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EOCHIONELASMUS PAQUENSIS, NEW SPECIES (CIRRIPEDIA: BALANOMORPHA), FROM 17°25'S, NORTH OF EASTER ISLAND: FIRST RECORD OF A SESSILE HYDROTHERMAL BARNACLE FROM THE EAST PACIFIC RISE

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ABSTRACT

The first sessile barnacle from a deep-sea hydrothermal vent of the East Pacific Rise (EPR) has been recovered by the French submersible *Nautile* from 17°25'S, north of Easter Island. It is similar in general appearance to the most primitive living balanomorph barnacle *Eochionelasmus ohtai* known from the North Fiji, Lau, and Manus Basins, in the Southwest Pacific (Yamaguchi and Newman, 1990; Galkin, 1992), but the morphology of its opercular plates, mouthparts, and cirri is distinct. Therefore, it is recognized here as a new species of the previously monotypic genus *Eochionelasmus*. However, it is anticipated that even greater differences will be found between the two species when fully developed individuals of the Easter Island form are found. If so, distinction at the genus-group level will need to be evaluated. The new species is not only the first record of a sessile vent barnacle from the East Pacific Rise, but it is also the first from a midocean ridge. This discovery corroborates the hypothesis that biotic exchange between midocean ridges and back-arc basins occurs relatively infrequently or was curtailed a long time ago.

A new genus and species, *Eochionelasmus ohtai* Yamaguchi, the most primitive living balanomorph barnacle known, was based on eight specimens collected from the North Fiji Basin (NFB) hydrothermal vent in 1987 (16°59'S, 173°55'E, 1,990 m; Yamaguchi and Newman, 1990). Additional large specimens, collected from NFB in 1989 (18°49'S, 173°29'E, 2,765 m) were also available for this study. Specimens of *Eochionelasmus* were also collected from the Lau Basin to the east in 1989 (cf. Newman and Yamaguchi, 1995), and from the Manus Basin in 1990 (Galkin, 1992). All three of these populations appear to be conspecific (Yamaguchi and Newman, in press).

While this and other sessile barnacles are known from vents at back-arc basins in the western Pacific (Newman and Yamaguchi, 1995), the new species to be described here, *Eochionelasmus paquensis,* is not only the first known from the eastern Pacific, but it is the first known from a midocean ridge.

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 paquensis, new species

Figs. 1, 2, 4–6, and Tables 1–3

Material Examined.—The specimens were collected at the Rehu site (17°24.85'S, 113°12.15'W) on the East Pacific Rise (EPR) off Easter Island, in the eastern Pacific (Geistdoerfer *et al.*, 1995). One subadult was collected from the Rehu site (ND 06–3–1B) and 1 subadult and 1 juvenile were collected 10–20 m distant from the site (ND 06–2–1B) at an approximate depth of 2,578 m [Dive 6 of a *NAUDUR* cruise (J.-M. Auzende, Chief Scientist)] by the French submersible *NAUTILE* on 11 December 1993. A first subadult, designated as the holotype (EPR–1), was collected from a dead chimney at the base of an active edifice (ND 06–3–1B), and the other 2 specimens, designated the first and second paratypes (EPR–2 and –3), were collected with the mussel *Bathymodiolus* sp. (ND 06–2–1B) on an active area (Segonzac, personal communication). All were coated with black manganese deposits. The 3 type specimens are deposited as follows: holotype (EPR–1), rostrocarinal diameter (RC) 5.0 mm, carinolateral diameter (LC) 4.1 mm, in the Muséum national d'Histoire naturelle, Paris (MNHN Ci 2493) (Fig. 2). First paratype (EPR–2), RC diameter 4.5 mm, CL diameter 4.6 mm, in the National Science Museum, Tokyo (NSMT–Cr11433) (Fig. 1). Second paratype (EPR–3), RC diameter 1.4 mm, CL diameter 1.0 mm, in the Muséum national d'Histoire naturelle, Paris (MNHN–Ci2494).

The largest specimen (EPR–1, Fig. 2) is small in comparison with those of the western Pacific populations of *Eochionelasmus*. The third and subsequent whorls of the basal imbricating plates, for example, are incomplete, but the specimen was morphologically mature at least as a male. The smallest specimen (EPR–3) had a complete 6-plated wall but had yet to add any of the imbricating plates.

