holotype (UMUT RA-18631): *A*, labrum flanked by mandibular palps, setae on left palp deleted; *B*, crest of labrum enlarged, interior view; *C*, right mandible; *D*, spines of second and third tooth of right mandible enlarged; *E*, right first maxilla; and *F*, intermediate segments of right sixth cirrus. All scale bars = 0.1 mm.

TABLE 1

NUMBER OF ARTICLES OF THE CIRRI (I–VI) AND CAUDAL APPENDAGES (c.a.) OF THREE SPECIMENS OF *Eochionelasmus ohtai*

		I	II	III	IV	V	VI	c.a.
Paratype (UMUT RA-18632)								
	a	21	33	37	51	55	60	
R	–	—	—	—	—	—	—	16
	p	6	36	46	58	56	68	
	a	22	30	34	1+	30+	57	
L	–	—	—	—	—	—	—	12+?
	p	6	30+	37	1+	56	61	
Holotype (UMUT RA-18631)								
	a	22+	32+	44	26+	68+	60+	
R	–	—	—	—	—	—	—	16
	p	7	22+	47	60+	21+	70+	
	a	16+	25+	44	62	64+	35+	
L	–	—	—	—	—	—	—	17
	p	7	33+	49	62	71+	48+	
Paratype (UMUT RA-18633)								
	a	15+	32+	43	62	66+	73+	
R	–	—	—	—	—	—	—	16
	p	8	28+	51	67	74	68+	
	a	22+	18+	37+	47+	29+	23+	
L	–	—	—	—	—	—	—	16+
	p	7	44+	28+	69	75+	65+	

NOTE: a and p = anterior and posterior cirri of right and left cirri.

Branchiae, found within the mantle cavity near the base of the scuta, are simple, sacklike, and without the unusual filaments seen in *Chionelasmus*. No ovigerous fraena were found, but none of the specimens was ovigerous and therefore even the largest may not have been fully mature [*Catomerus polymerus* is remarkable in possessing both ovigerous fraena and branchiae (Walker 1983), while *Neoverruca* has fraena but lacks branchiae (Newman and Hessler 1989)].

AFFINITIES: The primitive nature of the basal whorls of imbricating plates and the specialized feeding structures distinguish *Eochionelasmus* from *Chionelasmus*. *Eochionelasmus* has five full plus as many as four partial distinct whorls of basal monomorphic imbricating plates, while *Chionelasmus* has but three full and one partial whorl, the plates of which are integrated into a single whorl in adult specimens. The integration, resulting in the development of three different types of imbricating plates, has been derived from separate whorls of monomorphic plates as seen in *Eochionelasmus*, and, therefore, the latter is deemed more primitive. Unfortunately, in lieu of the discovery of living species, unless relatively complete specimens are encountered in the fossil record, intermediates between the two forms will be difficult to recognize.

Trophic structures of *Eochionelasmus* are quite different from those of *Chionelasmus* (Pilsbry 1907, Nilsson-Cantell 1928). Instead, they closely resemble those of two previously described but very distantly related hydrothermal barnacles, the most primitive living scalpellomorph, *Neolepas zevinae* (Newman 1979), and the most primitive living verrucomorph, *Neoverruca brachylepadoformis* (Newman and Hessler 1989). The development of uniquely similar and highly specialized trophic structures in these three hydrothermal barnacles, each the most primitive living member of its lineage, must be a convergence adaptation to feeding on extremely fine suspended particles transported by gentle currents (Newman 1979, Newman and Hessler 1989). Thus, while *Chionelasmus* likely did not evolve from *Eochionelasmus* per se, it must have evolved from some similar but nonhydrothermal ancestor.

Genus *Chionelasmus* Pilsbry

A Monotypic Genus

Until the present paper, *Chionelasmus darwini* (Pilsbry, 1907) was the sole representative of the subfamily Chionelasmatinae, and it therefore has figured prominently in our considerations of the new genus, *Eochionelasmus*. Pilsbry assigned *C. darwini* to *Catophragmus*, but the description was based on two or three mutilated individuals from 417 to 430 m depth near Kauai, Hawaiian Islands [*Albatross* station 3998 (hard parts, NMNH cat. no. 32407; soft parts, NMNH cat. no. 32408)]. He inferred that the wall of the barnacle was composed of two whorls in addition to the paired scuta and terga (S and T): (1) the rostrum (R), paired rostro-latera (RL), median latera (L) and carino-latera (CL), and the carina (C); and (2) the basal imbricating whorl of plates. However, he actually observed only six plates in the first whorl; the only lateral plate observed was in contact with the carina and therefore it was assumed to be CL as in the eight-plated primary wall of *Catophragmus*. He also noted that bathyal *C. darwini* was distinguished from the two littoral species, *Catophragmus imbricatus* Sowerby and *C. polymerus* Darwin [=*Catomerus polymerus* (Darwin) Pilsbry, 1916], in having well-developed caudal appendages and basal imbricating plates arranged in a single rather than in multiple whorls. He pointed out the possibility that *C. darwini* might belong to a distinct genus, or at least a distinct subgenus, which he considered might be intermediate between *Catophragmus* and *Pachylasma*, and he proposed *Chionelasmus*, which he used at the subgeneric level (Pilsbry 1911).

