THE VELIGER
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The Veliger 44(2):116–231 (April 2, 2001)

Gastropoda and Monoplacophora from Hydrothermal Vents and Seeps; New Taxa and Records

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Abstract. A monoplacophoran species and about 100 species of gastropods are recorded from hydrothermal vents and various kinds of seeps from the Atlantic and Pacific Oceans. Previously described species are supplemented with new information on distribution, ecology, morphology, and systematics. The zoogeography of these faunas is discussed and it is noticed that there is a good resemblance in generic composition between the vent and seep localities, while the species usually occur in only one of the two environments. More than 95% of the species found in vents have not been found outside this environment, and the endemic species make up more than 99.5% of the individuals. The fauna of the seeps is less well demarcated. Two species of *Provanna* (Caenogastropoda, Provannidae) are recorded from sunken drift wood in the NE Pacific. The genus was previously thought to be endemic to vent and seep environments. The fauna of the recently investigated vent system at the East Pacific Rise, 17°S is very similar to that of the more northern (9–21°N) localities; 14 species out of 16 are shared. Available evidence for a hypothesized relict character of the gastropod fauna is evaluated and failed to support the hypothesis. Spermatophores were found in *Melanodrymia* sp., the first known case in Neomphalina. A possible case of imposex is reported from the conid genus *Phymorhynchus.* The first monoplacophoran from hydrothermal vents is described, ***Rokopella segonzaci,*** sp. nov. (Family Neopilinidae), from the Mid-Atlantic Ridge at about 38°N. The following new gastropod taxa are described. Patellogastropoda. Family Neolepetopsidae: *Paralepetopsis* ***ferrugivora,*** sp. nov., from the Mid-Atlantic Ridge, 37°N; *P.* ***lepichoni,*** sp. nov., from the Nankai Trough off south-eastern Honshu, Japan. Vetigastropoda. Family uncertain: *Adeuomphalus* ***trochanter,*** sp. nov., from the Juan de Fuca Ridge; ***Sahlingia xandaros,*** gen. et sp. nov., from the Aleutian Trench. Family Lepetodrilidae: *Lepetodrilus* ***atlanticus,*** sp. nov., from the Mid Atlantic Ridge, 23–38°N. Family Sutilizonidae: *Sutilizona* ***pterodon,*** sp. nov., from the Mid-Atlantic Ridge, 23°N; *S.* ***tunnicliffae,*** sp. nov., from the Juan de Fuca Ridge. Skeneidae: *Bruceiella* ***athlia,*** sp. nov., from seeps in the Aleutian Trench. Trochidae: *Falsimargarita* ***nauduri,*** sp. nov., from vents at the East Pacific Rise at 17°S; *Fucaria* ***mystax,*** sp. nov., from vents off eastern New Guinea. Uncertain position. Family Neomphalidae: *Melanodrymia* ***galeronae,*** sp. nov., from the East Pacific Rise at 13°N; ***Retiskenea diploura,*** gen. et sp. nov., from the Aleutian Trench; *Lacunoides* ***vitreus,*** sp. nov., from the Juan de Fuca Ridge. Family Peltospiridae: *Lirapex* ***costellata,*** sp. nov., from the Mid-Atlantic Ridge at 37°N; *Nodopelta* ***rigneae,*** sp. nov., from the East Pacific Rise at 13°N; *Peltospira* ***smaragdina,*** sp. nov., from the Mid-Atlantic Ridge, 15–38°N. *Depressigyra*? *statura* Goedert & Benham, 1999, from Eocene seep deposits in the state of Washington is transferred to ***Retiskenea.*** Neritimorpha. Family Phenacolepadidae: *Shinkailepas* ***briandi,*** sp. nov., from the Mid-Atlantic Ridge, 15–38°N. Caenogastropoda. Family Cerithiopsidae: ***Speculator cariosus,*** gen. et sp. nov. from the Juan de Fuca Ridge. Family Vitrinellidae: ***Neusas,*** gen. nov., *marshalli* (Sykes, 1925), from the bathyal Northeast Atlantic. Family Elachisinidae: *Laeviphitus* ***desbruyeresi,*** sp. nov., from the Mid-Atlantic Ridge, 37°N. Buccinidae: *Bayerius* ***peruvianus,*** sp. nov., from seeps off Peru; *Eosipho* ***auzendei,*** sp. nov., from vents at the East Pacific Rise at 17°S. Conidae: *Bathybela* ***papyracea,*** sp. nov., from Gulf of California, off Jalisco; *Phymorhynchus* ***major,*** sp. nov., from the East Pacific Rise at 13°N; *P.* ***carinatus,*** sp. nov., from the Mid-Atlantic Ridge, 15–23°N; *P.* ***ovatus,*** sp. nov., from the Mid-Atlantic Ridge, 15–37°N. Heterobranchia. Family Hyalogyrinidae: *Hyalogyrina* ***globularis,*** sp. nov., from the Juan de Fuca Ridge; *H.* ***umbellifera,*** sp. nov., from seeps in the Aleutian Trench. Family Orbitestellidae: ***Lurifax vitreus,*** gen. et sp. nov., from the Mid-Atlantic Ridge, 37–38°N. Family Xylodisculidae: *Xylodiscula* ***analoga,*** sp. nov., from the Mid-Atlantic Ridge, 37°N.

