The hydrothermal vent barnacle *Eochionelasmus* (Cirripedia, Balanomorpha) from the North Fiji, Lau and Manus Basins, South-West Pacific

Toshiyuki YAMAGUCHI
Department of Earth Sciences, Chiba University,
1-33 Yayoi-cho, Inage, Chiba 263-8522 (Japan)

William A. NEWMAN
Scripps Institution of Oceanography, La Jolla,
CA 92093-0202 (USA)

Yamaguchi T. & Newman W. A. 1997. — The hydrothermal vent barnacle *Eochionelasmus* (Cirripedia, Balanomorpha) from the North Fiji, Lau and Manus Basins, South-West Pacific. *Zoosystema* 19 (4) : 623-649.

ABSTRACT

The most primitive living balanomorphan barnacle, *Eochionelasmus ohtai* Yamaguchi, 1990 was described from abyssal hydrothermal vents in the North Fiji Basin, West Pacific (Yamaguchi & Newman 1990). Since then, *Eochionelasmus ohtai* has been discovered at two other hydrothermal sites; one at the Lau Basin (west of the Tonga Islands; Desbruyères *et al.* 1994) and the other from the Manus Basin (north of Papua New Guinea; Tufar 1990, Galkin 1992a, b). These are back-arc basins, separated from the North Fiji Basin by approximately 1200 km east and 3000 km north-west, respectively. Back-arc basins are, unlike mid-oceanic ridges, discreet unities unconnected with each other. Despite this, the three populations of *Eochionelasmus* differ little in external appearance, except for some small but distinct difference in the ontogenetic development of the imbricating plates in the Manus population. Therefore, while it has been concluded that the North Fiji and Lau Basins populations represent the same form, *E. ohtai ohtai*, a new subspecies, *E. ohtai manusensis,* is being proposed for the Manus population.

KEY WORDS
hydrothermal vent barnacle, South-west Pacific, *Eochionelasmus*, Balanomorpha, Cirripedia, geographic isolation, speciation.

RÉSUMÉ
Le cirripède balanomorphe vivant le plus primitif, *Eochionelasmus ohtai ohtai* Yamaguchi, 1990, a été décrit de sources hydrothermales du bassin nord des Fiji, Pacifique occidental (Yamaguchi & Newman 1990). Depuis, *Eochionelasmus ohtai* a été trouvé dans deux autres sites hydrothermaux ; l'un dans le bassin de Lau (ouest des îles Tonga, Desbruyères *et al.* 1994) et l'autre dans le bassin de Manus (nord de la Papouasie-Nouvelle Guinée ; Tufar 1990, Galkin 1992a, b). Ce sont des bassins en forme d'arc, distants du bassin nord des Fiji d'environ 1200 km à l'est et 3000 km au nord-est, respectivement. Ces bassins, contrairement aux rides médio-océaniques, sont des unités de petite taille sans connection entre elles ; malgré cela, les trois populations d'*Eochionelasmus* diffèrent peu dans leur aspect extérieur, mais de petites différences ont été observées dans le développement ontogénique des plaques dans la population de Manus. En conséquence, tandis que l'on considère que les populations des bassins nord des Fiji et de Lau représentent la même forme *E. ohtai ohtai*, une nouvelle sous-espèce, *E. ohtai manusensis* est proposée pour la population de Manus.

MOTS CLÉS
Cirripedia, source hydrothermale, Pacifique sud occidental, *Eochionelasmus*, isolement géographique, spéciation.

INTRODUCTION

Eochionelasmus ohtai Yamaguchi, 1990 was discovered associated with an abyssal hydrothermal vent at 1990 m depth in the North Fiji Basin, South-West Pacific (Yamaguchi & Newman 1990). It is distinguished from its only close relative, *Chionelasmus darwini* (Pilsbry, 1907), an Indo-West Pacific bathyal species, in having multiple whorls of unspecialized basal imbricating plates, which is a generalized or primitive morphological character. Therefore it was evaluated as the most primitive living member of the suborder Balanomorpha.

The other known vent barnacles, the lepadomorphs *Neolepas zevinae* and *N. rapanuii*, the verrucomorph *Neoverruca brachylepadoformis*, and the brachylepadomorph *Neobrachylepas relica* (Newman 1979; Jones 1993; Newman & Hessler 1989; Newman & Yamaguchi 1995; respectively) not only also represent the most primitive living members of their respective suborders, but *N. relica* represents the only known living species of the brachylepadomorpha. These and other vent barnacles (unpublished data) are largely endemic to Indo-West Pacific vents, especially those of the South-West Pacific, and members of all four suborders are known from the Lau Basin, Tonga (Newman & Yamaguchi 1995).

Knowledge of the organization and ontogeny of the shell wall in *Eochionelasmus* has profoundly altered our understanding of the evolution of balanomorph barnacles, and the hypothesis of Yamaguchi & Newman (1990), that the 6-plated wall was more primitive than the 8-plated wall, has had a significant impact on our understanding of the relationship of the primitive balanomorphs (Buckeridge & Newman 1992; Newman 1993; Buckeridge 1995; Newman 1996; Ross & Newman 1996).

Detailed knowledge of the arrangement of the wall plates in thoracican cirripeds began with Darwin (1851, 1854), and he developed a nomenclature so that the plates and their arrangements in different forms could be accurately described and compared (*cf.* Newman 1996). He also made observations on the ontogeny of the balanomorph wall, and further details were elucidated by subsequent investigators such as Runnström (1925) and Costlow (1956).

Darwin also studied the arrangement of the basal plates forming the imbricating whorls that surround the wall plates in the intertidal and shallow water species of *Catophragmus* s.l., the only sessile barnacles known at the time to have them. Since then five other extant genera of sessile barnacles having basal whorls of imbricating plates have been discovered: *Chionelasmus* Pilsbry, 1911 (*cf.* Newman 1987); *Waikalasma* Buckeridge, 1983 (*cf.* Buckeridge & Newman 1992; Buckeridge 1996); *Neoverruca* Newman, 1989 (*cf.* Newman & Hessler 1989); *Eochionelasmus* Yamaguchi, 1990 (*cf.* Yamaguchi & Newman 1990; Yamaguchi & Newman 1997); and *Neobrachylepas* Newman *et* Yamaguchi, 1995 (*cf.* Woodward 1901; Newman 1987). Of these, all but *Chionelasmus* and *Waikalasma* are from hydrothermal vents and only in *Neoverruca* has the ontogeny of the imbricating plates been studied in detail (Newman 1989). While this shed light on the organization of the imbricating whorls in the early verrucomorphs, and by inference in the more primitive brachylepadomorphs, its relevance to the origin and hence the ontogeny of the basal imbricating whorls in balanomorphs is not yet known.

As for the balanomorphs themselves, there have been studies reconstructing the ontogeny of the basal imbricating whorls from adult morphology in *Catophragmus* and *Chionelasmus* (Newman 1987), and the nomenclature developed to describe the patterns has been emended (Yamaguchi in prep.). But none has actually been based on a complete ontogeny sequence, from the earliest post-metamorphic juvenile to the fully developed adult, much less have any been detailed enough to elucidate ontogenetic variation within and between populations. Such studies would be relatively easy to carry out with an intertidal form such as *Catomerus* in Australia, but they will always be difficult when it comes to deep-sea forms because of their inaccessibility. Therefore, since it does not seem likely appropriate collecting in the deep sea will be carried out in the foreseeable future, the present study was undertaken on the limited material available to date.

The present study involves a detailed analysis of the ontogeny of the basal whorls of imbricating plates in *Eochionelasmus ohtai*. Seventeen specimens from hydrothermal vents of the North Fiji Basin (NFB), ranging from very young to completely mature were used to infer a "generalized"

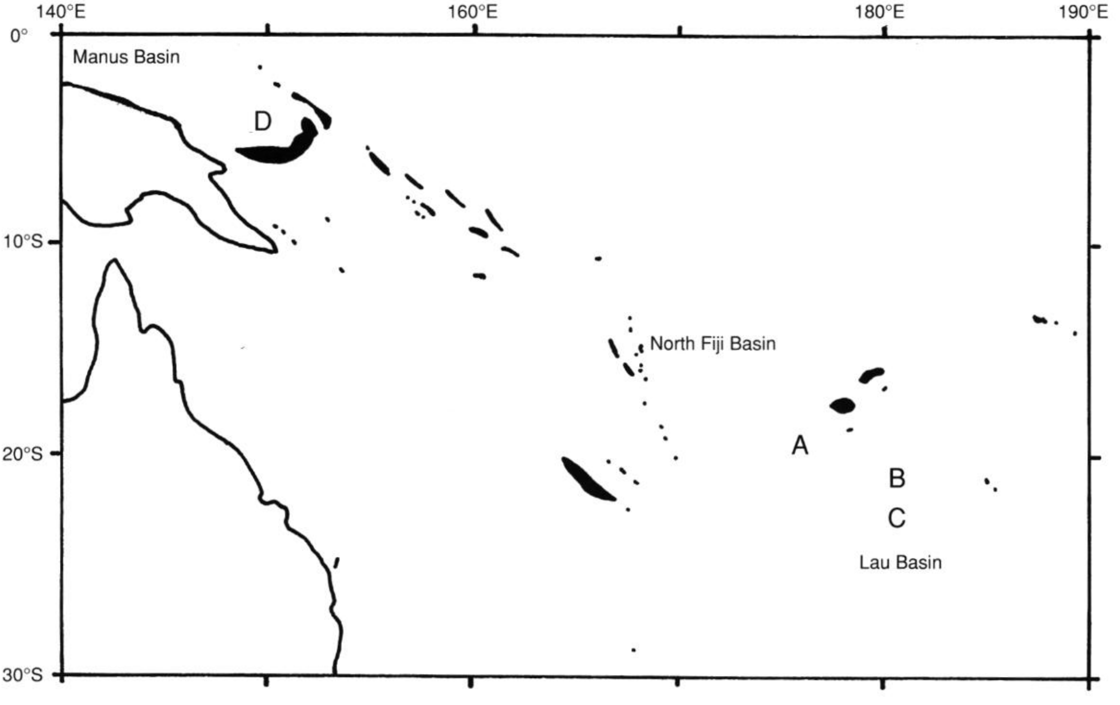

FIG. 1. — Locations of hydrothermal vents where *Eochionelasmus ohtai* was taken: North Fiji (**A**, White Lady), Lau (**B**, Hine Hina; **C**, Vailili) and Manus (**D**) Basins.

ontogenetic pattern up through the first four whorls of imbricating plates. This pattern was then compared to that found in eight early ontogenetic stages from Lau and eight from the Manus Basin. The results are significant because, while no important differences were found between the North Fiji and Lau populations, small but distinct differences distinguish these two populations from the Manus population. Therefore the Manus population has been proposed as distinct at the subspecific level, *E. o. manusensis*. The results of this ontogenetic study have not only been useful in fleshing out our knowledge for the balanomorphs in general, but in recogni-

TABLE 1. — North Fiji (NFB), Lau and Manus Basin specimens examined. **R-C**, rostrum-carina diameter; **CL**, carinolateral diameter (values in mm).

Eochionelasmus ohtai ohtai Yamaguchi, 1990 (Yamaguchi & Newman 1990)

No.	R-C	CL	Condition	Depository
NFB-A	14.3	12.7	Dissected	UMUT-RA18631 (Yamaguchi & Newman 1990)
NFB-B	9.5	8.1	*id.*	UMUT-RA18632 (*id.*)
NFB-C	19.5	16.0	*id.*	UMUT-RA18633 (*id.*)
NFB-1	2.4	2.0	*id.*	NSMT-Cr11945
NFB-2	2.6+	1.9+	Not dissec.	MNHN-Ci2495
NFB-3	3.9	2.3	*id.*	USNM-282771
NFB-4	4.7	4.2	Dissected	NSMT-Cr11946
NFB-5	5.8	5.0	Not dissec.	MNHN-Ci2496
NFB-6	7.4	6.4	Dissected	USNM-282770
NFB-7	10.2	10.0	Not dissec.	NSMT-Cr11947
NFB-8	10.4	10.0	*id.*	MNHN-Ci2497
NFB-9	12.1+	8.2	Dissected	USNM-282769
NFB-10	14.2	11.9	Not dissec.	NSMT-Cr11948
NFB-11	14.3	13.3	*id.*	NSMT-Cr11949
NFB-12	15.5	6.7	*id.*	MNHN-Ci2498
NFB-13	16.7	14.7	*id.*	USNM-282768
NFB-14	20.4	13.7	*id.*	MNHN-Ci2499
LAU-1	4.0	3.7	Dissected	NSMT-Cr11950
LAU-2	9.6	7.6	*id.*	MNHN-Ci2500
LAU-3	13.1	10.5	*id.*	USNM-282767
LAU-4	14.1	13.6	Not dissec.	NSMT-Cr11951
LAU-5	17.0	16.7	Dissected	MNHN-Ci2501
LAU-6	25.8+	27.2	*id.*	USNM-282766
LAU-7	26.1	17.9+	*id.*	NSMT-Cr11952
LAU-8	29.0	20.5	*id.*	MNHN-Ci2502

Eochionelasmus ohtai manusensis n.ssp.

No.	R-C	CL	Condition	Depository
MANUS-1	2.0	1.7	Dissected	NSMT-Cr11953 6th paratype
MANUS-2	3.8	3.1	Not dissec.	
MANUS-3	3.7	3.6	Dissected	USNM-282765 5th paratype
MANUS-4	4.8	4.0	*id.*	ZMMSU-Mg-1138 4th paratype
MANUS-5	7.4	6.2	*id.*	NSMT-Cr11954 holotype
MANUS-6	23.2	25.0	*id.*	ZMMSU-Mg-1137 1st paratype
MANUS-7	23.5	25.0	*id.*	USNM-282764 2nd paratype
MANUS-8	30.1	23.8	*id.*	NSMT-Cr11955 3rd paratype

zing genetic distance or divergence at the subspecies level. Furthermore, a generalized ontogeny of *Eochionelasmus*, based on the Lau population, has proved useful in demonstrating that a few immature specimens of *Eochionelasmus* collected from a vent near Easter Island in the South-east Pacific represent a distinct species (Yamaguchi & Newman 1997).