Nilsson-Cantell (1928) studied a complete individual [British Museum (Natural History) reg. no. 1928 5 23 84] collected from a telegraph cable in the western Indian Ocean at 526 m, 15.3 km north and 64.4 km west of Port Mathurin, Rodrigues Island. He identified it as *Chionelasmus darwini* (Pilsbry, 1907) and gave a relatively complete description and discussion of its phylogenetic significance. Contrary to Pilsbry's expectations, Nilsson-Cantell found that the primary wall consisted of six plates, rather than eight, as in *Catophragmus*, and he identified them as R-RL-L-C.

Additional specimens were subsequently collected from south of Molokai, Hawaiian Islands [Newman and Ross 1976 (frontispiece) and Stanley and Newman 1980, fig. 3A, R/V *Te Vega* station 23-95] and from 30°34′ S, 178°30′ W, near the Kermadec Islands at 501 m (Foster 1981, R/V *Tangaroa* station K858). Many specimens of *Chionelasmus darwini* from deep water off the Hawaiian Islands, and some from off Madagascar, are also deposited at the Scripps Institution of Oceanography (SIO).

The Primary Wall

Nilsson-Cantell (1928) noted the difficulty of determining whether a plate was CL or L, because both have an ala on one side. In the six-plated, complete specimen of *Chionelasmus* he decided the latera were L and suggested the possibility that the ancestor of *Chionelasmus* had possessed CL, as in eight-plated *Catophragmus*; that is, the low number of wall plates may be due to reduction rather than being primitive.

Foster (1981) reported, in a young stage of *Chionelasmus darwini* from near the Kermadec Islands, the presence and the presumed evolutionary significance of a small but apparently distinct plate in the "CL position" among the first plates to appear after the primary ones during ontogeny. Newman (1987:26 + figs. 4A and 11C) noted that the inferred homology of CL in *Chionelasmus* with that of *Catophragmus* might not be correct; namely, the plate dubbed CL could in fact be c^1 and therefore not previously part of the primary wall. However, following Foster (1981), he ended up favoring the view that the primary wall in *C. darwini* was R-RL-L-(CL)-C, and that CL had been secondarily relegated to the basal whorl during ontogeny rather than being lost.

Primary Latera

A pollicipedine scalpellomorph ancestry of Balanomorpha has been accepted without significant modification since Darwin (1854). However, a contemporary understanding of the organization of the capitular plates in pollicipedines and calanticines is useful if hypotheses concerning the organization of the plates in primitive sessile barnacles are to be understood. The necessary principal plates are present in calanticine scalpellomorphs (Figure 7 A2), and they are surrounded by several basal whorls of imbricating plates in pollicipedines (Figure 7 A3).

There are four extant species of pollicipedines, all known to Darwin: *Pollicipes pollicipes*, *P. elegans*, *P. polymerus*, and *Capitulum mitella* [formerly referred to *Pollicipes* (cf. Foster 1978)]. In this group RL and CL overlap R and C, respectively, but not L. Furthermore, l^1 is also separated from RL and CL, unlike the arrangement in the basic plan of the Brachylepadomorpha, Verrucomorpha, and Balanomorpha (Newman 1987, Newman and Hessler 1989; present paper). It should also be noted that although L covers the basal portion of the suture between S and T, it is more closely associated with the primary whorl in *Pollicipes* than in *Capitulum*.

A somewhat more appropriate plate arrangement can be seen in the calanticine scalpellomorph *Scillaelepas*, a genus having an abundant shallow-water fossil record in the Mesozoic and, following the discovery of the first living specimen in the abyss off Greenland at the turn of the century, considered a model for the ancestor of the Balanomorpha (Aurivillius 1894, Newman et al. 1969, Anderson 1983). In *Scillaelepas*, the basic wall, in addition to S-T, includes R-RL-L-CL-C plus a subcarina (sc) and in some species one or two subrostra (sr) (Newman 1980). But unfortunately, unlike pollicipedines, *Scillaelepas* is without the basal imbricating whorls of plates.

Furthermore, although the arrangement of the principal plates in *Scillaelepas* is closer to that of balanomorphs than is that of the pollicipedines, it differs in having L overlapped by rather than overlapping CL. Newman et al. (1969, fig. 90 1a–b) simply reversed the relationship to accommodate the hypothetical *Scillaelepas*-like ancestor of balanomorphs, with no more explanation than that if the latter evolved from the former, the plates would have to have been that way. As it turns out, the plate designated "L" in balanomorphs ever since Darwin (1854) is not homologous to L in calanticines and pollicipedines. In recognition of this, and because the latter have multiple whorls of basal imbricating capitular plates, the calanticine model for the origin of the sessile barnacles was combined to form a calanticine/pollicipedine model; that is, an intermediate between the two forms (Newman 1987, fig. 10E).