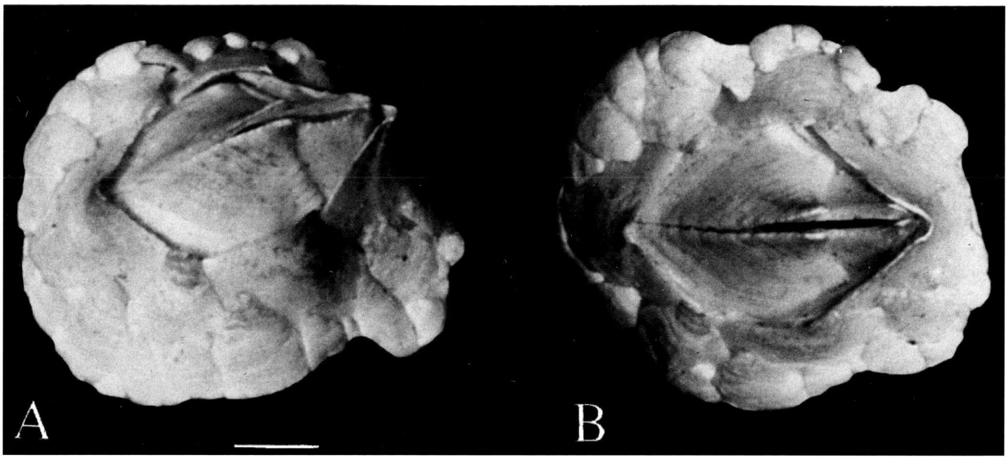

Fig. 1. *Eochionelasmus paquensis,* new species, paratype EPR–2 (NSMT–Cr11433). A and B, from right side and from above, respectively. Scale bar = 1 mm.

Two specimens of *E. ohtai* of comparable size from the North Fiji Basin (NFBH–1 and –4) were used for the comparisons between the trophi and cirri, and between the proportions and characteristics of the shell wall and opercular plates. The order in which the basal whorls of imbricating plates were added during ontogeny was also determined and compared with the "generalized" pattern determined from numerous specimens from the North Fiji Basin (Yamaguchi and Newman, in press).

Diagnosis.—*Eochionelasmus paquensis* differs externally from *E. ohtai* in the alae of primary plates being very indistinct and by the rostrum rising obliquely rather than nearly vertically to the orifice of the wall. The basal imbricating plates, rl^1 and sometimes cl^1, appear in the third rather than in the fourth whorl as is more commonly the case. The scutum is very distinct in lacking an articular ridge and adductor muscle pit, and in having a lateral depressor muscle pit, a wider articular furrow, and a tergal margin that is indented rather than straight. The tergum has a produced articular ridge. The first tooth of the mandible is low and inconspicuous, the lower margin of the cutting edge supports three or four spines rather than a single row of fine, short, sharp comblike spines.

Differential Description.—Hard parts (Figs. 1, 2, 4, 5, Table 1) of the two largest specimens (EPR–1 and –2) include the scuta and terga forming the operculum (S–T), the rostrum (R), rostrolatera (RL), carinolatera (CL), and carina (C) forming a 6-plated primary wall (R–RL–CL–C), and as many as 27 (EPR–1) and 34 (EPR–2) basal imbricating plates of the 74 expected by the end of the fourth whorl in specimens from the North Fiji Basin (cf. Fig. 4). While the EPR–3 juvenile lacks imbricating plates, the two EPR specimens, judged mature at least as males, lack the one additional major and three minor whorls of imbricating plates found in the wall of *E. ohtai.*

The shell is low conic, its orifice large and rhomboidal, and the rostrum slopes obliquely toward the orifice rather than standing at nearly right angles to the base as in *E. ohtai.* The arrangement of the six primary wall plates and the first two whorls of monomorphic, basal imbricating plates is identical to that in *E. ohtai* (Fig. 5). However, rl^1, and to some extent cl^1, appear precociously in the third whorl, while in *E. ohtai* they generally appear in the fourth whorl (Figs. 4, 5). The third and fourth whorls in *E. paquensis* (EPR) are almost destitute of r^3, r^4, c^3, and c^4 imbricating plates (Fig. 5), whereas 12 of each, in each whorl, are typical of the (NFB) population of *E. ohtai.* Furthermore, sr^1 and l^2, seen in the fourth whorl in NFB, had yet to appear in the EPR specimens. If the polarity of these differences is not simply retardation but reduction, the full complement of imbricating plates seen in NFB will not materialize. If this proved to be the case, it would be indicative of a substantial genetic distance between the EPR population and those to the west, in which case the genus-group status of the EPR population would be in need of reevaluation.