Expeditions that collected the material

The Japanese-French Cruise *Kaiyo* 87 (E. Honza & J.-M. Auzende co-chief scientists), 1987, North Fiji Basin; site B of station 4 (White Lady site), 16°59.4'S, 173°54.9'E, 1990 m in depth; type-locality of *Eochionelasmus ohtai* (Yamaguchi & Newman 1990; Fig. 1A).
The French submersible *Nautile* BIOLAU Cruise (A.-M. Alayse-Danet chief scientist), 1989, the Lau Basin, BL 02, 03 & 05 of station 1 (Hine Hina) (22°32'S, 176°43'W), around 1900 m in depth (Fig. 1B) and BL 12 of station 2 (Vailili) (23°13'S, 176°37'W), 1764-1707 m in depth (Fig. 1C) (Desbruyères *et al.* 1994; Newman & Yamaguchi 1995).
The French submersible *Nautile* STARMER II Cruise (D. Desbruyères & S. Ohta co-chief scientists), 1989, the North Fiji Basin; White Lady site (Desbruyères *et al.* 1994; Fig. 1A).
The German R/V *Sonne* OLGA II Research Cruise, 1990, Manus Back-Arc Basin (Bismarck Sea, Papua New Guinea); present observations based on the photographs (Tufar 1990, figs 10, 11a, b, 12a-e) of barnacles from the hydrothermal field (3°9.85'-3°9.88'S, 150°16.78'-150°16.80'E, 2489-2500 m in depth; Fig. 1D).
The Russian R/V *Akademic Mstislav Keldysh* 21st Research Cruise with submersible *Mir-2*, 1990, Manus Back-Arc Basin, station 2255 (3°10'S, 150°17'E; Fig. 1D), about 2500 m in depth, coll. S. V. Galkin (Galkin 1992a, b).

Material examined

Specimens examined have been deposited in the Muséum national d'Histoire naturelle, Paris (MNHN); National Science Museum, Tokyo (NSMT); United States National Museum of Natural History, Washington, DC. (USNM); Zoological Museum of Moscow State University (ZMMSU) (see Table 1).

SUPPLEMENTARY DESCRIPTION OF *Eochionelasmus ohtai* FROM THE NORTH FIJI BASIN BASED ON SPECIMENS COLLECTED DURING THE STARMER CRUISES

The original description of *Eochionelasmus ohtai* was based on the eight individuals collected by a dredge attached to the deep-tow used by the Japanese-French *Kaiyo* 87 cruise (Yamaguchi & Newman 1990). Subsequently, during STARMER II, the French submersible *Nautile* collected a total of 551 individuals of *E. ohtai* from near the type-locality of *Kaiyo* Cruise. According to the cruise report, gastropods (5404 individuals) were the most abundant of the megafauna. In the collection list, there were 2109 polychaetes, 1094 copepods, 586 bivalves, 551 barnacles, 134 macrures, 59 shrimps, 17 crabs, etc. Therefore, vent barnacles appear to be an important part of the fauna in the North Fiji Basin abyssal hydrothermal field. Most of barnacles were the balanomorph, *E. ohtai*. However, there were a few specimens of a neolepadine and a neoverrucid, and each represents at least a new species.
While 551 specimens of *E. ohtai* were collected, only 237 undamaged specimens were suitable for this study. These ranged from one cyprid larva attached to glassy basalt to many adults of which but one was brooding eggs.

Shells of *Eochionelasmus* from the North Fiji Basin

The shell is as high as wide, and the orifice is rather large and rhomboidal. The shell includes the scuta (S) and terga (T) forming the operculum (S-T), and the rostrum (R), rostrolatera (RL), carinolatera (CL), and carina (C) forming the primary wall (R-RL-CL-C). The carina stands at approximately right angles to the base, while the rostrum slopes obliquely toward the orifice. The number of whorls of monomorphic basal imbricating plates found around the primary wall range from zero to eight, depending on the ontogenetic stage, the same maximum number as in the original description of *E. ohtai*. However, in the present study it became evident that while there is no variation in the arrangement of the basal imbricating plates up to the second whorl, there is variation in the following whorls. Some of this variation is depicted in the holotype (NFB-A, Yamaguchi & Newman 1990,

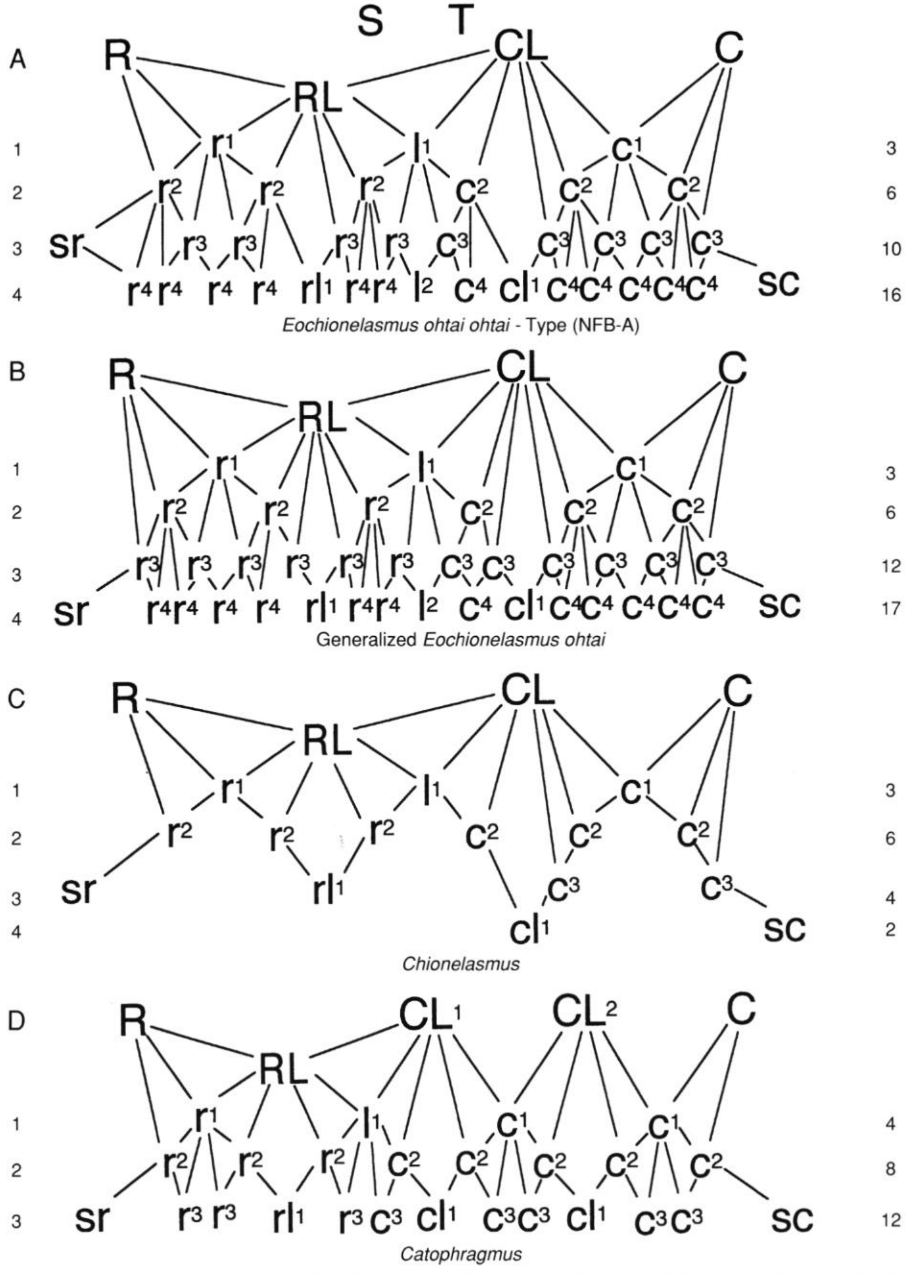

FIG. 2. — Arrangement of the plates in the wall and first four whorls of imbricating plates in **A**, holotype *E. ohtai ohtai*, in **B**, generalized, in **C**, *Chionelasmus darwini*, and in **D**, *Catophragmus* s.l. (see text for explanation).

figs 4, 5; *cf.* Figs 2A, B, 3). The anomalies include the appearance of sr in the third rather than in the fourth whorl which otherwise remains the same, the reduction of the r^3 plates from 6 to 4 and of the c^3 plates from 6 to 5 on each side. These differences are important to recognize because a frame of reference is needed when it comes to comparing different populations, as is the case in the present study. Therefore the most common or "generalized" NFB pattern was determined (Figs 2B, 3).

It is important to note that the generalized or basic pattern in *Eochionelasmus* is similar to that in *Chionelasmus* (Newman 1987, fig. 5A; see Fig. 2B herein for nomenclatural adjustments reflecting present knowledge). A similarity is expected because the latter has evidently been derived from the former (Yamaguchi & Newman 1990). From a superficial inspection of *Chionelasmus* it was reported that there was but a single whorl of basal imbricating plates (Pilsbry 1907; Nilsson-Cantell 1928; Newman *et al.* 1969), but actually there are four whorls (Newman 1987). It will be observed (Fig. 2B, C herein) that, while the first two whorls include the same plates in both *Eochionelasmus* and *Chionelasmus*, not only has the number of plates in the third whorl been reduced in the latter,

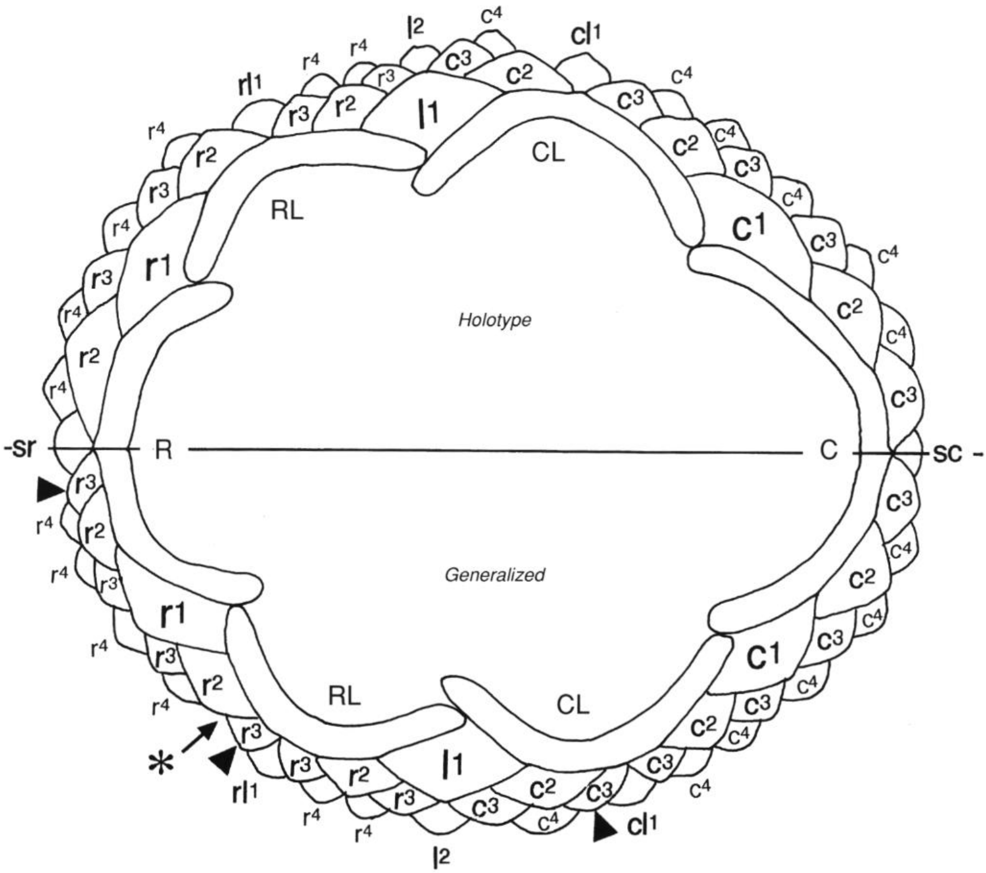

FIG. 3. — *Eochionelasmus ohtai ohtai*, plan views of the wall and first four whorls of imbricating plates for the holotype (NFB-A, upper) and the more common or generalized pattern encountered in additional specimens from North Fiji Basin. The three arrows indicate the addition plates found in the generalized form and the asterisk indicate the position of a plate that was not found. **R**, rostrum; **RL**, rostro-latus; **CL**, carino-latus; **C**, carina; **r**, imbricating plates added between R and l^1; **c**, imbricating plates added between l^1 and C; **sr** and **sc**, imbricating plates added below R and C.

from twelve to four, but that the homologs of two of the four plates (sr and rl[1]) have been brought up from to the fourth to the third whorl. Thus, not only is the number of plates in the third whorl in *Chionelasmus* reduced, but part of the fourth whorl has been transferred or condensed into it. Further reduction is seen in the fourth whorl in *Chionelasmus*, which consisted of seventeen or perhaps eighteen plates in *Eochionelasmus*. It now consists of but two plates, due to the elimination of six r^4, six c^4 and one l^2 on each side, as well as to the transfer of the sr and rl[1] to the third whorl mentioned above.