In the classical interpretation of balanomorphs, "CL" overlaps C, but it is overlapped by "L." Evidence for how this peculiar arrangement may have become established came from a study of the arrangement of plates in the extinct brachylepadomorph *Brachylepas cretacea* (Newman 1987), the little-appreciated intermediate between lepadomorphs and balanomorphs advocated by Woodward (1901). In *Brachylepas*, the central three vertical tiers of imbricating plates closing the gap between R and C are larger than the numerous adjacent ones, and Woodward called them "... sublatera, as in the capitulum of *Pollicipes*." Newman (1987) noted that when observed from without, the uppermost latera of these three tiers appear to be arranged in the same way as RL-L-CL in the higher balanomorphs; namely, "L" overlaps CL rather than being overlapped by it. However, L belongs to the operculum in *Brachylepas*, and, therefore, the median plate in question must be l^1. After the chalky matrix was removed from the shell cavity of the fossil, the arrangement from within could be studied and an interesting thing was revealed; namely, there was a plate hidden beneath the presumed RL, and although it appeared vestigial it overlapped R and therefore it was apparently the true RL. It follows that a plate overlapping RL from without must be rl^1. Therefore it was

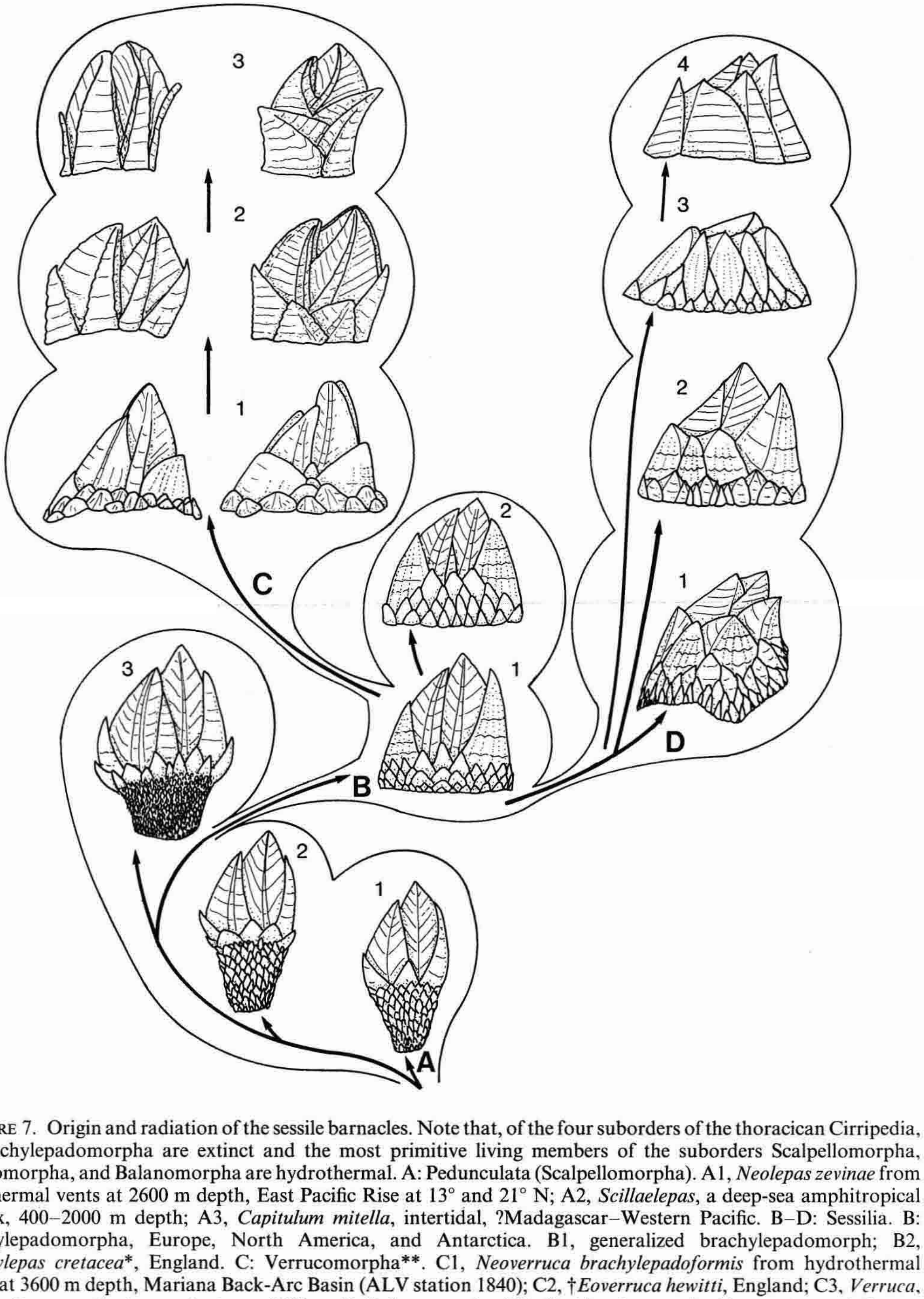

FIGURE 7. Origin and radiation of the sessile barnacles. Note that, of the four suborders of the thoracican Cirripedia, the Brachylepadomorpha are extinct and the most primitive living members of the suborders Scalpellomorpha, Verrucomorpha, and Balanomorpha are hydrothermal. A: Pedunculata (Scalpellomorpha). A1, *Neolepas zevinae* from hydrothermal vents at 2600 m depth, East Pacific Rise at 13° and 21° N; A2, *Scillaelepas*, a deep-sea amphitropical complex, 400–2000 m depth; A3, *Capitulum mitella*, intertidal, ?Madagascar–Western Pacific. B–D: Sessilia. B: †Brachylepadomorpha, Europe, North America, and Antarctica. B1, generalized brachylepadomorph; B2, †*Brachylepas cretacea**, England. C: Verrucomorpha**. C1, *Neoverruca brachylepadoformis* from hydrothermal springs at 3600 m depth, Mariana Back-Arc Basin (ALV station 1840); C2, †*Eoverruca hewitti*, England; C3, *Verruca*, cosmopolitan, mostly deep water to ca. 5000 m. D: Balanomorpha. D1, *Eochionelasmus ohtai* (present paper), from a hydrothermal vent at 1990 m depth, North Fiji Basin; D2, *Chionelasmus darwini*, deep water (ca. 500 m depth), islands of the Indo-West Pacific; D3, generalized *Catophragmus* s.l.