The primary wall plates, while smooth, have shallow, narrow external grooves radi-

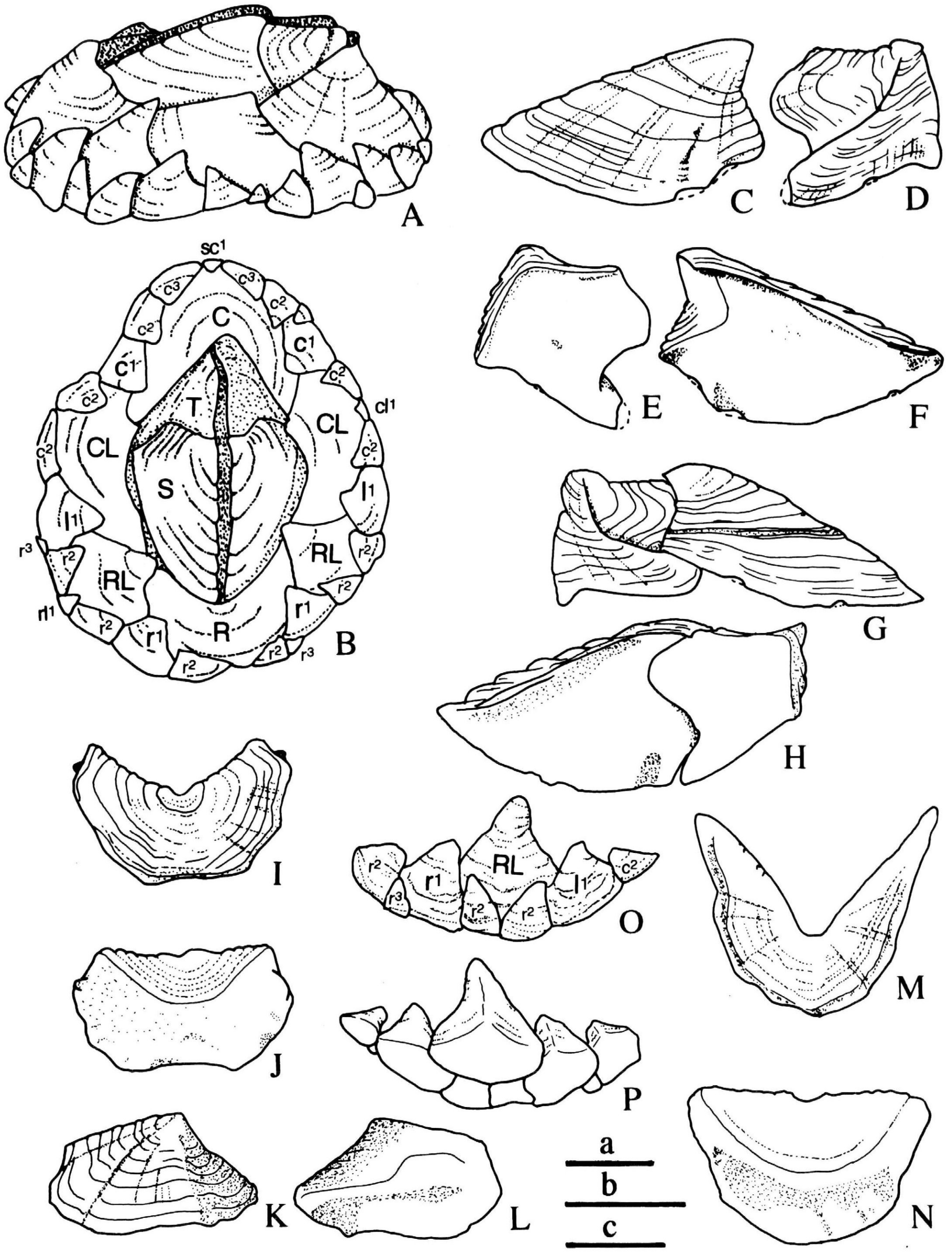

Fig. 2. *Eochionelasmus paquensis*, new species, holotype (MNHN–Ci2493). A and B, viewed from the right side and from above, respectively; C, D, and E, F, exterior and interior views of the right scutum (S) and tergum (T), respectively; G and H, exterior and interior views of the articulated left scutum and tergum (S+T), respectively; I and J, exterior and interior views of the rostrum (R); K and L, exterior and interior views of the right carinolateral (CL); M and N, exterior and interior views of the carina (C); and O and P, exterior and interior views of right rostrolateral (RL) and its surrounding imbricating plates. Letters in 2 B and O are for the principal wall plates (R, RL, CL, and C), the opercular plates (S and T), and the imbricating plates (r^1, r^2, r^3, rl^1, l^1, cl^1, c^1, c^2, c^3, and sc^1). Scale bars a–c = 1 mm, a for A and B; b for C–H; c for I–P.