It is instructive to note that not only is the basic pattern similarity between *Eochionelasmus* and *Chionelasmus*, but also between them and *Catophragmus* s.l. (Newman 1987, fig. 5B; see Fig. 2D herein), including the condensation and some of the reduction seen in NFB-A, compared to the more generalized NFB pattern (*cf.* Fig. 2D with Fig. 2A, B). Specifically, the sequential transfer of sr, then rl[1], and then cl[1] and sc, from the fourth to the third whorl in these genera, reduces the number of plates protecting the basal margin and the sutures of RL and CL, from seven to six to five. It is notable that the configuration below RL and CL, created by this reduction in *Catophragmus*, turns out to be identical to that under CL[2], the plate infered to be a replication of CL[1] in *Catophragmus* and higher balanomorphs (Yamaguchi & Newman 1990; Buckeridge & Newman 1992). It will be important to see how these patterns correlated in other primitive balanomorphs, such as the former Miocene fossil *Waikalasma* recently discovered living at 700-800 m depths off the New Hebrides (Buckeridge 1996), because they should help us better understanding the reduction and loss of the basal imbricating plates in the evolution of early sessile barnacles, and understanding unlikely to be gained from the fossil record.

SIZE OF *Eochionelasmus* FROM THE NORTH FIJI BASIN

Yamaguchi & Newman (1990) had but three complete specimens to measure (NFB-A, B and C); the other five were incomplete. In these (Table 1), the ratios of the rostro-carinal (R-C) to carino-lateral (CL) basal diameters are 1.13, 1.17

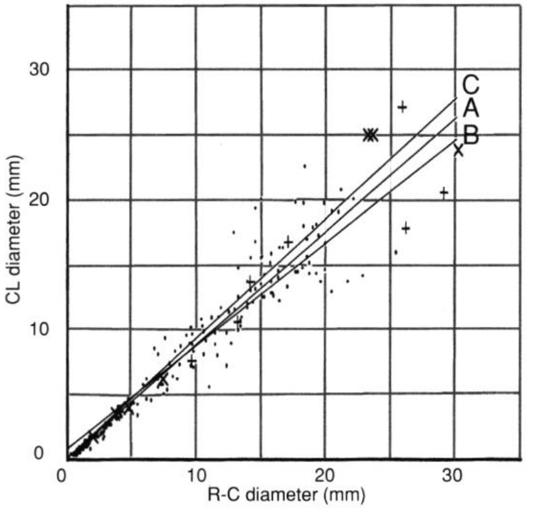

FIG. 4. — *Eochionelasmus ohtai ohtai*, size distribution of R-C and CL diameters for 237 specimens (dots) from the North Fiji Basin and **A**, their corresponding regression line compared to the regression lines for the Lau (**B**) and Manus (**C**) populations. **+**, 8 specimens from the Lau Basin; **x**, 8 specimens from the Manus Basin.

and 1.22, respectively. These were considered fully mature because there was one damaged specimen brooding eggs (NFB-10) which was slightly smaller than the holotype of *E. ohtai* (NFB-A).

The R-C and CL diameters of the 237 individuals were measured (Fig. 4). The mean (x), standard deviation (s) and range were 7.29 mm, 6.77 mm and 0.34-25.5 mm for the R-C diameters, and 6.43 mm, 6.17 mm and 0.37-22.7 mm for the CL diameters. The ratio between means of the R-C and CL diameters is 1.23 ($s = \pm 0.22$, range = 0.72-2.00). The chi-square (χ^2) of 2.9 is not significant at the 10% level (Pr ($\chi^2 >= 9.23$) = 0.1), indicating that the 237 individuals represent a random sample from a population having a normal distribution. The regression line is $y = 0.88\ x + 0.0004$ (Fig. 4) and the correlation coefficient (r) is 0.967.

The ratios for the holotype and the two paratypes (NFB-A, B and C) are nearly equal to the mean ratio (1.23) for the 237 individuals. Therefore, the ratios of the R-C and CL diameters do not distinguish the 237 individuals from the North Fiji Basin from the three type specimens of *E. ohtai* from the same population.

ONTOGENY OF *Eochionelasmus* FROM THE NORTH FIJI BASIN

The appearance of the wall and the first two whorls of imbricating plates

The shell is composed of the operculum (S-T), and the primary wall (R-CL-C) and these appear first during ontogeny. They are followed by RL and then by as many as eight basal whorls of imbricating plates. The basal whorls are added sequentially each outside the previous whorl, but only the first four were studied here (Figs 2A, B, 3). The plates of the first whorl (r^1, l^1 and c^1) are invariably found over the three pairs of sutures between the primary wall plates on each side, while the plates of the second whorl (r^2 r^2 r^2 c^2 c^2 c^2) are invariably found overlapping the lateral margins of r^1, l^1 and c^1 on each side. However, the third and fourth whorls of imbricating plates do not necessarily follow a consistent pattern.

In the 237 individuals, ninety-three individuals are smaller than 2 mm in R-C diameter. Of these, twenty-eight individuals have six to seventeen plates in addition to the four opercular plates. Of these, twenty-one had a 6-plated wall (R-RL-CL-C) but no imbricating plates, two had a 7-plated wall (6-plates plus a c^1), three had an 8-plated wall (6-plates plus the c^1 pair), one had a 15-plated wall, and one had a 17-plated wall (Table 2). The individuals with a 6-plated wall are within the range of 0.58-1.10 mm R-C and 0.37-0.89 mm CL diameters. Individuals with 7- and 8-plated walls are within the range of 1.03-1.30 mm R-C and 0.74-1.04 mm CL diameters. While the observed ranges in R-C and CL diameters for 6-, 7- or 8-plated walls overlap, the R-C and CL mean diameters for 6-plated walls are significantly different from 7- or 8-plated walls (student *t*-test). The growth from 6- to 7- and 8-plated walls involves the addition of c^1 which, without exception, covers with the suture between the C and CL (Fig. 3).

After the addition of c^1, the imbricating plates l^1 and r^1 appear over the sutures between RL-CL, and RL-R, respectively. Unfortunately it could not be determined which appeared first, l^1 or r^1,

TABLE 2. — North Fiji Basin (STARMER II, Dive 16, station 4): measurements for one cyprid and 28 juveniles (5 additional juveniles unmeasured) with a 6-plated wall plus 1, 2, 9 and 11 imbricating plates; or a total of 6, 7, 8, 15 and 17-plates, respectively. **R-C**, rostrum-carina diameter; **CL**, carinolateral diameter. Statistical values for R-C and CL diameters for 6-plated and the 7- to 8-plated juveniles: **std.**, standard deviation; **var.**; variance; **O.R.**, range (values in mm).

Specimen	Carapace Length	Height
1 cyprid	0.86	0.29

Specimen	No. of plates	R-C	CL
1	6	0.58	0.37
2	6	0.61	0.41
3	6	0.61	0.51
4	6	0.62	0.43
5	6	0.63	0.41
6	6	0.63	0.50
7	6	0.67	0.57
8	6	0.72	0.43
9	6	0.72	0.58
10	6	0.74	0.41
11	6	0.76	0.58
12	6	0.76	0.60
13	6	0.80	0.53
14	6	0.80	0.69
15	6	0.83	0.55
16	6	0.89	0.77
17	6	0.93	0.74
18	6	0.96	0.68
19	6	0.96	0.69
20	6	0.98	0.89
21	6	1.10	0.86
22	7 c	1.03	0.74
23	7 c	1.06	1.04
24	8 c	1.06	0.86
25	8 c	1.22	1.03
26	8 c	1.30	0.92
27	15	1.68	1.58
28	17	1.72	1.31

6-plated	mean	std.	var.	O.R.
R-C diameter	0.78	0.14	0.02	0.58-1.10
CL diameter	0.58	0.15	0.02	0.37-0.89

7- and 8-plated	mean	std.	var.	O.R.
R-C diameter	1.13	0.11	0.01	1.03-1.30
CL diameter	0.92	0.11	0.01	0.74-1.04

although, since l^1 is slightly larger, it may have been first.

There was little information on juveniles between 9 and 15-plates but, judging from observations on a 15-plated juvenile, the second whorl apparently begins with the appearance of c^2 over the suture between the l^1 and CL. If so, c plates generally appear before r and l plates.

Addition of imbricating plates of the third and fourth whorls

The first whorl of basal imbricating plates, consisting of a pair each of r^1, l^1 and c^1, is invariably followed by three pair each of r^2 and c^2 plates at the six pairs of the sutures between R-RL-CL-C-r^1-l^1-c^1. This brings us to the third and fourth whorls of basal imbricating plates in which some individual variation was encountered among the fourteen individuals studied (Table 1: NFB-1 to 14; Figs 5, 6). As we shall see, the variation can be greater between than within populations and, therefore, it apparently has a geographical as well as a random basis.

In holotype (NFB-A) (Yamaguchi & Newman 1990, fig. 4), imbricating plate sr^1 appeared in the third whorl. However, as we shall see, sr occurs more frequently in the fourth whorl along with rl^1, l^2, cl^1 and sc (Fig. 6). Therefore this and other variations need to be addressed now.

Of the fourteen specimens from NFB (Fig. 6),

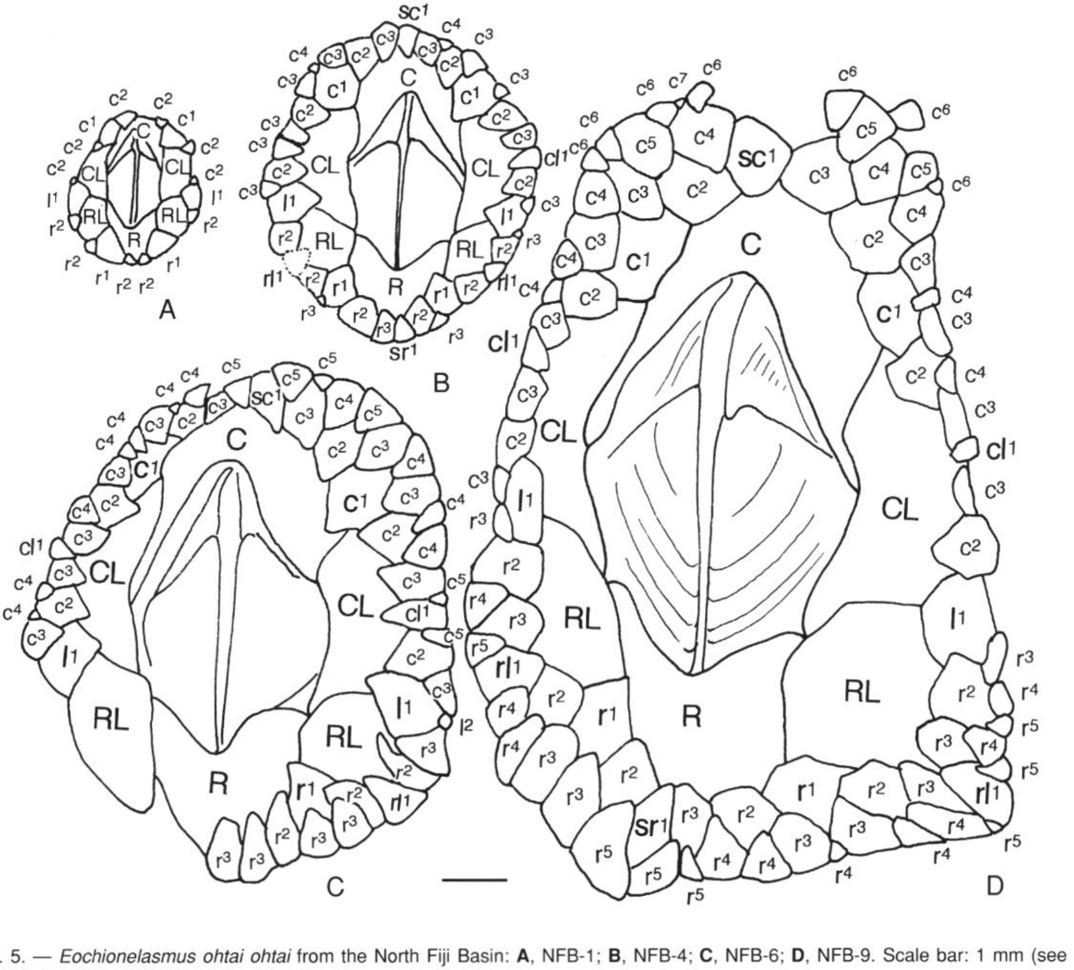

FIG. 5. — *Eochionelasmus ohtai ohtai* from the North Fiji Basin: **A**, NFB-1; **B**, NFB-4; **C**, NFB-6; **D**, NFB-9. Scale bar: 1 mm (see figure 3 for abbreviations).