*, three extant species, intertidal, Bermuda and Caribbean Islands, offshore islands on the Pacific side of Panama and Costa Rica, and southeast Australia and Tasmania; D4, *Hexelasma*, western Atlantic and western Pacific; Bathylasmatidae, deep water, 100–3000 m depth. †, extinct; *, unessential basal imbricating plates in rostral and carinal sides omitted; **, right and left sides (one or the other a mirror image) (modified from Newman and Hessler 1989).

inferred that the arrangement R-rl^1-l^1-CL-C, seen from without in *Brachylepas*, gave rise to the eight-plated balanomorph having basal imbricating whorls, *Catophragmus* s.l. (Newman 1987).

As a result of these observations and considerations, it seemed that the homology between the plates of the scalpellomorphs and the brachylepadomorphs was established; the loss of RL and L, and their replacement by rl and l^1 in *Brachylepas*, led to the balanomorphs. However, although *Chionelasmus* came close, there was the supposed problem that "CL" (now considered to be c^1) overlapped rather than underlapped the median plate. It was concluded that this median plate represented L rather than l^1, and, therefore, it was possible that *Chionelasmus* evolved from a different brachylepadomorph-like ancestor (Newman 1987).

Then came the discovery of the most primitive living sessile barnacle, *Neoverruca brachylepadoformis*, from an abyssal hydrothermal vent at 3600 m depth in the Mariana Back-Arc Basin (Newman and Hessler 1989). Although *Neoverruca* is a verrucomorph, if all that were known of it was the normal, movable side, it would be classified as a brachylepadomorph: L is situated in the suture between S and T [a situation previously unknown in sessile barnacles except brachylepadomorphs, in which, before its discovery in fossil remains, its existence and opercular position had been inferred by Woodward (1901)]. Also, as in brachylepadomorphs, the primary wall plates (R-C) in *Neoverruca* are supported above the substratum by multiple whorls of imbricating plates. Thus, it became perfectly clear that the scalpellomorph L had become part of the operculum in the primitive sessile barnacles, Brachylepadomorpha and Verrucomorpha, and this fact strengthened the inference that the opercular L had been lost in higher balanomorphs (*Catophragmus* s.l.). But does it follow that l^1 replaced L in *Catophragmus* s.l. as it had in *Brachylepas*? If so, something must be wrong with our understanding of the primary wall in *Chionelasmus*, unless it came from a different brachylepadomorph-like ancestor, as Newman (1987) had allowed for.