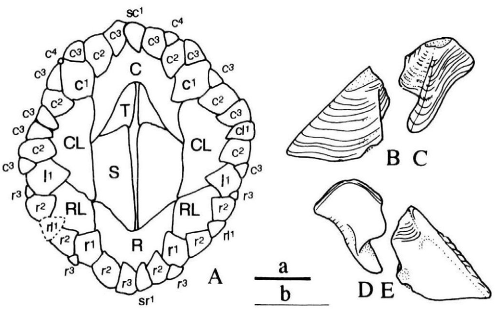

Fig. 3. *Eochionelasmus ohtai* (NFB–4) from North Fiji Basin (Yamaguchi and Newman, in press) comparable in size to EPR–1 and –2. A, viewed from above; B, C, and D, E, exterior and interior views of right scutum and tergum, respectively. Scale bars a, b = 1 mm, a for A, and b for B–E (abbreviations as in Fig. 2).

ating from the apex to the base, and there is no distinct boundary between the alae and paries of the primary plates (R, CL, C) as there is in *E. ohtai.* The growth lines are faint,

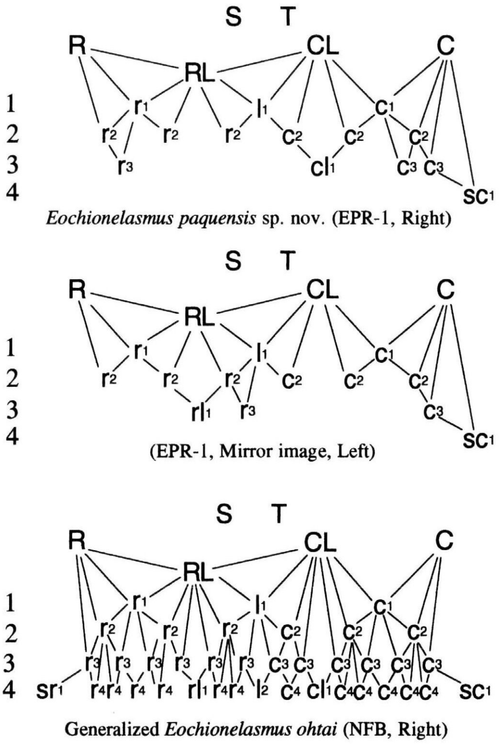

Fig. 4. Shell arrangement (right or mirror image of left side) in *Eochionelasmus paquensis,* new species (EPR–1) and *E. ohtai* (NFB generalized; Yamaguchi and Newman, in preparation). The fifth and lower whorls of imbricating plates are omitted in *E. ohtai.* Note that the differences between the two species begin to appear after the second whorl of imbricating plates, and that subsequently there may be differences between the right and left sides in the same individual as illustrated here.

Whorl	Imbricating Plates	Specimen no.
1	r1 l1 C1	All specimens
2	r2 r2 r2 C2 C2 C2	All specimens
3	r3 r3 r3 r3 r3 r3 C3 C3 C3 C3 C3 C3	NFB Generalized
3	r3 cl1 C3 C3	EPR-1(R)
3	rl1 r3 C3	EPR-1(L) (Mirror Image)
3	r3 r3 r3 rl1 r3 cl1 C3 C3 C3	EPR-2(R)
3	r3 r3 r3 rl1 c3 C3	EPR-2(L) (Mirror Image)
4	Sr1 r4r4 r4 r4 rl1 r4r4 l2 C4 cl1C4C4C4C4C4 SC1	NFB Generalized
4	SC1	EPR-1(R & L)
4	cl1	EPR-2(L) (Mirror Image)

Fig. 5. Arrangement of the first four whorls of imbricating plates in *E. ohtai* (NFB generalized; Yamaguchi and Newman, in preparation) and *E. paquensis*, new species (EPR–1 and –2; EPR–3 lacked imbricating plates). The first and second whorls of imbricating plates (r^1, l^1, c^1, and three pairs of r^2 and c^2) are the same in all specimens. Note, however, that rl^1 and cl^1 may appear in the third whorl rather than the fourth whorl, and that $r^{3,4}$ and $c^{3,4}$ are few in *E. paquensis* compared to *E. ohtai* (open c^3 for EPR–2 (L) indicates ontogenetic misplacement).