INTRODUCTION

The importance of chemosynthetically nourished environments in the sea is becoming more and more obvious. These environments include many biotopes, from a normal sea bottom with an inflow of organic material higher than the available oxygen can oxidize, to hydrothermal vents. In the latter, sulfides or other oxidizable compounds are released from deeper sediments or rocks where they have been trapped as minerals, via phreatic water. When the outflow is slow, especially when there are no defined outlets for the water, usually the term seep or seepage is used. Among the compounds used by the bacteria are, in addition to sulfides, methane, reduced iron, and manganese compounds.

High concentrations of sulfides, hydrocarbons, and heavy metals are toxic for most animals. These biotopes may therefore become isolated, and most areas around hydrothermal vents harbor a specialized fauna (Carney, 1994; Fustec et al., 1987; Grassle, 1986b; Hessler & Lonsdale, 1991a, b; Hessler, 1985; Hessler & Smithey, 1983; Tunnicliffe, 1988, 1991; Hessler & Kaharl, 1995). When the availability of oxidizable compounds is high, the biomass and number of individuals may become very high, but the number of species is low (Grassle, 1986b, 1989).

We here report on previously unstudied collections of Gastropoda (and two specimens of Monoplacophora) made by several investigators and research organizations in various vent and seep environments.

MATERIALS AND METHODS

The present study is based mainly on the French (IFREMER/DRO/EP) explorations of the hydrothermal activity at the East Pacific Rise [thereafter EPR] and the Mid-Atlantic Ridge [thereafter MAR]. We have, however, also included material from other localities, vents and seeps, when such has been available. All localities are listed in Appendix 1, where also references to further information on the biotopes and expeditions are given. Material collected by French (IFREMER) expeditions is deposited in MNHN. No museum number is allocated to individual lots, but the material reported in this paper is unambiguously designated (and retrievable) through the combination of expedition acronym, e.g., MARVEL, and station/dive number, e.g., dive 1195. This information is present on labels accompanying individual lots.

The specimens on which our work is based are listed under each species. They are there listed according to locality (north to south), by expedition and a reference number to the sampling. More detailed position data are given in Appendix 1. Unless otherwise stated, the material is stored in Muséum national d'Histoire naturelle.

Much of the French material was found after dives in the "retrieval box" ("panier"), which means that the specimens were gathered there during the dive, without detailed notes on their origin. They can, however, be localized to the area where the dive was made and constitute important material for variation, abundance, and anatomical investigation.