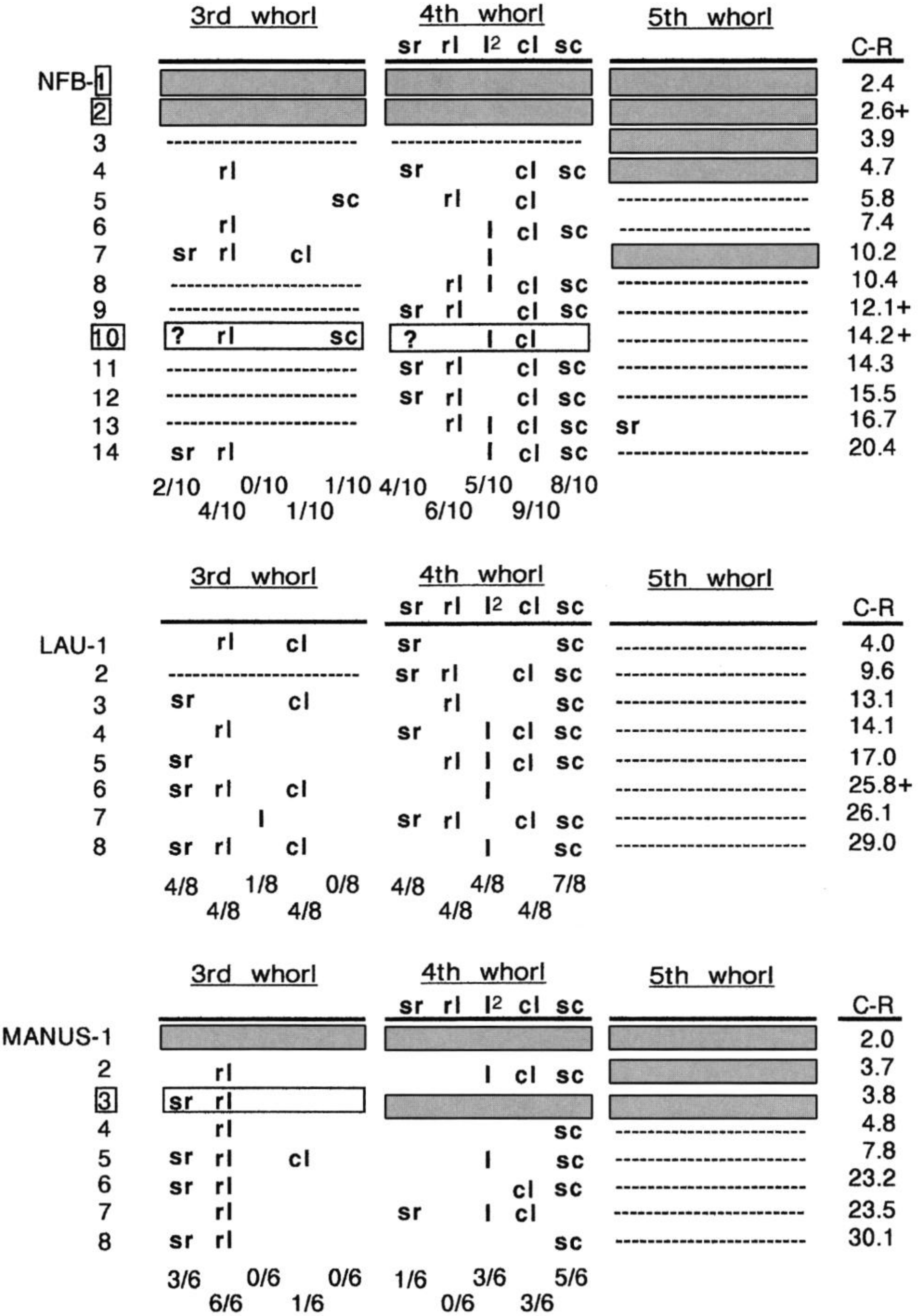

FIG. 6. — *Eochionelasmus ohtai*, shell arrangements in specimens from North Fiji, Lau and Manus Basins. The first two whorls of the imbricating plates in all three populations are same and are therefore omitted. The first appearance of sr^1, rl^1, l^2, cl^1 and sc^1, from the third to fourth whorls in each specimen is shown. Superscripts are included in the figure only where essential. Shade, no plates of the whorl present; ---, some r and/or c plates present; boldface, appeared; specimens in box which have no plates of the whorl or lack a part of imbricating plates did not count the first appearance of sr^1, rl^1, l^2, cl^1 and sc^1 (see table 3 for summary).

TABLE 3. — Comparison of the frequencies of the first appearance of imbricating plates sr, rl[1], l[2], cl[1] and sc in the 3rd and 4th whorls from the North Fiji (**NFB**), Lau (**LB**) and Manus (**MB**) Basins. The denominator = number of specimens sufficiently complete to make the comparison and the numerator = number of specimens in which the plates have appeared on either the right or left side.

	Loc.	3rd whorl		4th whorl	
sr	NFB	2/10	(20%)	4/10	(40%)
	LB	4/8	(50%)	4/8	(50%)
	MB	3/6	(50%)	1/6	(17%)
rl[1]	NFB	4/10	(40%)	6/10	(60%)
	LB	4/8	(50%)	4/8	(50%)
	MB	6/6	(100%)	0/6	(0%)
l[2]	NFB	0/10	(0%)	5/10	(50%)
	LB	1/8	(13%)	4/8	(50%)
	MB	0/6	(0%)	3/6	(50%)
cl[1]	NFB	1/10	(10%)	9/10	(90%)
	LB	4/8	(50%)	4/8	(50%)
	MB	1/6	(17%)	3/6	(50%)
sc	NFB	1/10	(10%)	8/10	(80%)
	LB	0/8	(0%)	7/8	(88%)
	MB	0/6	(0%)	5/6	(83%)

NFB-1, 2 and 3 had yet to develop imbricating plates and NFB-10 was too damaged to be useful in determining the order of appearances. This leaves seven specimens that had completed the fourth whorl of imbricating plates. Because NFB-4, 5 and 7 have no plates marking the fifth whorl, their fourth whorls may not have been complete. However, being incomplete would simply lower the frequency of appearance of certain plates, and since generally at least half the plates expected are present, the difference would not be appreciable.

If one normalizes the data by calculating the percentages at which the plates appear in the third and fourth whorls (Table 3; percentages may not add up to 100% because some of the plates occasionally appear after the fourth whorl), it will be observed that for the ten NFB individuals, the frequencies are: sr^1 20-40 %, rl^1 40-60%, l^2 0-50%, cl^1 10-90%, and sc^1 10-80%. Thus, these plates are more likely to fall in the fourth than in the third whorl, and the variability appears to be greater in the rostral than in the carinal half of the shell. How does this compare to the Lau and Manus populations (Table 3)?

It can be observed that, of the eight individuals from Lau, the frequency of occurrence in the third and fourth whorls for sr^1, rl^1 and cl^1 is 50-50%, for l^2 13-50%, and for sc 0-88%. Thus, these plates are as likely or more likely to fall in the fourth than in the third whorl, with the variability again somewhat greater in the rostral half of the shell. While these frequencies are not considered to be substantially different from those encountered in the NFB population, that cl^1 have a frequency of 50-50% rather than 10-90% is a potential difference that will need to be watched, should more material become available.

It will be observed that in the six individuals available from Manus apparently having complete third and fourth whorls, the appearance of sr^1 is 50-17%, rl^1 100-0%, l^2 0-50%, cl^1 17-50%, and sc 0-83%. While variability again appears to be greatest in the rostral half of the shell, it needs to be noted that rl^1 has an unprecedented frequency of 100-0% while in the other populations it was distributed approximately 50-50 between the third and fourth whorls. So, if we assume that the probability of rl^1 occurring in the third or fourth whorl is 0.5 in the NFB/Lau populations, then the probability of its occurring in the third whorl alone in all six individuals from the Manus population is 0.015; *e.g.*, unlikely due to chance alone. Therefore this divergent configuration is considered an important taxonomic character.

A generalized arrangement for the basal imbricating plates

There are as many as eight whorls of basal imbricating plates in *Eochionelasmus*. The first (r^1, l^1, c^1) and second (three r^2 and c^2) whorls are arranged in the same way in all populations known to date. However, beyond the second whorl, the pattern not only becomes very complex but quite variable, probably owing to crowding and/or to the uneven substratum.

In the previous section, the arrangement of the basal imbricating plates of the third to fourth whorls of various ontogenetic stages was used to compare individuals both within a population and between populations (Fig. 6; Table 3). It was observed that individuals having a complete or almost complete shell, such as NFB-7, 9, 12, 13 and A, had few variations and were bilaterally symmetrical. From such forms a generalized arrangement of basal imbricating plates was deduced, as follows: the third whorl of imbricating plates generally consists of six r^3 and six c^3 plates; *e.g.*, twelve rather than ten plates as previously believed (*cf.* Fig. 2A, B). They appear, with minor variations, at the sutures between the primary wall and the previous imbricating plates, or only at the sutures of the imbricating plates of the preceding whorls (Figs 2, 3). Furthermore, while sr^1, rl^1 or cl^1 usually appear in the fourth whorl, one or more may appear in the third whorl, in which case they replace the r^3 and/or c^3 plates that were expected to appear there. This pattern of variation in plate arrangement is found in the holotype (NFB-A) and NFB-7.

The fourth whorl also generally consists of six r^4's and six c^4's plus five additional plates; sr, rl^1, l^2, cl^1 and sc. The distribution of the r^4's and c^4's is uneven however; *e.g.*, rl^1 and cl^1 are divided in 4-2 and 1-5, respectively. Furthermore, due to spaces between the r^3's and c^3's of the previous whorl, r^4's and c^4's not only tend to double up but even to cover sutures between plates of the second and third whorls rather than just of the third whorl alone. For example, two r^4's occupy the space between the two r^3's adjacent to the l tier, and there are two similar pairing among the c^4's. From these considerations, a generalized arrangement of the imbricating plates for *Eochionelasmus ohtai* from North Fiji Basin was deduced (Figs 2B, 3). This gave us a point of reference to which different populations could be compared.

Maturity and sexuality of *Eochionelasmus* from the North Fiji Basin

There is little known about the reproduction of deep-sea hydrothermal vent barnacles. Information on sexual maturity or on the reproductive cycle was not obtained in the morphologic analysis. As mentioned above, only one of the 237 individuals (STARMER II, Dive 10, North Fiji Basin) was brooding eggs in the mantle cavity. Its R-C and CL diameters were 14.2 × 11.9 mm, but it was lacking some imbricating plates near the rostrum and therefore was likely a little longer. Nevertheless, individuals of 14 mm or larger in the R-C diameter are likely functional hermaphrodites. No complemental males have been observed, such as in *Chionelasmus* (Hui & Moyse 1984; Yamaguchi & Newman 1990).

Table 4. — Egg size in specimen of *Eochionelasmus ohtai ohtai* from North Fiji Basin (in mm).

0.27 × 0.45	0.27 × 0.46	0.28 × 0.46
0.28 × 0.46	0.28 × 0.47	0.28 × 0.49
0.28 × 0.49	0.29 × 0.45	0.29 × 0.49
0.30 × 0.44	0.30 × 0.45	0.30 × 0.45
0.30 × 0.45	0.30 × 0.45	0.30 × 0.46
0.30 × 0.46	0.30 × 0.47	0.30 × 0.47
0.30 × 0.48	0.30 × 0.49	0.30 × 0.49
0.30 × 0.49	0.30 × 0.50	0.31 × 0.47
0.31 × 0.50	mean: 0.293 × 0.470	

Eggs of *Eochionelasmus ohtai* from the North Fiji Basin

Eggs have been found in the mantle cavity of *Neolepas zevinae* (Newman 1979: 158; 0.3 × 0.5 mm in size), *Neoverruca brachylepadoformis* (Newman & Hessler 1989: 265; 0.25 × 0.5 mm) and *Neolepas rapanuii* (Jones 1993: 939; 0.3 × 0.5 mm). Eggs of the individual *E. ohtai* noted above occurred in a pair of saucer-shaped ovigerous lamellae. There were seventy-seven eggs in the left ovigerous lamella, and, therefore, it is estimated that the number of eggs is approximately 150 in all. The egg size ranged from 0.27 to 0.31 mm in width (mean, 0.29 mm) and from 0.5 to 0.44 mm in length (mean, 0.47 mm) (Table 4), essentially the same size as those of other vent barnacles. While this egg-bearing individual was but one among 236 barren individuals, three of the five individuals of *Neoverruca* examined were brooding (Newman & Hessler 1989). Whether or not the eggs were held in place by ovigerous frena, as in most pedunculate barnacles, *Neoverruca*, and *Catophragmus* s.l. has not been confirmed in *Chionelasmus*, *Waikalasma* or *Eochionelasmus*.

The study of eggs and larvae of the hydrothermal vent animals is very important to our understanding of their dispersal capabilities. However, little evidence is available (Lutz 1988). The large eggs of the vent barnacles, and the large but likely non-feeding nauplii of *N. rapanuii* described by Jones (1993) suggests that they have non-planktotrophic larvae, as does the giant clam

Calyptogena magnifica from the Galapagos Rift (Berg & Turner 1980). Since this barnacle had few but large size of eggs, it is likely that it has lecithotrophic larvae (Barnes 1989), but unfortunately, no nauplii or cyprids were found in any of the *Eochionelasmus* examined.

MOUTH PARTS OF *Eochionelasmus* FROM THE NORTH FIJI BASIN

The mouth parts are essentially the same as described for the type from the North Fiji Basin, except for the less specialized second and third teeth of mandible in the youngest stages, and they closely resemble those of the other hydrothermal barnacles: *Neolepas*, *Neoverruca* and *Neobrachylepas*.