and those of the rostrolatus and carinolatus do not form small knobs where they overlap adjacent plates, as they do in *E. ohtai.*

Although the general appearance, shape, and ornamentation of the opercular valves resembles *E. ohtai,* there are some notable differences. The scutum is triangular in both species, but its tergal margin differs in being deeply indented rather than straight, its basal length is greater than its height rather than the reverse, an articular ridge is absent rather than prominent, the adductor muscle pit is absent rather than faint, and a pit for the lateral depressor muscle is present. Furthermore, the tergum is square rather than triangular, and, while smooth, it has very faint growth lines and striations radiating from the apex. While its carinal margin is straight and the basal margin concave near the basicarinal angle, as in *E. ohtai,* its scutal margin is slightly concave rather than slightly convex, its articular ridge is longer and wider, its surface area is nearly equal to that of the tergum, and there are no crests for the tergal depressor muscle near the basicarinal angle where they are distinctly expressed in *E. ohtai.*

In the soft parts (Fig. 6, Tables 2, 3) the trophi and cirri of *E. paquensis* are similar to those of *E. ohtai,* as well as the other hydrothermal barnacles, *Neolepas, Neoverruca,* and *Neobrachylepas* (Newman, 1979, and

Table 1. Comparison between *Eochionelasmus paquensis,* new species (EPR–1), and *E. ohtai* (generalized; Yamaguchi and Newman, in preparation).

	E. paquensis	*E. ohtai*
Shell size (RC × L mm)	5.0 × 4.1 mm	4.7 × 4.2 mm
Appearance of shell wall	no obvious difference	no obvious difference
Appearance of rl^1	few by third whorl	fourth whorl
Appearance of cl^1	usually third whorl	fourth whorl
Appearance of r^3 and c^3	few by third whorl	all by fourth whorl
Boundary between ala and paries	indistinct	distinct
Basal length/tergal length of scutum	basal > tergal	equal
Tergal margin of scutum	not straight	straight
Articular ridge of scutum	absent	very high
Adductor muscle pit	absent	faint
Pit for lateral depressor muscle	present	absent
Tergal depressor crest along basal margin	absent	faint
First tooth of mandible	low, small	erect, large
Lower margin of mandible	rounding to inferior angle	straight to inferior angle
Notch of first maxillae	absent	shallow
Ratio of length of anterior versus posterior rami of CI	1.7:1	2.7:1
Ratio number of articles of anterior versus posterior rami of CI	1.8:1	2.6:1
Length of anterior three pairs of cirri	short	long

Jones, 1993; Newman and Hessler, 1989; and Newman and Yamaguchi, 1995, respectively). The crest of the labrum is concave, without a notch, and supports a single row of minute sharp teeth behind a row of bristles, and it is flanked by large, oval mandibular palps clothed with soft simple spines, as in all hydrothermal species. In *E. paquensis,* the superior and inferior margins of the mandible support soft spines and the cutting edge supports three teeth (a simple superior tooth, and two teeth supporting small spines) followed by a long row of single, fine, sharp, comblike spines to the inferior angle, as in juveniles of *E. ohtai* in the North Fiji, Lau, and Manus Basins (Yamaguchi and Newman, in preparation). However, all stages of *E. ohtai* have a stronger and higher superior tooth (Yamaguchi and Newman, in preparation) and, in adults, more comblike and spinous superior margins on the second and third teeth (Yamaguchi and Newman, 1990). There are a few small differences in some of the other parts when compared closely with those of *E. ohtai.* While the superior and inferior margins of the first maxilla are clothed with soft spines, the straight cutting edge of about 16 spines differs from that of *E. ohtai* in lacking a small shallow notch below the two or three large spines near the superior angle. The second maxilla, clothed with soft simple spines, and a few spines near the inferior angle, may or may not have a shallow notch and therefore is indistinguishable from that of *E. ohtai.*

The cirri of all three specimens consist of long, delicate, slender, multiarticulate rami clothed with fine setae, like other hydrothermal barnacles. The number of articles in the cirri and caudal appendages of specimens EPR–1 and –2 were compared with specimen NFB–4 which was essentially the same size. The first cirri have broadly inflated, profusely setose proximal segments and, of the unequal rami, the anterior is antenniform and longest (Table 3). The second pair of cirri are similar but less inflated. The third and the following pairs have long, slender, subequal rami with ctenopod setation; the proximal articles of the rami are wider than high and support one or two pairs of setae, while the distal articles are more than twice as high as wide and each supports three to five pairs of setae on the lesser curvature. The cirral counts are given in Table 3.