As usual with material from "general" samplings, the fixation is highly variable. Gastropods need to be individually anesthetized to allow the fixative quick access to the soft parts. When preserved in bulk mixed with bottom material, the results are highly variable. Occasional specimens may be good, especially such where the shell has been damaged. Nevertheless, one can usually find specimens good enough to allow an informative picture of the external morphology. Such specimens have been used for critical-point drying, via 99.5% alcohol and carbon dioxide. For anesthetization of gastropods we recommend isotonic magnesium chloride ($MgCl_2 \times 10H_2O$, 72.3 gram per liter of fresh water). This is slowly added to the jar with seawater where the crawling specimens are kept, during 10 minutes to a few hours and in small portions. When they do not react to touch, try transferring the least important specimen to the fixative. Different species may take different times to get ready for fixation.

Patellogastropod radulae (see McLean, 1990a) as well as those of chitons (Macey et al., 1997) and to some extent those of Monoplacophora (Warén & Gofas, 1997), contrary to most other gastropod radulae, are sensitive to treatment with strong potassium hydroxide, which usually is employed to clean the organ from the surrounding tissues (Figures 2a, d). After tests with various concentrations and times, we have instead macerated the radular sac or small specimens in 0.5% KOH at 40–50°C for 10–20 hours. This causes no damage, but much organic material remains. The radulae were then cleaned in diluted commercial bleach (3 parts water: 1 part bleach) for a short time (1–30 seconds depending on size), carefully rinsed in distilled water, and mounted on histological cover slips. For large radulae we used a thin layer of carefully dried polyvinyl acetate glue to make them stick better to the substrate. Comparison with the most anterior part of the same radula, from the buccal cavity, which had been dissected out, showed no destruction (Figures 2b, e, g).

In descriptions and figures of radulae, we have numbered the teeth sequentially, counting the central tooth as "0," the first lateral tooth "1," etc.

ABBREVIATIONS

CENTOB	Centre de Tri d'Océanographie Biologique, Brest
EPR	East Pacific Rise
FMNH	Field Museum of Natural History, Chicago
IFREMER	
DRO/EP	Institut Français de Recherches pour l'Exploitation de la Mer/Direction de la Re-

	cherche Océanographique/ Département Environnement Profond
JdF	Juan de Fuca Ridge system, from southern Juan de Fuca to Explorer Ridge
LACM	Los Angeles County Museum of Natural History, Los Angeles
MAR	Mid-Atlantic Ridge
PL	Plongée (dive)
MNHN	Muséum national d'Histoire naturelle, Paris
SMF	Senckenbergisches Museum und Forschungsinstitut, Frankfurt
SMNH	Swedish Museum of Natural History, Stockholm
sh(s)	shell(s) with no soft parts
spm(s)	live taken specimen(s)
TVG	TV monitored grab, 1.82 m^2
TVGKG	TV monitored box corer
USNM	National Museum of Natural History, Washington, D.C.
WP	West Pacific vent systems

DESCRIPTIONS AND SYSTEMATIC LIST OF NEW SPECIES AND RECORDS

Class MONOPLACOPHORA

Family NEOPILINIDAE Knight & Yochelson, 1958

Rokopella Starobogatov & Moskalev, 1987

Rokopella Starobogatov & Moskalev, 1987:10.

Type species: *Neopilina oligotropha* Rokop, 1972; by original designation; north of Hawaii, abyssal.

Remarks: Warén & Gofas (1997) reviewed the small species of Monoplacophora with reticulate sculpture and recognized *Rokopella* and *Veleropilina* Starobogatov & Moskalev, 1987, as distinct genera, with three and five species, respectively. They summarized the distinctive features, and we refer to there for further information.

We have classified the new species described below in *Rokopella* because its sculpture is very similar to other species of the genus; the foot and gills are very small; and the pallial furrow is very broad and shallow. The arrangement of the perioral ridges and tentacles agrees as far as the poor preservation allows comparison. *Rokopella* ***segonzaci*** does, however, differ in having the apex situated well outside the margin of the shell, and in having three pairs of gills only (Haszprunar, personal communication).

The apical area of the two specimens is badly corroded, but there seems not to be a pitted zone around the "apical cap" as in *Veleropilina*; instead the first sculpture to appear is the network of concentric and radial ribs, as in other species of *Rokopella*.

Rokopella ***segonzaci*** Warén & Bouchet, sp. nov.