In adults, the mandible has a cutting edge provided with a pointed superior tooth followed by three low teeth, each of which, like the inferior angle, supports a single row or comb of fine,

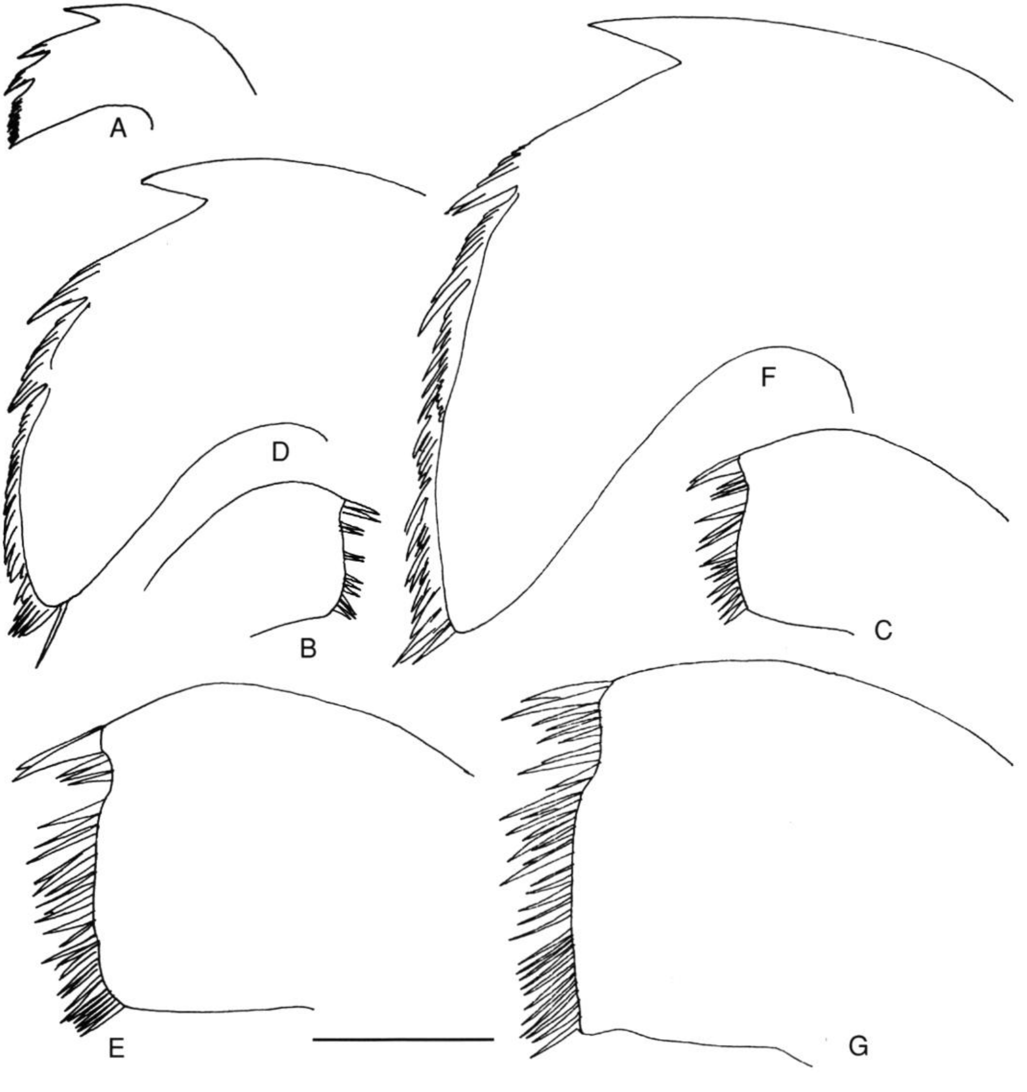

FIG. 7. — *Eochionelasmus ohtai ohtai* from the North Fiji Basin: **A**-**G**, mandibles and first maxillae; **A**, right mandible of specimen NFB-1; **B**, left first maxilla of NFB-1; **C**, right first maxilla of NFB-4; **D**, right mandible of NFB-6; **E**, right first maxilla of NFB-6; **F**, right mandible of NFB-9; **G**, right first maxilla of NFB-9. The mandible of NFB-4 was missing. Scale bar: 0.1 mm.

TABLE 5. — *Eochionelasmus ohtai ohtai* from the North Fiji Basin, size and ratios of the specimen. **aL/pL**, ratios of the lengths of the anterior and posterior rami of cirrus I; **L/W**, ratios of the lengths and widths of the 12th, 20th, 30th, 40th, 50th and 60th articles of cirrus VI with in parenthesis, the number of pairs of setae per article of cirrus VI; –, articles missing; **R-C**, rostrum-carina diameter (in mm). Article indicated in [ ] when designated article was broken off.

	aL/pL	L/W of articles of C VI						Size
	C I	12th	20th	30th	40th	50th	60th	R-C
NFB-1	2.4	2.2 (3) [11th]	–	–	–	–	–	2.4
NFB-4	2.7	1.2 (3)	2.1 (4) [19th]	–	–	–	–	4.7
NFB-6	2.5	0.8 (3)	1.1 (4)	1.8 (5)	2.3 (4)	2.7 (4)	3.6 (3)	7.4
NFB-B	2.8	0.8 (4)	1.1 (5)	1.5 (6)	1.8 (6)	2.1 (6)	2.9 (3)	9.5
NFB-9	3.3	0.8 (3)	1.1 (4)	1.3 (4) [27th]	–	–	–	12.1+
NFB-A	2.8+	0.7 (4)	1.1 (6)	1.4 (7)	1.7 (7)	2.4 (8)	2.6 (6)	14.3
NFB-C	2.6+	0.7 (5)	1.0 (7)	1.3 (8)	1.5 (8)	1.9 (7)	2.1 (7)	19.5

sharp spines. However, in juveniles, the second and third teeth are pointed and divided into but a few spines, and therefore they look more like those of ordinary deep-sea thoracicans. The length of the superior margin of the second and third teeth in juveniles grows more rapidly than the inferior margin, and it becomes more spinous as it does so, and this produces the form seen in the adult (Fig. 7A, D, F). The relatively generalized second and third teeth of the mandible are also found in the smallest specimens of LAU-1 and MANUS-1 from the Lau and Manus Basins, respectively (Fig. 10C, D). A similar ontogenetic change, from generalized to specialized, was also seen in certain chthamalids (Pope 1965).

In the first maxillae, the number of spines on cutting edge increases with growth (Fig. 7B, C, E, G), but a marked change does not occur in them or in the other mouth parts.

CIRRI AND CAUDAL APPENDAGES OF *Eochionelasmus* FROM THE NORTH FIJI BASIN

The delicate cirri have long, slender, multiarticulate rami clothed with fine setae. The rami of first pair are unequal, the anterior being the longest and antenniform. The ratios of lengths of the anterior and posterior rami of cirrus I are shown in table 5. The second and following pairs have long, slender, subequal rami and ctenopod setation. The proximal articles in the second and the following pairs are wider than high and support one or two pairs of setae, while the distal articles are more than twice as long as wide and each

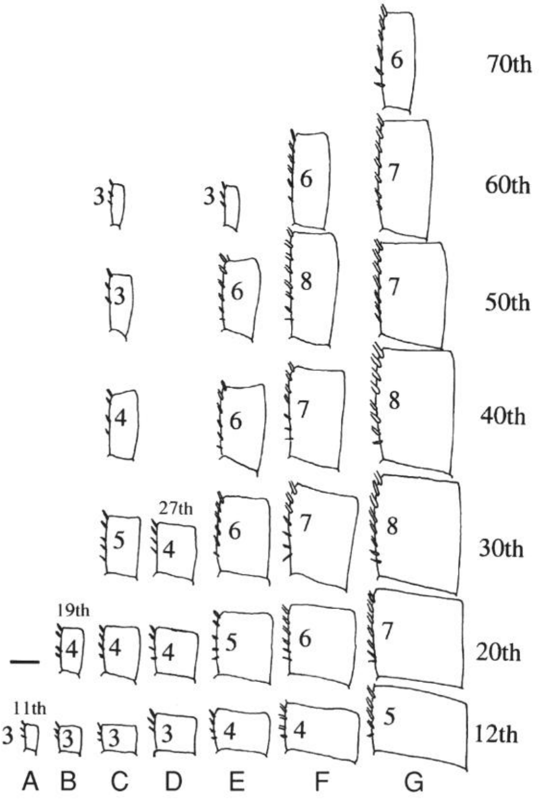

FIG. 8. — Shape and number of pairs of setae in the 12th, 20th, 30th, 40th, 50th, 60th and 70th articles of anterior ramus of the cirrus VI in specimen **A**, NFB-1; **B**, NFB-4; **C**, NFB-6; **D**, NFB-9; **E**, type specimens of NFB-B; **F**, type specimens of NFB-A; **G**, type specimens of NFB-C. The number within each figure corresponds with the number of pairs of setae. In cases of lacking where the appropriate article was the next available article, indicated by its numbers, was used. Scale bar: 0.1 mm.

TABLE 6. — *Eochionelasmus ohtai ohtai* from North Fiji Basin. Number of articles of the right anterior (**R:a**), right posterior (**R:p**), left anterior (**L:a**), and left posterior (**L:p**) rami of cirri I-VI and caudal appendages (**c.a.**); **R-C × CL**, rostrum-carina and carinolateral diameters (in mm), respectively.

		Number of articles of cirri						c.a.	R-C × CL	Remarks
		I	II	III	IV	V	VI			
NFB-1	R:a	8	5	6	11	13+	12+	(4)	2.4 × 2.0	no penis
	R:p	4	4	9	15+	17+	13+			
	L:a	9	5	6	11+	12+	12+	(6)		
	L:p	4	4	8	10+	11+	14+			
NFB-4	R:a	13	11	18	19+	20+	19+	(10)	4.7 × 4.2	penis tiny
	R:p	5	13	18+	19+	20+	23+			
	L:a	13	9	18	20+	19+	20	(10)		
	L:p	5	13	20+	17+	19+	22+			
NFB-6	R:a	18	16+	30	45	44+	61	(13)	7.4 × 6.4	penis small
	R:p	6	24+	33	47	45+	46+			
	L:a	18	21+	24+	27+	22+	20+	(14)		
	L:p	6	22+	23+	22+	22+	25+			
NFB-B	R:a	21	33	37	51	55	60	(16)	(First Paratype) 9.5 × 8.1	penis long
	R:p	6	36	46	58	56	68			
	L:a	22	30	34	1+	30+	57	(12+)		
	L:p	6	30+	37	1+	56	61			
NFB-9	R:a	20	17+	20+	22+	23+	27+	(15)	12.1+ × 8.2	penis long
	R:p	6	21+	22+	22+	23+	23+			
	L:a	17	20+	26+	32+	31+	24+	(15+)		
	L:p	5	17+	27	33+	25+	26+			
NFB-A	R:a	22+	32+	44	26+	68+	60+	(16)	(Holotype) 14.3 × 12.7	penis long
	R:p	7	22+	47	60+	21+	70+			
	L:a	16+	25+	44	62	64+	35+	(17)		
	L:p	7	33+	49	62	71+	48+			
NFB-C	R:a	15+	32+	43	62	66+	73+	(16)	(Second Paratype) 20.4 × 13.7	penis long
	R:p	8	28+	51	67	74	68+			
	L:a	22+	18+	37+	47+	29+	23+	(16+)		
	L:p	7	44	28+	69	75+	65+			

supports three to eight pairs of setae along its lesser curvature (Fig. 8, Table 5). The number of articles for the rami of the cirri and caudal appendages are given in table 6.

The cirri were examined in seven individuals of different sizes in order to determine how they changed with growth. The seven individuals include the holotype and two paratypes of *E. ohtai* and they range from 2.4 mm to 19.5 mm in the R-C diameter (Tables 2, 6). Two of the type specimens are the largest and one is the fourth largest (9.5 mm) of the seven individuals examined.

In cirrus I, the anterior ramus is from 2.4 to 3.3 times as long as the posterior ramus (Table 5, *cf.* Tables 7, 9). Even the number of segments of the anterior ramus of cirrus I is from 2 to 3.6 times greater than for the posterior ramus (Table 6). The ratios, for the length and the number of articles of the anterior and posterior ramus in cirrus I, increase with growth. In comparison with the smallest (NFB-1), the ratios for the increase in number of articles for the largest (NFB-C) examined are × 3 for the anterior and × 2 for the posterior ramus (Table 6).

The remaining five pairs of cirri of *Eochionelasmus* are almost equal in the number of articles and in the length of each ramus, though there is considerable variation in both. The number of articles and the length of the rami of the posterior cirri also increase with growth of shell. The number of articles in the largest was five times that found in the smallest individual (Table 6). Individuals smaller than the NFB-B show marked increases with growth of these two characters. However, the number of articles of the cirri do not increase markedly with growth in individuals larger than the NFB-B (9.5 × 8.1 mm) nor does the length of penis. Therefore, individuals larger than approximately 10 mm in R-C diameter, rather than 14 mm or so, may be reproductively active at least as males.

The unequal rami of cirrus I mentioned above are characteristic of and apparently distinguished *Eochionelasmus* from other vent barnacles, for the rami of their cirrus I are almost equal in length and number of articles. While the number of articles of cirrus I in other vent barnacles is substantially greater than in young specimens of *Eochionelasmus* from the North Fiji Basin, the number is nearly equal to that of cirrus I in large specimens of *Eochionelasmus*. It is assumed that in other vent barnacles the number of articles in the cirri also increases with growth and, therefore, young individuals of other vent barnacles likely have a small number of articles in the posterior rami of cirri I.

The unequal rami of cirrus I, and the equal number of articles and subequal length of the rami of the remaining pairs of cirri are also characteristic of *Eochionelasmus* from the Lau and Manus Basins. Therefore, as with the mouth parts, *E. ohtai* of the North Fiji Basin cannot be distinguished from *Eochionelasmus* of the Lau and Manus Basins by the nature of the cirri, even though these three basins are relatively isolated from each other (see next section).

While nature of cirri of *Eochionelasmus* apparently does not differ significantly from that of other vent barnacles, except for cirri I, there is no information on changes with growth for them. The rami of cirrus III to VI are essentially equal in the number of articles and in length in all three forms, as they are for cirrus I in other vent barnacles. However, in *Eochionelasmus* the rami of cirrus I are unequal in number of articles and in length. As for cirrus II, while that of *Neolepas* and *Eochionelasmus* has subequal rami and numbers of articles, that of *Neoverruca* has unequal rami and numbers of articles.

The caudal appendages of those specimens of *Eochionelasmus* examined ranged from six to seventeen articles (Table 6). Like the cirri, the number of articles also increase with growth. In other vent barnacles the caudal appendage are rudimentary.