The holotype of *E. paquensis* and a specimen of *E. ohtai* from the North Fiji Basin (NFB–4 specimen, Yamaguchi and Newman, in preparation) have almost the same size. While the number of articles of the anterior three pairs of cirri of EPR–1 is clearly less than in NFB–4, that of the posterior three pairs of cirri is almost the same (Table 3). The ratios between the lengths of the anterior and posterior rami of cirrus I (aL/pL) are 1.7 and 2.7, respectively (Tables 1, 2). While the anterior ramus of the holotype is about twice as long as the posterior ramus, it is nearly three times longer in the NFB–4 specimen. The difference

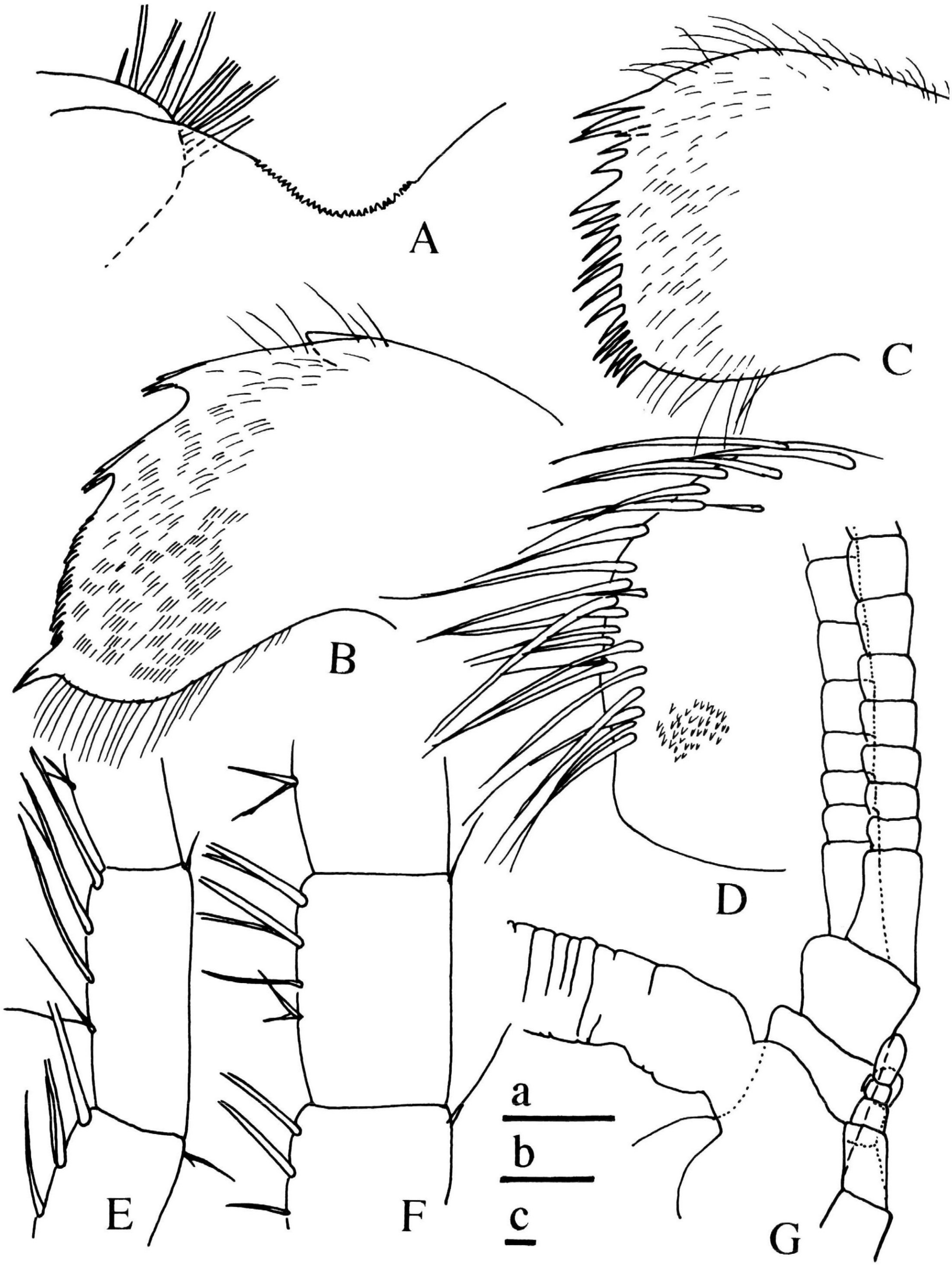

Fig. 6. *Eochionelasmus paquensis*, new species, holotype (MHNH-Ci2493) (EPR–1): A, labrum; B, right mandible; C, right first maxilla; D, right second maxilla; E, right cirrus VI, anterior ramus, nineteenth to twenty-first articles; F, right cirrus VI, anterior ramus, ninth to eleventh articles; G, base of left cirrus VI, cirrus caudal appendage, and penis (setae ignored for simplicity). Scale bars a–c = 0.05 mm; a for A–D, b for E and F, and c for G.