An Alternative Hypothesis

From the foregoing it is evident that the hypothesis of previous authors for the arrangement of plates in *Chionelasmus* needs to be modified. If we assume that L in chionelasmatines went with the operculum, as it did in brachylepadomorphs (Woodward 1901), in the verrucomorph *Neoverruca brachylepadoformis* (Newman and Hessler 1989), and as inferred in *Catophragmus* s.l. (Newman 1987), then the plate designated L in *Chionelasmus* (Nilsson-Cantell 1928, Newman et al. 1969, Foster 1981, Newman 1987) is either l^1 or CL. If L went with the operculum, l^1 could take its place and overlap the suture between RL and CL. However, in *Chionelasmus*, the plate in question is overlapped by RL and therefore it cannot be l^1. If the latus between RL and C in chionelasmatines is not L or l^1, it must be CL, whereby the plate previously designated CL becomes c^1, that previously designated median r^1 becomes l^1, and the rostral r^1 of the same whorl remains unchanged (see Figures 4 and 5).

The resulting chionelasmatine primary wall, R-RL-CL-C, corresponds to that of the calanticines and more closely to the basic wall in brachylepadomorphs and the movable side of neoverrucids and eoverrucids than it does with that of the higher Balanomorpha. This focuses attention away from the affinity between the Brachylepadomorpha and the Balanomorpha to that between the chionelasmatines and the higher Balanomorpha. But before dealing with that, we need to look at some new evidence derived from the ontogeny of *Chionelasmus*.

Ontogenetic Corroboration

The early postlarval or juvenile stages of hermaphrodites of *Chionelasmus darwini* were described by Newman (1987) based on material found on a bathyal coral, *Enallopsammia*, from Nihoa Bank, Hawaiian Islands [SIO reg. no. C6236]. The wall of the earliest juvenile stage found consisted of the opercular plates (S-T) and a four-plated primary wall (R-"L"-C; Newman 1987, fig. 6A). However, from the foregoing analysis of the primary wall of

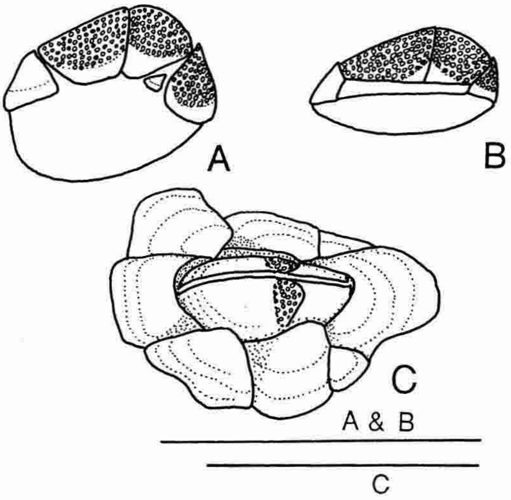

FIGURE 8. *A* and *B*, Two complemental males representing early postcyprid eight-plated ontogenetic stages provided with rudimentary peduncle, found attached on the opercular valves of an adult specimen, *Chionelasmus darwini* (Pilsbry) from Makapuu, Oahu, Hawaiian Islands [SIO reg. no. C6665]. Note that primordial valves are found on the carinae as well as the scuta and terga; in *A*, CL is very small, immature, and associated closely with C, and a semiglobular, naked peduncle forms approximately half of the body. Note that in *B*, CL is more fully developed and extends over to contact R, and the peduncle is proportionally smaller and constitutes little more than a slightly swollen basal membrane. *C*, An early juvenile (UMUT RA-18634) of *Eochionelasmus ohtai* composed of the scuta and terga forming the operculum, R-RL-CL-C forming the primary wall, and c^1, the first imbricating plate. The primordial valves are found on scuta, but they are easily knocked off, as they probably have been on the terga and carina. Scale bars = 1 mm.

chionelasmatines, the wall of this stage should be designated R-CL-C.

In the search for younger ontogenetic stages than those utilized in previous studies, two complemental males were found attached to the opercular valves of an adult specimen of *Chionelasmus darwini* [SIO reg. no. C6665] from Makapuu, Oahu, Hawaiian Islands (Figures 8*A* and *B*). The presence of a complemental male was first reported by Hui and Moyse (1984), attached to the scutal apex and accommodated by a notch in the tergum of the same side, in an adult *Chionelasmus* [BM(NH) reg. no. 1928 5 23 84] from Rodrigues Island studied by Nilsson-Cantell (1928). According to Hui and Moyse, the primary wall of this male was distorted and some of the plates were missing. The size was not given, but from the figure it appears to be ca. 1.9 mm in R-C diameter.

In the Hawaiian material, one male was found in the exposed articular furrow and another near the apex on the inside of the left tergum. The latter was in the same location as that of Hui and Moyse (1984), although no notch or pit accommodating it was found. The R-C and lateral diameters of these two males are 0.63 mm × 0.35 mm and 0.65 mm × 0.31 mm (Figures 8*A*, 8*B*, respectively), significantly smaller than that described by Hui and Moyse (1984). In these individuals, the paired S and T form the operculum and R, a pair of latera, and C form the primary wall, the same number of plates forming the primary wall in juvenile hermaphrodites (Newman 1987, fig. 6A). However, the individuals are almost 1/3 smaller, their latera are less well developed, and although all plates are calcified, only C, S, and T have primordial valves. Furthermore, the partially naked capitulum of the first individual is supported by a semiglobular, naked peduncle forming approximately half of the body. In the larger male, the peduncle is proportionally smaller and constitutes little more than a slightly swollen basal membrane. Thus it is evident that the males pass through a few transitory pedunculate stages during early ontogeny, and it is likely that the earliest stages of the hermaphrodite do so also.