PENIS OF *Eochionelasmus* FROM THE NORTH FIJI BASIN

In the smallest individual examined (NFB-1: 2.4 × 2.0 mm in R-C and CL diameters) no

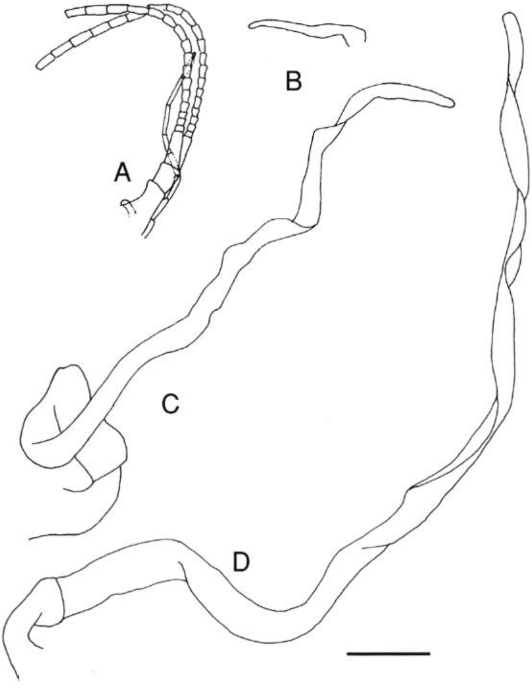

FIG. 9. — Ontogenetic growth of penis; **A**, NFB-4, a tiny penis is found at the base of the protopod of cirrus VI; **B**, NFB-6; **C**, NFB-9; **D**, paratype (UMUT-RA18632), specimens from the North Fiji Basin. No penis was found in NFB-1 specimen. Scale bar: 0.1 mm.

TABLE 7. — *Eochionelasmus ohtai ohtai* from Lau Basin, size and ratios of the specimen. **aL/pL**, ratios of the lengths of the anterior and posterior rami of cirrus I; **L/W**, ratios of the lengths and widths of the 12th, 20th, 30th, 40th and 50th articles of cirrus VI with, in parenthesis, the number of pairs of setae per article of cirrus VI; –, articles missing; **R-C**, rostrum-carina diameter (in mm). Article indicated in [ ] when designated article was broken off.

	AL/pL	L/W of articles of C VI					Size
	CI	12th	20th	30th	40th	50th	R-C
LAU-1	2.3	2.0 (2)	2.2 (2)	–	–	–	4.0
LAU-2	2.4	0.9 (3)	1.6 (6)	2.3 (5)	–	–	7.6
LAU-3	2.9	0.8 (3)	1.2 (5)	1.8 (6) [29th]	–	–	13.1
LAU-5	2.7	0.6 (4)	0.8 (5)	1.3 (7)	2.1 (8) [41st]	1.6 (5)	17.0
LAU-8	2.7	0.5 (4)	0.7 (5)	1.0 (7)	1.2 (8)	1.6 (7)	29.0

TABLE 8. — *Eochionelasmus ohtai ohtai* from Lau Basin. Number of articles of the right anterior (**R:a**), right posterior (**R:p**), left anterior (**L:a**) and left posterior (**L:p**) rami of cirri I-VI and caudal appendages (**c.a.**); **R-C × CL**, rostrum-carina and carinolateral diameters (in mm), respectively.

		Number of articles of cirri						c.a.	R-C × CL	Remarks
		I	II	III	IV	V	VI			
LAU-1	R:a	12	11	10	16	14+	23	(9)	4.0 × 3.7	penis tiny
	R:p	5	14+	10	13+	18+	24			
	L:a	12	9	17	15	22	24	(7+)		
	L:p	5	14	20	18	23	23			
LAU-2	R:a	14	21	24	22+	17+	19+	(12)	9.6 × 7.6	penis long
	R:p	6	18	29	31	21+	19+			
	L:a	17	24	28	38	38	38	(13)		
	L:p	7	28	26	37	47	37			
LAU-3	R:a	21	21+	32	42	42	29+	(14)	13.1 × 10.5	penis long
	R:p	6	21+	37	43	26+	33+			
	L:a	21	22+	21+	24+	33+	33+	(15)		
	L:p	6	23+	26+	28+	34+	34+			
LAU-5	R:a	23	36	3+	36+	51	56+	(15)	17.0 × 16.7	penis long
	R:p	7	42	13+	27+	33+	43+			
	L:a	23	26+	42	31+	31+	20+	(16)		
	L:p	7	38	27+	38+	52	63+			
LAU-6	R:a	27	27+	24+	63+	50+	69+	(18)	25.8+ × 27.2	penis long
	R:p	8	31+	38+	47+	69	59+			
	L:a	26	36	31+	60	81	61+	(20)		
	L:p	7	31+	32+	59+	72+	57+			
LAU-7	R:a	25	37	45	44+	66	73	(16)	26.1 × 17.9+	penis long
	R:p	7	47	26+	55	69	70			
	L:a	26	27+	6+	57	40+	66	(16)		
	L:p	6	43	48	62	65	48+			
LAU-8	R:a	22	25	45	57	64	56+	(17)	29.0 × 20.5	penis long
	R:p	7	33	54	62	55+	70			
	L:a	24	30	39	50+	23+	74	(16+)		
	L:p	7	38	46	54+	65	72			

penis was found between the pedicles of cirri VI. A tiny penis (0.1 mm in length) was found in specimen NFB-4 (Fig. 9A: 4.7 × 4.2 mm in R-C and CL diameters) and in specimen NFB-6 (Fig. 9B: 7.4 × 6.4 mm in R-C and CL diameters) the penis was about 0.6 mm, or as long as the posterior rami of cirrus I. Finally, specimen NFB-9 (Fig. 9C: 12.1 × 8.2 mm in R-C and CL diameters) had a penis about 7 mm in length, again as long as the anterior rami of the cirrus I. As mentioned in the section on sexual maturity, the specimen brooding eggs was around 14.2 × 11.9 mm in R-C and CL diameters. Therefore, although eggs were not found in the mantle cavity of a specimen of comparable size (NFB-9), its penis was apparently functional and therefore it was probably mature.

Eochionelasmus FROM THE LAU AND MANUS BASINS

Eochionelasmus FROM THE LAU BASIN

Eight individuals of *Eochionelasmus* from station BL12 in the Lau Basin were studied. The smallest and the largest were 4.0 × 3.7 mm and 29.0 × 20.5 mm in R-C and CL diameters, respectively (Fig. 9, Table 1). The regression line between CL (y) and R-C (x) diameters is $y = 0.79\ x + 0.95$ and the correlation coefficient (r) is 0.937. Thus, the specimens from the Lau Basin closely resemble the regression line for those from the North Fiji Basin (Fig. 4: $y = 0.88\ x + 0.0004$, $r = 0.967$), as well as in the characteristics of the shell, in corroboration of "Spivey's Law" for species of *Balanus*; *e.g.* every species has its own shape (Spivey 1989).

Besides shell size and form, the opercular plates, the primary wall plates, and the basal imbricating plates, are essentially the same in morphology and arrangement as those of the *E. ohtai* from the North Fiji Basin. The sr, rl^1, l^2, cl^1 and sc plates appear in the third whorl in 50, 50, 13, 50 and 0% individuals and in the fourth whorl in 50, 50, 50, 50 and 83%, respectively. Therefore, by the fourth whorl 100, 100, 100, 100 and 83% of the individuals have gained these respective plates (Fig. 5, Table 3). Since sr, rl^1 and cl^1 generally appear in the fourth whorl in the North Fiji Basin population, it is remarkable that they have appeared in half of eight specimens from Lau.

As for the mouth parts, there is no notable difference between those from the North Fiji and Lau Basins populations (Fig. 10). The second and third teeth of the mandible in the smallest dissected specimen (LAU-1, Fig. 10C) have very few and very fine comblike spines as does the smallest individual from the North Fiji Basin and from the Manus Basin (Fig. 11D). With regard to the cirri, as already noted, the number of articles increases with growth (Tables 7 and 8). Generally speaking, when individuals of same sized from Lau and North Fiji Basins are compared, such as NFB-4 (4.7 × 4.2 mm) and LAU-1 (4 × 3.7 mm), NFB-B (9.5 × 8.1 mm) and LAU-2 (9.6 × 7.6 mm), and NFB-9 (12.1+ × 8.2 mm) and LAU-3 (13.1 × 10.5 mm), the number of articles, while similar, is slightly less in the specimens from the Lau Basin. Otherwise, no morphological difference between the cirri of these two populations were found.

The number of articles of the caudal appendages range from nine to twenty, a greater range than for the North Fiji Basin population. However, when same sized individuals were compared, the number was almost the same. Therefore, there appear to be no significant difference between these two populations, in any of the characters examined, and therefore it is concluded that they represent the same species.

Eochionelasmus FROM THE MANUS BASIN

Seven individuals of *Eochionelasmus* from the Manus Basin were studied. The smallest and largest individuals were 2.0 × 1.7 mm and 23.8 × 25.0 mm in R-C and CL diameters, respectively (Fig. 11, Table 1). The regression line between the CL (y) and R-C (x) diameters is $y = 0.93\ x + 0.12$ and the correlation coefficient (r) is 0.973. Thus, the Manus Basin regression is similar to that of the North Fiji Basin population ($y = 0.88\ x + 0.0004$, $r = 0.967$). The specimens from the Manus Basin also closely resemble those of *E. ohtai* from the North Fiji Basin in the morphology of their opercular plates, the primary wall plates and the basal imbricating plates.

As for the mouth parts and cirri I and II, there is

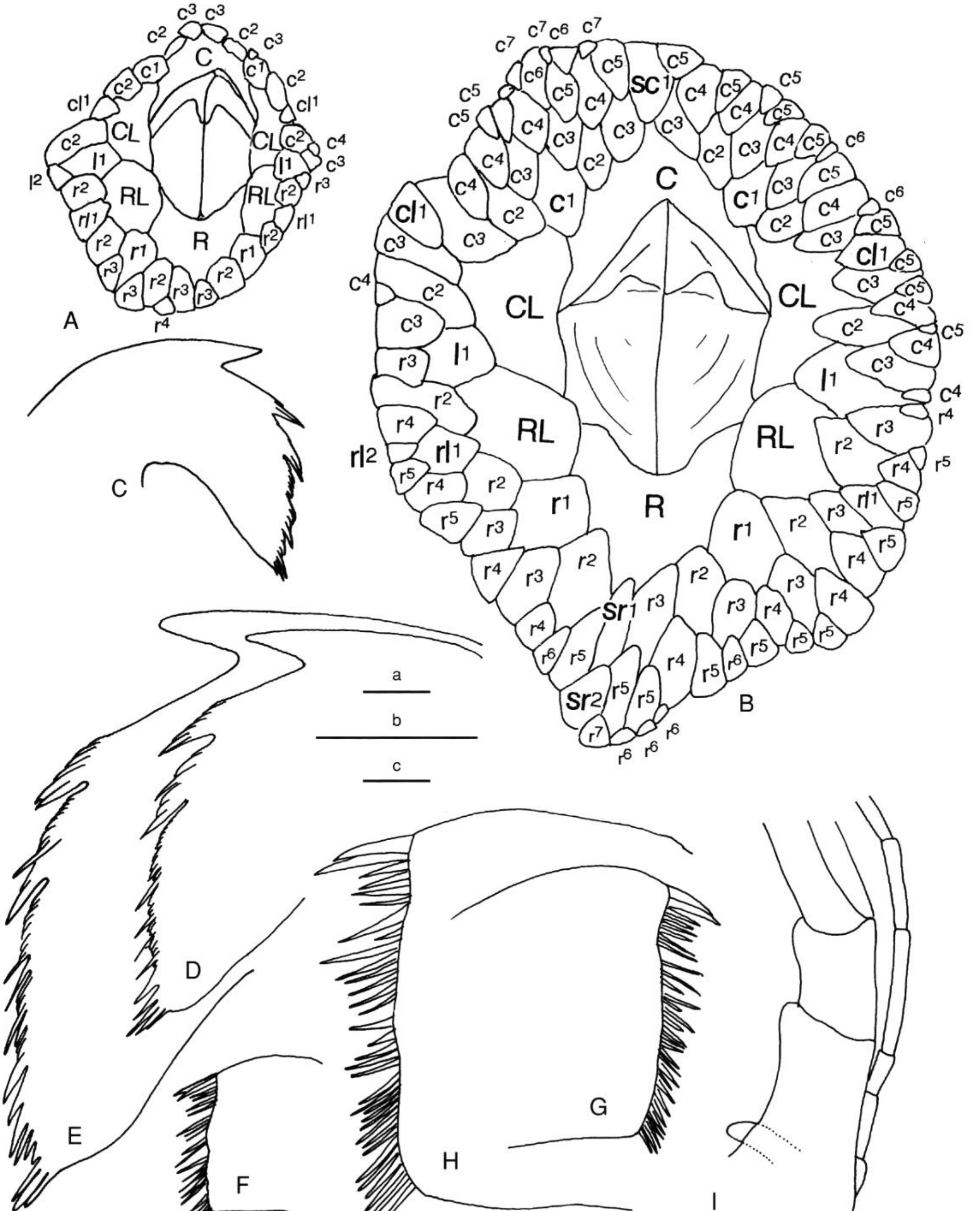

FIG. 10. — Specimens from the Lau Basin. **A**, LAU-1; **B**, LAU-2; **C**, right mandible of LAU-1; **D**, right mandible of LAU-2; **E**, right mandible of LAU-3; **F**, right first maxilla of LAU-1; **G**, left first maxilla of LAU-2; **H**, left first maxilla of LAU-3; **I**, a tiny penis; right cirrus VI and caudal appendage. Scale bar: **a** (A, B), 1 mm; **b** (C-H), 0.1 mm; **c** (I), 0.1 mm.