Table 2. Ratios in *Eochionelasmus paquensis*, new species, of lengths of anterior and posterior rami of cirrus I (aL/pL), ratios between length and width (L/W) of twelfth and twentieth articles of cirrus VI, and (in parentheses) number of pairs of setae per article. Data for NFB–1 and –4 specimens are from Yamaguchi and Newman (in preparation). L/W ratios of the eleventh and nineteenth articles are shown in brackets [ ].

	aL/pL	L/W		Shell size		
	CI	Twelfth	Twentieth	RC	L (mm)	
EPR–2	1.5	0.9(3)	2.0(4) [nineteenth]	4.5	4.6	first paratype (NSMT–Cr11433)
EPR–1	1.7	1.4(4)	2.5(5)	5.0	4.1	holotype (MNHN–Ci2493)
NFB–1	2.4	2.2(3) [eleventh]	—	2.4	2.0	
NFB–4	2.7	1.2(3)	2.1(4) [nineteenth]	4.7	4.2	

between aL/pL increases allometrically with growth in both populations (Table 2).

A comparison of the ratios of length and width (L/W) in the twelfth and twentieth articles of cirrus VI and the number of pairs of setae of those articles, between the EPR–1 and EPR–2, NFB–1 to NFB–9 (Yamaguchi and Newman, in preparation), and the holotype and two paratypes of *E. ohtai* (NFB, A–C), shows that while L/W increases with growth from the EPR–2 (4.5 × 4.6 mm) to EPR–1 (5.0 × 4.1 mm) in both the twelfth and twentieth articles, L/W decreases with growth in the twelfth article in the NFB specimens (Table 2).

The caudal appendages are shorter rather than larger than the protopod of the posterior cirri and the number of articles is less, compared to NFB–4 (Yamaguchi and Newman, in preparation) (Table 3).

The probosciform penis, which is as long as cirrus VI in EPR–1, is shorter than the protopod of cirrus VI in NFB–4. On the other hand, the simple, saclike branchiae found within the mantle cavity near the base of the terga are similar in both species. No oviger-

Table 3. Comparison between the appendages of *E. paquensis*, new species, and *E. ohtai* of approximately the same size. *Eochionelasmus paquensis* has fewer articles in both the cirri and caudal appendages than *E. ohtai* (NFB–4 specimen). Data for NFB–1 and –4 from Yamaguchi and Newman (in preparation). (R and L = right and left cirri, respectively; a and b = anterior and posterior rami, respectively; C.A. = caudal appendages).

			Number of articles of cirri							
			I	II	III	IV	V	VI	C.A.	Remarks
E. paquensis										
EPR–2	R	a	9	8	15	19	21+	20+	(3)	4.5 × 4.6 mm
		p	5	7	19	25	20+	20+		first paratype, a large penis
	L	a	9	8	14	18+	18+	23+	(4)	
		p	5	7	16+	17+	19+	19+		
EPR–1	R	a	9	6	13	17	22	24	(4)	5.0 × 4.1 mm holotype,
		p	5	7	16	21	23	26		a large penis
	L	a	9	6	13	17	22	23	(3)	
		p	5	7	16	21	23	25		
E. ohtai										
NFB–1	R	a	8	5	6	11	13+	12+	(4)	2.4 × 2.0 mm,
		p	4	4	9	15+	17+	13+		no penis
	L	a	9	5	6	11+	12+	12+	(6)	
		p	4	4	8	10+	11+	14+		
NFB–4	R	a	13	11	18	19+	20+	19+	(10)	4.7 × 4.2 mm,
		p	5	13	18+	19+	20+	23+		a tiny penis
	L	a	13	9	18	20+	19+	20	(10)	
		p	5	13	20+	17+	19+	22+		

ous frena have been observed in *Eochionelasmus* or *Chionelasmus.*

Etymology.—The species has been named for its proximity to the Isle de Pâques (Easter Island), the focal point of the Rapanuian subprovince or district at the southeastern margin of the Indo-West Pacific.