Having a number of pedunculate stages, and having them provided with the full complement of primordial valves in *Chionelasmus*, represents the most generalized (primitive) developmental sequence known in the balanomorphs, one more comparable to that of *Neoverruca* (see Newman 1989). More important in the present context, the latus of the smaller male in *Chionelasmus* (Figure 8*A*) is not only small, it is in the carino-lateral (CL) position; that is, located between T and C. In the larger, more mature male (Figure 8*B*) it extends across the capitulum to meet R. In light of these facts, the pair of latera of these males evidently represents CL rather than L and therefore the four-plated primary wall consists of R-CL-C, rather than R-L-C as previously believed in four-plated juveniles. The arrangement becomes R-RL-CL-C in the six-plated juveniles, before c^1 is added as in Figure 8*C*. These findings corroborate the conclusion, based on the arrangement of plates in adult *Eochionelasmus* noted above, that the principal latus in chionelasmatines is the carino-latus.

SOME EVOLUTIONARY ASPECTS OF SESSILE BARNACLES

Ontogenetic Trends

A simple transitory pedunculate stage is known in the higher sessile barnacles such as *Verruca stroemia* (Runnström 1926), *Semibalanus balanoides* (Darwin 1854:130, Runnström 1925, Stubbings 1975), and *Balanus "amphitrite"* (Bernard and Lane 1962), and it presumably represented an ancestral reminiscence. However, the most primitive living sessile barnacle, *Neoverruca brachylepadoformis*, passes through several distinct pedunculate stages (Newman 1989, Newman and Hessler 1989), and now we find that the chionelasmatines also have some pedunculate stages. From these findings it is evident that the evolution of sessility was a relatively gradual process, with all traces of the peduncle finally being all but eliminated following the first postcyprid metamorphic or juvenile stage in higher sessile barnacles.

Trends from lower to higher Sessilia following cyprid metamorphosis involved the reduction in number of pedunculate stages from several (containing phylogenetic information) to essentially one highly specialized form. The steps included (1) the development of rapid metamorphosis from the pedunculate to the sessile mode; (2) reduction of the peduncle before metamorphosis into the sessile mode; (3) reduction of the number of stages between cyprid metamorphosis and metamorphosis to the sessile mode; (4) replacement of the primordial chitinous valves (S-T and C) by simple chitinous valves (S-T and C); (5) appearance of simple chitinous rather than calcareous valves during the pedunculate phase; (6) delay in the appearance of discrete chitinous valves (S-T) until the sessile stage; (7) delay of calcification until the juvenile is fully sessile; and (8) integration of metamorphoses of the cyprid and the last pedunculate juvenile to the sessile mode into a single metamorphosis (Newman 1989).

The chionelasmatines, *Eochionelasmus* and *Chionelasmus*, can be ranked among the sessile barnacles according to the evolutionary trends enumerated above: (1) they have fewer pedunculate stages and the peduncle is reduced compared to that of *Neoverruca*; (2) the peduncle persists longer than in *Verruca* and *Semibalanus*; (3) the primordial valves have yet to be replaced by chitinous valves; and (4) calcification begins in the earliest pedunculate stage. Therefore, the chionelasmatines rank closer to verrucomorphs (and, concomitantly, the brachylepadomorphs) than to the balanomorphs as far as postcyprid metamorphosis and the earliest juvenile stages are concerned. It is important to note here that the addition of basal imbricating whorls to the primary wall, from the inside out, is as in *Chionelasmus* and *Catophragmus* s.l. However, in *Neoverruca brachylepadoformis*, and inferred in *Brachylepas cretacea*, the basal imbricating whorls are added from the outside in; that is, between the primary whorl of plates (R-C) and the first two whorls (RL-l^1-Cl; Newman 1989, Newman and Hessler 1989).

Homologies of the Latera

Since Darwin (1854), the primitive eight-plated wall in balanomorphs, such as *Catophragmus* s.l., *Pachylasma*, *Octomeris*, and *Chelonibia*, has been considered to consist of R-RL-L-CL-C with CL overlapping C and underlapped by L. The overlap/underlap of CL has been a stumbling block in understanding the evolution of the wall of the balanomorphs because in calanticines like *Scillaelepas* and in the basic plan of brachylepadomorphs, CL overlaps L rather than being overlapped by it (Newman et al. 1969, Newman 1987).