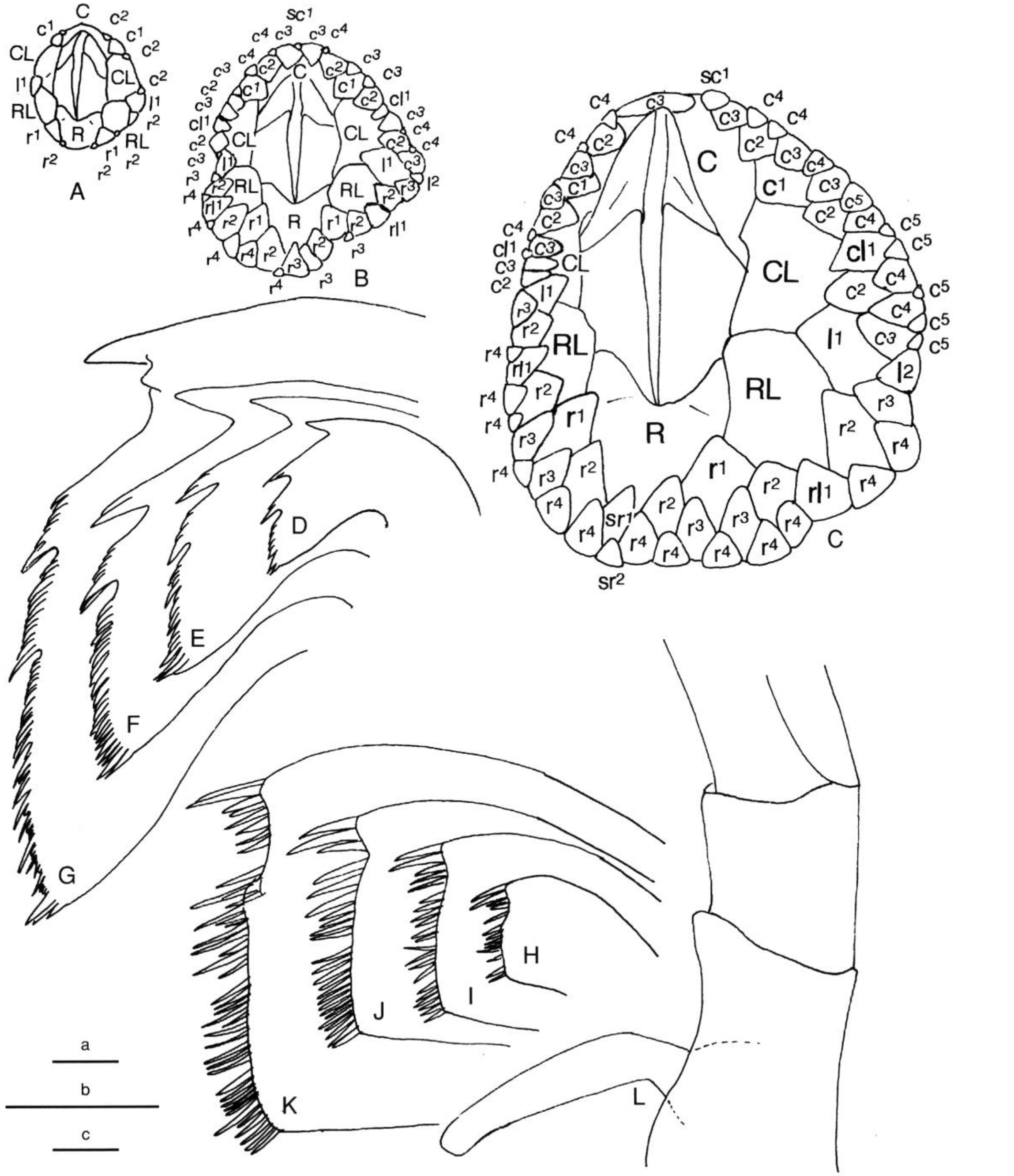

FIG. 11. — Specimens from the Manus Basin. **A**, MANUS-1; **B**, MANUS-3; **C**, MANUS-5; **D**, left mandible of MANUS-1; **E**, left mandible of MANUS-4; **F**, right mandible of MANUS-5; **G**, right mandible of MANUS-6; **H**, left first maxilla of MANUS-1; **I**, right first maxilla of MANUS-4; **J**, left first maxilla of MANUS-5; **K**, right first maxilla of MANUS-6; **L**, a small penis, right cirrus VI and caudal appendage of MANUS-5. Scale bar: **a** (A-C), 1 mm; **b** (D-J), 0.1 mm; **c** (L), 0.1 mm.

TABLE 9. — *Eochionelasmus ohtai ohtai* from Lau Basin, size and ratios of the specimen. **aL/pL**, ratios of the lengths of the anterior and posterior rami of cirrus I; **L/W**, ratios of the lengths and widths of the 12th, 20th, 30th, 40th, 50th and 60th articles of cirrus VI with, in parenthesis, the number of pairs of setae per article of cirrus VI; –, articles missing; **R-C**, rostrum-carina diameter (in mm). Article indicated in [ ] when designated article was broken off.

	aL/pL	**L/W of articles of C VI**						**Size**
	C I	**12th**	**20th**	**30th**	**40th**	**50th**	**60th**	**R-C**
MANUS-1	2.4	2.5 (3)	–	–	–	–	–	2.0
MANUS-4	2.6	–	–	–	–	–	–	4.8
MANUS-5	2.5	0.9 (3)	1.7 (4) [21st]	2.3 (4)	–	–	–	7.4
MANUS-6	4.0	0.6 (4)	0.8 (6)	1.0 (7)	1.2 (8)	1.6 (9) [51st]	2.0 (9)	23.2

TABLE 10. — *Eochionelasmus ohtai manusensis* n.ssp. from Manus Basin. Number of articles of the right anterior (**R:a**), right posterior (**R:p**), left anterior (**L:a**) and left posterior (**L:p**) rami of cirri I-VI and caudal appendages (**c.a.**); **R-C × CL**, rostrum-carina and carinolateral diameters (in mm), respectively.

		Number of articles of cirri						**c.a.**	**R-C × CL**	**Remarks**
		I	**II**	**III**	**IV**	**V**	**VI**			
MANUS-1	R:a	8	5	6+	5+	5+	14+	(5+)	2.0 × 1.7	no penis
	R:p	4	4	5+	5+	30	6+			
	L:a	8	5	6+	12	22+	+	(5+)		
	L:p	4	5	6	5+	7+	+			
MANUS-3	R:a	11	10	9+	9+	8+	9+	(9+)	3.7 × 3.6	no penis
	R:p	5	10	6+	8+	10+	9+			
	L:a	11	6	9+	12+	10+	10+	(10+)		
	L:p	5	10	13+	11+	10+	11+			
MANUS-4	R:a	12	1+	2+	1+	1+	1+	(4+)	4.8 × 4.0	no penis
	R:p	5	3+	3+	1+	1+	1+			
	L:a	14	12	3+	4+	3+	1+	(6+)		
	L:p	5	1+	2+	6+	6+	1+			
MANUS-5	R:a	17	12+	11+	16+	19+	32+	(14)	7.4 × 6.2	penis small
	R:p	6	13+	22+	17+	20+	19+			
	L:a	15	12+	26	18+	28+	20+	(13)		
	L:p	6	14+	16+	19+	32+	20+			
MANUS-6	R:a	30	45	60	68+	73+	68+	(12+)	23.2 × 25.0	penis long
	R:p	7	41	52	64	73+	80+			
	L:a	27	37+	42+	75	86+	86	(18)		
	L:p	7	42	52+	52+	76+	8+			
MANUS-7	R:a	17+	30	29+	41+	64+	54+	(16)	23.5 × 25.0	penis long
	R:p	6	33	44+	54+	68+	76+			
	L:a	27	35	40	59+	60+	62+	(16)		
	L:p	7	35+	51	40+	52+	69+			
MANUS-8	R:a	32	44+	46	66	70	79	(18)	30.1 × 23.8	penis long
	R:p	7	45	50	73	82	51+			
	L:a	32	44	50	60	70	78	(18)		
	L:p	8	38	47	76	84	65+			

no notable difference between the North Fiji and Lau Basins (Fig. 10). The mandible (Fig. 11D) of the smallest individual in the dissected specimens has same morphological characteristics as found in the smallest individual from the Manus, North Fiji and Lau Basins. Though more than half of the seven individuals examined lack tips of cirri III to V, the number of articles in the few complete cirri are in the observed ranges for the specimens from the North Fiji Basin. As for the complete caudal appendages observed in half specimens, the number of articles is essentially the same as for those from the North Fiji Basin (Tables 9, 10). Furthermore, there is no notable difference in the ratio of length and width of the articles of the cirri, in the number of spines per article, or in the nature of mouth parts between the populations from the North Fiji and Manus Basins, as might be expected since they are likely eating very much the same thing.

The sr, rl^1, l^2, cl^1 and sc plates appear in the third whorl of 50, 100, 0, 17 and 0% of the individuals, and in the fourth whorl of 17, 0, 50 50 and 83%, respectively. Therefore, by the fourth whorl 67, 100, 50, 67 and 83% of the individuals have gained these plates, respectively (Fig. 5, Table 3). Since sr, rl^1 and cl^1 generally appear in the fourth whorl in the North Fiji population, it is very remarkable that rl^1 has appeared in the third whorl in all individuals of the six specimens from Manus. No notable difference in the order in which the other imbricating plates appeared was found.

DISCUSSION

Relationship between the *Eochionelasmus* populations from the North Fiji, Lau and Manus Basins

Unless endowed with excellent dispersal capabilities, one might expect that these three relatively isolated deep-sea hydrothermal vent populations would have speciated. However, despite the variety of morphological attributes investigated here, no demonstrable morphological differences attributable to the geographical isolation were found that could be used to distinguish the three isolated populations of the North Fiji, Lau and Manus Basins, except the small ontogenetic change in the appearance of the pair of rl^1 imbricating plates in the Manus population. Morphological species are often subject to question, and they can be a problem in accessible shallow-water as well as relatively inaccessible deep-water populations. To further explore this matter, it will likely be necessary to employ molecular methods. But until then, it would appear that these three remote populations represent the same species, *E. ohtai*. However, the difference in the position of rl^1 does distinguish the Manus population from the North Fiji and Lau populations, and it is isolated from them by approximately 3000 km and 4300 km, respectively. Therefore, the difference correlates with the geographic isolation of the Manus from the North Fiji/Lau populations, and this justifies designat-ing the Manus population as a subspecies, *E. ohtai manusensis* n.ssp.

Dispersal

For some, interests in the fauna in the deep-sea hydrothermal vents has shifted from discovery and description of new and often exotic taxa to considerations of endemism and dispersal over the long-distances between the East Pacific, West Pacific and/or Atlantic; *i.e.* the bresilid shrimp (Williams & Rona 1986), bythograeid crabs (Hessler & Martin 1989), and copepods of genus *Stygiopontius* (Humes 1987, 1989, 1990). The occurrence of closely related species at various remote deep-sea hydrothermal vents requires long-range albeit infrequent dispersal and/or more stepping stones along the mid-ocean ridge system, and between them and back-arc basins than there are today (Hessler & Lonsdale 1991; Tunnicliffe & Flower 1996), and for some surely cognate environments such as hydrocarbon and brine seeps are involved (Newman 1985; Smith *et al.* 1989).

Some animals inhabiting the deep-sea hydrothermal vents are survivors of higher taxa that originated in the Mesozoic or Paleozoic that have otherwise gone extinct (Barnacles: Newman 1979; Newman & Hessler 1989; Yamaguchi & Newman 1990; Jones 1993; Newman & Yamaguchi 1995. True crabs: Newman 1985. Limpets: McLean 1981; 1988a, b; 1989a, b. Pectinids:

Schein-Fatton 1988). If the present distribution of such primitive animals is terms of a 100 million years or more, it may be better explained move in terms of vicariance and relictism than of dispersal.

ECOLOGY

Desbruyères *et al.* (1994) reported on the habitats and temperatures where populations of *Eochionelasmus* and a new neolepadine similar to *Neolepas* (pers. obs.) are present in the Lau and North Fiji Basins. At the Vai Lili site of the Lau Basin, where temperatures reach but did not exceed 6 °C, few *Eochionelasmus* were found. On the other hand, along the outside rim of the Vai Lili site, where populations of *Eochionelasmus* accompanied by the neolepadine were present, temperatures ranged from 2 to 5 °C. At the Hine Hina site of the Lau Basin, where the temperature ranged from 2.5 to 4.5 °C, a population of the neolepadine was present, while at two sites dominated by mytilids, the temperature ranged was 5.3-12.2 °C and 3.7-17 °C (Chevaldonné *et al.* 1991). In the South Hine Hina and Momoko sites at Lau, the neolepadine was even found at sites where no thermal anomaly was detected during the sampling period. In the outer portion of the White Lady site of the North Fiji Basin, dense communities of *Eochionelasmus* occured with sparse individuals of neolepadine, where temperatures ranged from 2.5 to 4 °C (Desbruyères *et al.* 1994).

CONCLUSIONS

In the present study, numerous specimens of *Eochionelasmus ohtai* collected by the French submersible *Nautile* from the North Fiji Basin are compared with the type specimens of *E. ohtai* from the North Fiji Basin described previously by Yamaguchi & Newman (1990). No significant difference were found in the morphology of shell wall, opercular valves, trophi and cirri between these two populations, and they are considered representative of the same species. However, in studying the ontogeny of the basal whorl of imbricating plates, it was observed that there were a few small differences between what was generally observed and the arrangement depicted for the type specimen by Yamaguchi & Newman (1990).

The adjusted or generalized pattern stemming from these observation was then used for comparisons with populations of *Eochionelasmus* from the Lau Basin, Tonga and the Manus Basin, Bismarck Archipelago. It was observed that while there were minor differences between the North Fiji and Lau populations, there was a notable difference between them and the Manus population; *e.g.* (1) the rl^1 pair of imbricating plates in all six specimens from the Manus Basin occurred in the third whorl while in the specimens from the North Fiji and Lau Basins it occurred there in 40 and 50% of the ten and eight individuals examined, respectively; and (2) cl^1 appeared in all individuals from the North Fiji and Lau basins by the fourth whorl while in the Manus specimens it appeared in 50% of the individuals by the fourth whorl.