Ecology.—According to Geistdoerfer *et al.* (1995), the lobate lava between 17°24'S and 17°25'S was covered by extensive patches of orange and pink anemones, sometimes associated with many small gray anemones, pedunculate cirripeds, and colonies of the mussels, *Bathymodiolus* sp. The EPR–2 and –3 specimens of *E. paquensis* were sampled with the mussels, while the specimens at EPR–1 were collected on a piece of dead chimney at the base of an active edifice some 10–20 m distant. The pedunculate barnacle is similar to *Neolepas rapanuii* Jones, 1993, from 23°S, but a detailed comparison has yet to be made.

Geistdoerfer *et al.* (1995) indicated that the temperature of the shimmering waters was approximately 60°C, while the temperature where the barnacles were taken probably ranged between 5 and 15°C (M. Segonzac, personal communication).

Similarly, *Eochionelasmus ohtai,* a neolepadine, and a mussel were closely associated at the NFB and Lau sites. At the Vailili site, Lau, where populations of *E. ohtai* were associated with a neolepadine, the temperatures range from 2 to 5°C (Desbruyéres *et al.,* 1994), but the sessile barnacles are generally closer to mussels there (Newman and Yamaguchi, 1995), and the temperature of the association was almost the same as that at the Hine Hina Site at Lau and the White Lady Site, NFB (Desbruyéres *et al.,* 1994). No neolepadines were observed or taken with *E. ohtai* from the Vienna Woods Site or other vents of the Manus Basin at approximately 2,510 m, 03°5, 150°E, east of New Ireland (Tufar, 1990; Galkin, 1992), nor was *Neobrachylepas,* which at Lau appears to be associated with them (Newman and Yamaguchi, 1995). A neolepadid distinctly different, however, from those at Lau and NFB has recently been discovered in a depth of 1,450 m off Lihir Island, Bismarck Archipelago (WAN, personal observation; Tunnicliffe, leg.).

As noted by Desbruyéres *et al.* (1994), hydrothermal barnacles are analogous to the filter-feeding serpulids of the East Pacific Rise; that is, they tend to be peripheral compared to those animals with chemoautotrophic endosymbionts. The latter may require higher concentrations of sulfides, and/or the protection from certain predators that are unable to enter the ecotone.

The new species *Eochionelasmus paquensis* is based on two subadult and one juvenile specimens from approximately 17°S, north of Easter Island on the East Pacific Rise. The new species is similar in general appearance to *E. ohtai,* which ranges from the Manus to the Lau Basins in the Western Pacific. However, the order in which the imbricating plates are added, and details of the wall, opercular valves, mouthparts, cirri, and caudal appendages, are distinctly different from those of *E. ohtai.* Therefore, while it is concluded that the Rapanuian population represents a new species, *E. paquensis,* its genus-group status may have to be reevaluated once fully mature specimens have been discovered.

This is the first record of a sessile hydrothermal vent barnacle from the eastern boundary of the Indo-West Pacific faunal province, as well as from a ridge crest, and none are known from the East Pacific (Tunnicliffe, 1992). The Indo-West Pacific province is based on shallow-water organisms (Ekman, 1953). Do its characteristics in any way apply to the vent barnacles? The other barnacles associated with hydrothermal vents come from back-arc basins of the Southwest Pacific, and their greatest diversity is at Lau where representatives of three sessile and a pedunculate suborder are known (Newman and Yamaguchi, 1995). In the northern hemisphere, the East Pacific Rise swings into the East Pacific Faunal Province close to the Americas, where, of the vent barnacles, only *Neolepas zevinae* is known (10–21°N). This pattern of declining diversity of western Pacific forms, from the center of diversity in the Southwest Pacific, is also seen in the shallow-water fauna, where it also includes peripheral endemism (Zullo and Newman, 1964; Rehder, 1980; Foster and Newman, 1987). That the pattern should be similar in shallow and deep water may be surprising, but it is likely for many of the same reasons, namely, greater habitat diversity in the west, the loss and/or paucity of stepping stones for dispersal (e.g., the loss of ancient archipelagos and their remnants in shallow water (Newman and Foster, 1987) in the east, and the loss of hydrothermal vents between various outposts (Hessler and Lonsdale, 1991; Tunnicliffe and Fowler, 1996). The shallow-water endemics of Easter and adjacent islands characterize the Rapanuian Faunal District of the Indo-West Pacific Province, as do *Neolepas rapanuii* and *Eochionelasmus paquensis* in deep water.

Acknowledgements

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