As noted earlier, there are certain anomalies in the arrangement of the latera in the only nearly complete specimen of the primitive sessile barnacle *Brachylepas cretacea*, and these provide a possible way for the balanomorph wall to have evolved; namely, (1) because L went with the operculum it had been replaced by l^1; (2) RL was in the process of being replaced by rl^1; (3) the principal latera in *Brachylepas* were rl^1-l^1; and (4) these were presumably homologous with the latera of Balanomorpha (Newman 1987). However, with the discovery of *Neoverruca* and its ontogeny (Newman and Hessler 1989) it was found that the uppermost whorl of latera proved to be the youngest rather than the oldest (Newman 1989). Because the ontogenies of *Neoverruca* and *Brachylepas* were evidently comparable, this fact rendered the rl^1-l^1 substitution hypothesis untenable (Newman 1989). And so we were left with no firm explanation for the arrangement of the principal latera in the balanomorph wall, except that L, in having been incorporated into the operculum and subsequently lost, had not been part of the primary wall in any of the primitive sessile barnacles.

In light of this, a reevaluation of the homologies of the latera in chionelasmatines was obviously called for. It was therefore pleasing to find in the present study that what had previously been considered L in *Chionelasmus* was more readily interpreted as CL, and that ontogeny supported this conclusion; namely, that the wall of chionelasmatines is R-RL-CL-C. This configuration is very similar to that of calanticine/pollicipedines and the inferred basic wall of brachylepadomorphs (including that l^1 effectively replaces L in all three groups). But we are still in want of an explanation of how the wall of higher balanomorphs came to be made up of three rather than just two pairs of latera.

"CL" Replication: A New Hypothesis

Whether or not the six-plated chionelasmatine wall is entirely primitive, the eight-plated wall in balanomorphs departs significantly from that of all previous forms and therefore it must be highly derived. The third pair of latera in the balanomorph wall, known as the carino-latera (CL) since Darwin (1854), appears to have been intercalated between L and C of each side. Indeed, the pair of plates in question is ontogenetically intercalated into the wall of higher balanomorphs such as *Semibalanus balanoides* (L.) (Runnström 1925) and *Balanus improvisus* Darwin (Costlow 1956). That there is morphogenetic continuity between these two plates is vouched for by Runnström's (1925, figs. 13–17) observations that "CL" effectively buds off the carinal margin of the median plate; that is, the intercalation of "CL" is by an ontogenetic replication of the median plate (the true CL). The apparent budding seen by Runnström appears to be little more than a repeated wave of calcification emanating from the "carinolateral position" seen in the ontogeny of *Chionelasmus*. Therefore, it is hypothesized that it was through such an ontogenetic replication, in the wall of a chionelasmatine-like ancestor (R-RL-CL-C), that the eight-plated condition in higher balanomorphs (R-RL-CL-"CL"-C) evolved.

This hypothesis is eminently satisfactory, not only because it explains (1) how the additional third pair of latera was acquired and (2) the long perplexing enigma of why CL and "CL" of Darwin were virtually identical in their form and manner of overlap, but because (3) it is in parsimonious harmony with the facts of adult morphology and ontogeny (where known) of all the primitive forms involved (Figure 3). Knowledge of the early juvenile ontogeny in the eight-plated balanomorphs could be instructive in testing it.

CONCLUSIONS

Fossil Record

The two previously known hydrothermal barnacles, *Neolepas zevinae* (Newman 1979) and *Neoverruca brachylepadoformis* (Newman and Hessler 1989), are the most primitive living scalpellomorph and verrucomorph, respectively. Their respective antecedents were probably abundant in shallow marine waters of the lower Jurassic (Buckeridge and Grant-Mackie 1985) and Cretaceous (Newman 1985), and their generic ages (GA) have been estimated at 162 MY (million years) and 135 MY (Eolepadinae, Buckeridge 1983; Verrucidae, Newman 1985).

Eochionelasmus, the most primitive balanomorph, has no recognized fossil or living antecedents, but it does have a close living relative in *Chionelasmus*, which is represented in the late Eocene of New Zealand (Buckeridge 1983) and the Eocene of Tonga (Newman, unpubl. data; GA of 45 MY, Newman 1985). However, *Pachylasma* and *Bathylasma*, while both structurally more advanced than chionelasmatines, are known from the Paleocene (GA of 57 MY). Therefore, a GA of 45 MY for the Chionelasmatinae is likely an underestimate. *Eochionelasmus* is clearly more primitive than *Chionelasmus* in shell structure and likely dates back to the Paleocene if not the late Mesozoic. Therefore, like the two previously known hydrothermal barnacles, *Eochionelasmus* represents a relic of early Tertiary or perhaps even Late Mesozoic age, surviving in the refugium provided by deep-water hydrothermal springs.