(Figures 1a–e)

Type material: Holotype and 1 paratype in MNHN.

Type locality: MAR, Menez Gwen: DIVA 2 PL 11, 37°50.54'N, 31°31.30'W, 860–870 m, on shells of *Bathymodiolus* sp.

Material examined: Only known from the type material.

Distribution: Only known from the type locality.

Etymology: Named after Michel Segonzac at IFREMER, who has supervised the sorting of all material collected by French expeditions from hydrothermal vents.

Description: *Shell (Figures 1d–e).* Very small and flat for the group, transparent, fragile, with well visible sculpture and thick periostracum. The apical area is corroded in both specimens, but the sculpture starts already at a diameter of 0.1 mm. The apical cap forms an angle of about 30° with the basal plane of the shell. Only traces remain of the first sculpture but very soon it develops into a slightly irregular network of equally strong radial and concentric ribs. These ribs are slightly irregular and make little jerks and twists at the intersections, but do not form tubercles. The shell is covered by a thick and tough periostracum, but this was peeling in both specimens, and only traces remained at the first examination. The ratio length/breadth is 1.38, height/length is 0.29.

Dimensions. Maximum diameter of holotype 0.90 mm; paratype 0.82 mm.

Soft parts (Figure 1c). The foot is small and circular, its diameter corresponds to 0.22 of the length of the shell in critical-point dried specimens. The pallial furrow is wide and shallow; its width corresponds to a little less than half the diameter of the foot. There are three small, simple, fingerlike, and inconspicuous gills, of which the posterior one is twice as large as the others. They seem to lack ciliation, except a longitudinal strip along the anterior-inner side, but this may be an artifact of poor preservation. They are all strongly wrinkled transversally and seemingly capable of considerable elongation. In a broken gill two large longitudinal vessels can be seen. The perioral organs are low and inconspicuous; the anterior lip consists of a simple semicircular ridge. The vela are hardly connected in front of the lip; they are attached for the anterior third of their length; the posterior two-thirds is a simple skinfold. The posterior lip is a low and inconspicuous ridge. The posterior tentacle ridge is interrupted in the center; laterally there is a lappet, but no tentacles.

Radula (Figures 1a, b). Normal for the family, long and slender with 11 teeth per transverse row. Tooth number 0 has a strong denticle at each side of the main cusp. Teeth 1–3 are of similar size and shape with three-four, five, and four strong cusps, respectively. Tooth 4 has ca. 22 cusps. Tooth 5 has the usual scooplike appearance.