Those differences not only appear to be significant but they correlate with the geographic situation. Therefore, we feel justified in proposing that the Manus population be recognized as a distinct race or subspecies, *Eochionelasmus ohtai manusensis* n.ssp.

Only one individual (14.2 × 11.9 mm in R-C × CL diameters) of the dozens of mature specimens examined was brooding eggs, about 150 of which were divided between two ovigerous lamellae. The eggs were essentially of the same size as in previously known hydrothermal barnacles of *Neolepas zevinae*, *N. rapanuii* and *Neoverruca brachylepadoformis*. The holotype of *Eochionelasmus* is almost of the same size as the individual with eggs, and therefore it is considered to be a fully adult individual.

It was observed that the second and third teeth of the mandible in all three populations each changed from a point of a few fine spines to a long row of comb-like tooth during ontogeny. The ontogenetic change corroborates the view that the special mandible of *Eochionelasmus* was derived from an ancestor having normal mandibular teeth.

The morphological resemblance between the Manus, North Fiji and Lau populations, which are separated by 3000 and 1300 km respectively, suggests that they are conspecific; *e.g.*

Eochionelasmus ohtai. If so, this is the first report of a vent barnacle species having a range of over 4300 km.

SYSTEMATIC DESCRIPTION

Subclass CIRRIPEDIA Burmeister, 1834
Superorder THORACICA Darwin, 1854
Order SESSILIA Lamarck, 1818
Suborder BALANOMORPHA Pilsbry, 1916
Superfamily CHIONELASMATOIDEA Buckeridge, 1983
Family CHIONELASMATIDAE Buckeridge, 1983
Genus *Eochionelasmus* Yamaguchi, 1990

Eochionelasmus ohtai manusensis n.ssp.

MATERIAL. — Eleven individuals (including 6 adults and 5 juveniles) were recovered by Russian submersible *Mir-2*, 1990, Manus Back-Arc Basin, station 2255 (3°10'S, 150°17'E), at about 2500 m of depth. Eight individuals (including 3 adults and 5 juveniles) were used in this study.

DEPOSITION OF TYPES. — See table 1.

DIAGNOSIS

As for the species (Yamaguchi & Newman 1990), except that the rl^1 pair of imbricating plates appears in the third whorl rather than in the fourth whorl as is more commonly the case in the North Fiji and Lau Basin populations.

DESCRIPTION

As for the species.

Acknowledgements

We thank S. Galkin for the specimens from Manus Basin and M. Segonzac for the specimens from Lau Basin. The first author would like to acknowledge for the sponsorship and the support of the Japan Society for the Promotion of Science (JSPS) for a six months overseas research at Centers of Excellence Abroad to Scripps Institution of Oceanography (SIO). This study was supported in part by a Grant-in-Aid for Scientific Research from the Ministry of Education, Science and Culture, project Nos. 04804065 and 06404001 and the Tokyo Geographical Society, the Sumitomo Foundation and the Fujiwara Natural History Foundation.

REFERENCES

Barnes M. 1989. — Egg production in cirripedes. *Oceanography and Marine Biology Annual Review* 27: 91-166.

Berg C. J. & Turner R. D. Jr 1980. — Description of living specimens of *Calyptogena magnifica* Boss and Turner with notes on their distribution and ecology, Appendix 1, *in* Boss K. J. & Turner R. D. (eds), The giant white clam from the Galapagos Rift, *Calyptogena magnifica* sp. nov, *Malacology* 20: 183-185.

Buckeridge J. S. 1995. — Phylogeny and biogeography of the primitive Sessilia and a consideration of a Tethyan origin for the group, *in* Schram F. R. & Høeg J. T. (eds), New frontiers in barnacle evolution, *Crustacean Issues* 10: 255-267.

— 1996. — A living fossil *Waikalasma boucheti* n.sp. (Cirripedia, Balanomorpha) from Vanuatu (New Hebrides), Southwest Pacific. *Bulletin du Muséum national d'Histoire naturelle*, Paris, série 4, A, 18 (3-4) : 447-457.

Buckeridge J. S. & Newman W. A. 1992. — A reexamination of *Waikalasma* (Cirripedia: Thoracica) and its significance in Balanomorph Phylogeny. *Journal of Paleontology* 66 (2): 341-345.

Chevaldonné P., Desbruyères D. & Le Haitre M. 1991. — Time-series of temperature from three deep-sea hydrothermal vent sites. *Deep-Sea Research* 38 (11): 1417-1430.

Costlow J. D. 1956. — Shell development in *Balanus improvisus* Darwin. *Journal of Morphology* 99: 359-415.

Darwin C. R. 1851. — *A monograph on the sub-class Cirripedia. The Lepadidae; or pedunculated cirripedes*. Ray Society, London, 400 p.

— 1854. — *A monograph on the sub-class Cirripedia. The Balanidae (or sessile cirripedes); the Verrucidae, etc.* Ray Society, London, 684 p.

Desbruyères D., Alayse-Danet A.-M., Ohta S. & the Scientific Parties of *Biolau* and *Starmer* Cruises 1994. — Deep-sea hydrothermal communities in Southwest Pacific Back-arc basins (the North Fiji and Lau Basins): Composition, microdistribution and food web. *Marine Geology* 116: 227-242.

Galkin S. V. 1992a. — *Eochionelasmus ohtai* (Cirripedia, Balanomorpha) from hydrothermal vents in the Manus Back-Arc Basin. *Zoologicheskiy Zhurnal* 71 (11): 139-143.

— 1992b. — Bottom fauna of the Manus basin

hydrothermal. *Oceanology, Russian Academy Nauk* 32: 1102-1110.
Hessler R. R. & Longsdale P. 1991. — Biogeography of Mariana Trough hydrothermal vent communities. *Deep-Sea Research* 38 (2): 185-199.
Hessler R. R., Longsdale P. & Hawkins J. 1988. — Pattern on the ocean floor. *New Scientist* 24: 47-51.
Hessler R. R. & Martin J. W. 1989. — *Austinograea williamsi*, new genus, new species, a hydrothermal vent crab (Decapoda: Bythograeidae) from the Mariana Back-Arc Basin, Western Pacific. *Journal of Crustacean Biology* 9 (4): 645-661.
Hui E. & Moyse J. 1984. — Complemental males of the primitive balanomorph barnacle, *Chionelasmus darwini. Journal of the Marine Biological Association of the U. K.* 64: 91-97.
Humes A. G. 1987. — Copepoda from deep-sea hydrothermal vents. *Bulletin of Marine Science* 41: 645-788.
— 1989. — New species of *Stygiopontius* (Copepoda, Siphonostomatoida) from a deep-sea hydrothermal vent at the East Pacific Rise. *Zoologica scripta* 18 (1): 103-113.
— 1990. — Copepods (Siphonostomatoida) from a deep-sea hydrothermal vent at the Mariana Back-Arc Basin in the Pacific, including a new genus and species. *Journal of natural history* 24 (2): 289-304.
Jones D. S. 1993. — A new *Neolepas* (Cirripedia: Thoracica: Scalpellidae) from an abyssal hydrothermal vent, Southeast Pacific. *Bulletin of Marine Science* 52 (3): 937-948.
Lutz R. A. 1988. — Dispersal of organisms at deep-sea hydrothermal vents: a review. *Oceanologica Acta*, vol. sp. (8): 23-29.
McLean J. H. 1981. — The Galapagos Rift limpet *Neomphalus*: Relevance to understanding the evolution of a major Paleozoic-Mesozoic radiation. *Malacologia* 21: 291-336.
— 1985. — Preliminary report on the limpets at hydrothermal vents, *in* Jones M. L. (ed.), The Hydrothermal Vents of the Eastern Pacific: An Overview, *Bulletin of Biological Society of Washington* (6): 159-166.
— 1988a. — New archaeogastropod limpets from hydrothermal vents. Superfamily Lepetodrilacea. I. Systematic descriptions. *Philosophical transactions of the Royal Society of London*, Ser. B. 319: 1-32.
— 1988b. — New archaeogastropod limpet families in the hydrothermal vent community. *Malacological review*, Supplement 4: 85-87.
— 1989a. — New archaeogastropod limpets from hydrothermal vents, new family Peltospiridae, new superfamily Peltospiracea. *Zoologica scripta* 18: 49-66.
— 1989b. — New slit-limpets (Scissurellacea and Fissurelacea) from hydrothermal vents. Part 1. systematic descriptions and comparisons based on shell and radular characteristics. *Contributions in science*, Natural History Museum of Los Angeles County (407): 1-29.
Newman W. A. 1979. — A new scalpellid (Cirripedia); a Mesozoic relic living near an abyssal hydrothermal spring. *Transactions of the San Diego Society of Natural History* 19 (11): 153-167.
— 1985. — The abyssal hydrothermal vent invertebrate fauna: A glimpse of antiquity ? *Bulletin of the Biological Society of Washington* (6): 231-242.
— 1987. — Evolution of cirripedes and their major groups, *in* Southward A. J. (ed.), Barnacle Biology, *Crustacean Issues*, Balkema, Rotterdam 5: 3-42.
— 1989. — Juvenile ontogeny and metamorphosis in the most primitive living sessile barnacle, *Neoverruca*, from an abyssal hydrothermal spring. *Bulletin of Marine Science* 45: 467-477.
— 1992. — Biotic cognates of eastern boundary conditions in the Pacific and Atlantic: Relicts of Tethys and climatic change. *Proceeding of the San Diego Society of Natural History* 16: 1-17.
— 1993. — Darwin and cirripedology, *in* Truesdale F. (ed.), History of Carcinology, *Crustacean Issues*, Balkema, Rotterdam 8: 349-434.
— 1996. — Cirripedia : 453-540, *in* Forest J. (ed.), *Traité de Zoologie*, tome VII, Crustacés, fascicule II. Masson, Paris.
Newman W. A. & Hessler R. R. 1989. — A new abyssal hydrothermal verrucomorphan (Cirripedia; Sessilia); the most primitive living sessile barnacle. *Transactions of the San Diego Society of Natural History* 21 (16): 221-235.
Newman W. A. & Yamaguchi T. 1995. — A new sessile barnacle (Cirripedia; Brachylepadomorpha) from the Lau Back-arc Basin, Tonga; first record of a living representative since the Miocene. *Bulletin du Muséum national d'Histoire naturelle*, Paris, serie 4, A 18 (3-4) : 221-243.
Newman W. A., Zullo V. A. & Withers T. H. 1969. — Cirripedia: R206-R295, *in* Moore R. C. (ed.), *Treatise on Invertebrate Paleontology*, Part R, Arthropoda, 4, 1. Geological Society of America and University of Kansas Press, Lawrence.
Nilsson-Cantell C. A. 1928. — The cirripede *Chionelasmus* (Pilsbry) and a discussion of its phylogeny. *The Annals and Magazine of Natural History* ser. 10, 2 (1): 445-455.
Pilsbry H. A. 1907. — Hawaiian Cirripedia. *Bulletin Bureau of Fisheries* 26: 181-190.
Pope E. C. 1965. — A review of Australian and some Indomalayan Chthamalidae (Crustacea: Cirripedia). *Proceedings of the Linnean Society of New South Wales* 90 (1): 10-77.
Ross A. & Newman W. A. 1996. — A unique experiment in four-platedness by a Miocene barnacle (Cirripedia; Balanidae) that Darwin considered improbable. *Journal of Crustacean Biology* 16 (4): 663-668.
Runnström S. 1925. — Zur Biologie und Entwicklung von *Balanus balanoides* (Linné). *Bergens Mususeum Aarbok* 5: 1-46.
Schein-Fatton E. 1988. — A very primitive

Pectinacea (Bivalvia): *Bathypecten vulcani* from the 13°N hydrothermal site (East Pacific). *Oceanologica acta*, volume special, No. 8: 3-89.
Smith C .R., Kukert H., Wheatchroft R. A., Jumars P. A. & Deming J. 1989. — Vent fauna on whale remains. *Nature* 341: 27, 28.
Spivey H. R. 1989. — The size variable and allometric analysis in the barnacle genus *Balanus*. *Journal of natural history* 23: 1017-1032.
Tufar W. 1990. — Modern hydrothermal activity, formation of complex massive sulfide deposits and associated vent communities in the Manus Back-Arc Basin (Bismarck Sea, Papua New Guinea). *Mitteilungen der österreichischen geologischen Gesellschaft* 82: 183-210.
Tunnicliffe V. & Flower M. R. 1996. — Influence of sea-floor spreading on the global hydrothermal vent fauna. *Nature* 379: 531-533.
William A. B. & Rona P. A. 1986. — Two new caridean shrimps (Bresiliidae) from an hydrothermal field on the Mid-Atlantic Ridge. *Journal of Crustacean Biology* 2 (1): 136-147.
Woodward H. 1901. — On '*Pyrgoma cretacea*', a cirripede from the Upper Chalk of Norwich and Margate. *Geological Magazine* 8: 145-152 (erratum: 240; additional note: 528).
Yamaguchi T. & Newman W. A. 1990. — A new and primitive barnacle (Cirripedia: Balanomorpha) from the North Fiji Basin Abyssal Hydrothermal Field, and its evolutionary implications. *Pacific Science* 44 (2): 135-155.
— 1997. — *Eochionelasmus paquensis*, new species (Cirripedia, Balanomorpha) from 17°25'S, north of Easter Island: First record of an hydrothermal sessile barnacle from the East Pacific Rise. *Journal of Crustacean Biology* 17 (3): 488-496.

Submitted on 14 January 1997;
accepted on 22 May 1997.