Evolution of the Balanomorph Wall

The most primitive living balanomorph, *Eochionelasmus ohtai*, n. gen., n. sp., has a primary wall composed of R-RL-CL-C surrounded by several basal whorls of monomorphic imbricating plates, all of which can be traced back through a brachylepadomorph-like ancestor to the calanticine/pollicipedine scalpellomorphs having a primary wall of R-RL-(L)-CL-C (Figure 7) plus supplementary basal whorls of imbricating plates. It is now apparent that in primitive sessile barnacles, L became associated with the operculum, rather than with the primary wall, where it underwent reduction and loss except in most brachylepadomorphs and the early verrucomorphs.

Additional adaptations to a sessile way of life, including (1) the formation of dedicated latera in contact with the substratum rather than latera elevated above it by whorls of imbricating plates as in brachylepadomorphs and early verrucomorphs, and (2) the nearly complete loss of pedunculate ontogenetic stages following cyprid metamorphosis, have been all but completed at the chionelasmatine level of organization. It is postulated that the six-plated wall of chionelasmatines (R-RL-CL-C) evolved into the eight-plated wall of higher balanomorphs (R-RL-CL-"CL"-C) by ontogenetic replication and intercalation of "CL" from the CL primordial margin.

Compatibility of Barnacles with Hydrothermal Environments

At first glance, finding the most primitive living scalpellomorph and verrucomorph, and now what is evidently the most primitive living balanomorph, all associated with hydrothermal springs, seems like a remarkable coincidence. What are the underlying principles involved? The diverse adaptations of barnacles in general to a wide variety of inanimate and animate substrates in virtually all marine environments, and their adaptability to a wide range of rigorous conditions (freshwater-dominated estuaries; the highest reaches of the tides, even in the tropics; and the warm effluent from power plants tolerated by few other members of such communities) are well known. Therefore, unlike echinoderms for example, they are not unlikely candidates when it comes to hydrothermal and cognate environments. The key to the success of the three hydrothermal barnacle genera, despite their distinctive and antiquated shell morphologies, is that they share a highly adaptable setose feeding mechanism that has been uniquely and convergently modified to handle hydrothermally associated food sources in the form of very fine particles.

Hydrothermal Endemism

Abyssal hydrothermal and cognate environments are inhabited by remarkable assemblages of endemic invertebrates (Newman 1985, Hessler et al. 1988). The endemism includes family-group taxa as well as genera and species. There are two hypotheses explaining this high degree of endemicity: great age or rapid evolution (Cohen and Haedrich 1983). Although it is agreed that individual vents are ephemeral in space and time, proponents of the first hypothesis argue that major components of these communities are relics, descendants of nonhydrothermal lineages that no longer exist. This explains endemism at high taxonomic ranks, but it requires that the species involved have excellent dispersal capabilities (Newman 1979, 1985, McLean 1981, 1985, Batten 1984). Proponents of the second hypothesis argue that vents are too ephemeral and too widely separated for dispersal to maintain a relic fauna; they suggest that the unusual taxa are the result of rapid, recent evolution and that such similarities that may exist between hydrothermal and primitive, often extinct taxa are convergent (Hickman 1984).

The problem is, of course, convergence or reversion from what? As far as barnacles are concerned, reversion to a more primitive appearance via paedomorphosis cannot be completely ruled out, in *Neolepas* (Newman 1979, 1985) or in *Eochionelasmus* (present paper), because their ontogenies are such that some "reversion" is at least possible. However, there is no known living form from which *Neoverruca* might have reverted; all traces of a brachylepadomorph ancestry have been eliminated from the ontogeny and adult morphology of *Verruca* (Newman 1989) and from the ontogeny of all other sessile barnacles, including *Eochionelasmus* for that matter. To suggest that neoverrucid organization could have been achieved through progressive convergent evolution from a verrucid to essentially a brachylepadomorph is out of the question. Therefore, the hypothesis for reversion to or convergence with an extinct morphology has been fairly and fully falsified, at least as far as the hydrothermal barnacles are concerned. All three clearly represent relic stem forms, of late Mesozoic and earliest Tertiary radiations previously considered extinct, that have survived in the refuge provided by abyssal hydrothermal springs long after their nonhydrothermal predominantly shallow-water ancestors became extinct.

ACKNOWLEDGMENTS

We wish to thank co-chiefs of the mission, Eichi Honza (Geological Survey of Japan) and Jean-Marie Auzende (IFREMER), the organizing agencies IFREMER and STA (Science and Technology Agency, Japan), S. Ohta and many scientists of the R/V *Kaiyo* 87 shipboard party, and the Japan Marine Science and Technology Center for providing specimens of this primitive balanomorph. We also wish to thank Brian A. Foster and John S. Buckeridge for information on recent and fossil *Chionelasmus* from the Southwest Pacific, and Beatrice Burch for specimens from Hawaii having complemental males. One of us (T.Y.) wishes to thank the Ministry of Education, Science and Culture of Japan and University of California, San Diego, for supporting a sabbatical leave at the Scripps Institution of Oceanography for a period of ten months.

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