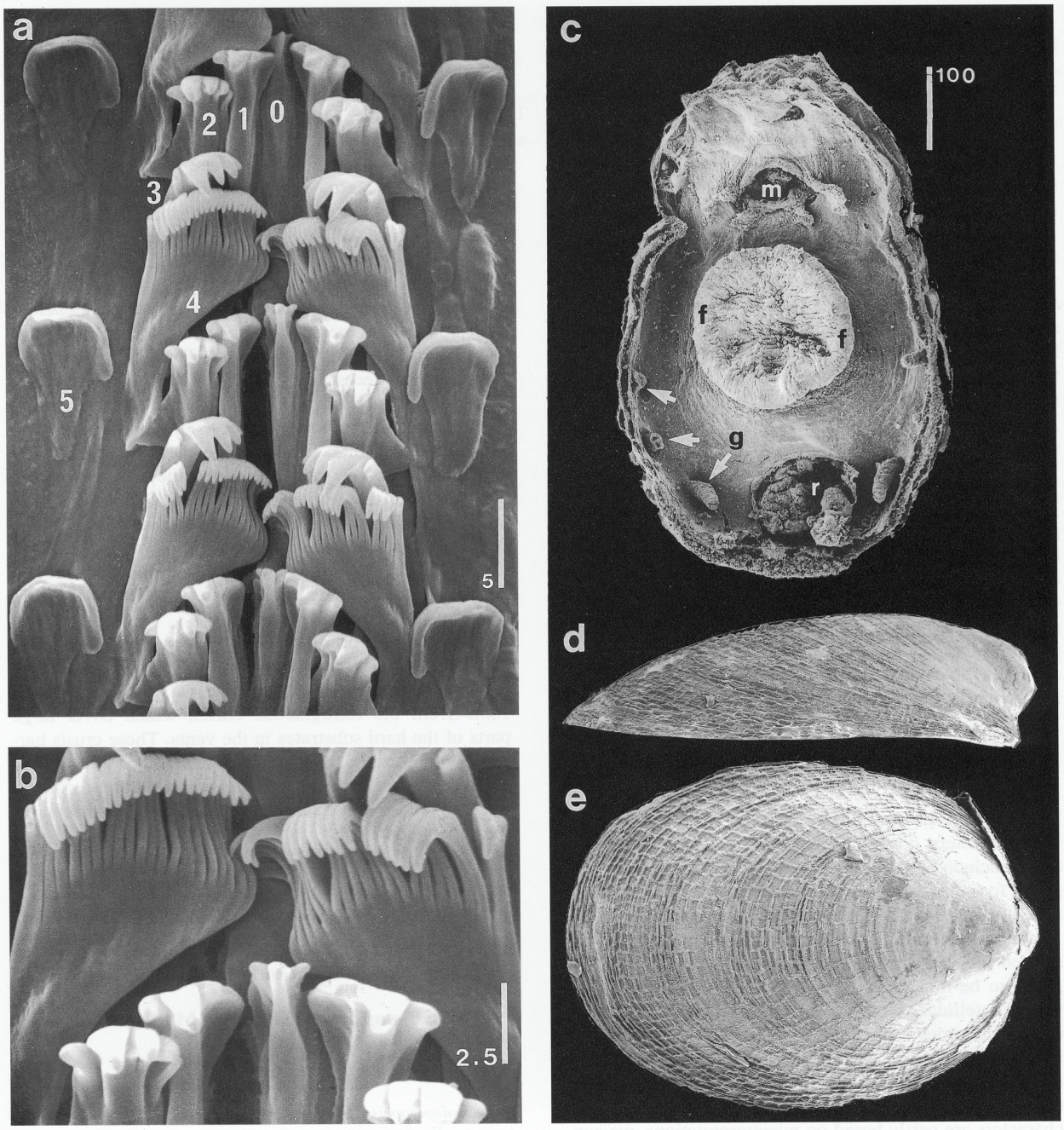


Figure 1. *Rokopella* ***segonzaci*** Warén & Bouchet, sp. nov. *a, b.* Radula. Numbers indicate sequential order of teeth with central tooth as 0. *c.* Ventral view of soft parts, body wall broken at anus. *d, e.* Shell of holotype, maximum diameter 0.90 mm. f - foot; g - gill; m - mouth; r - rupture of pallial roof. Scale bars in μm.

Remarks: The start of the sculpture at a diameter of only 0.1 mm indicates that the sculpture starts immediately after the apical cap, as in *R. euglypta* (Dautzenberg & Fischer, 1896), although in that (larger) species the corresponding diameter is 0.2 mm. The low profile of the shell may indicate that the specimens are juveniles; this is, however, contradicted by the sculpture being more crowded toward the edge.

Rokopella ***segonzaci*** differs from *R. euglypta* by being proportionally more elongate (L/B 1.38; 1.15 in *R. euglypta*) and by having fewer and coarser cusps on radular teeth 0–3 (five, 13, seven, and eight in *R. euglypta*).

The low number of gills, only three, is a difference from *Rokopella oligotropha* and *R. euglypta,* which have five pairs. This is probably connected with the small size, since *Micropilina minuta* Warén, 1989, which is also of a similar size, has only three pairs of gills.

This is the first monoplacophoran to be found at modern hydrothermal vents, but since it was found only once, we are not sure that *R.* ***segonzaci*** is a regular member of the vent fauna, although its habitat, on shells of *Bathymodiolus* may support this view. The species may also have been overlooked because of its small size. There are three additional species of Monoplacophora known from nearby parts of the Mid-Atlantic Ridge (Warén & Gofas, 1997).

Class GASTROPODA

We have largely followed the arrangement of the gastropods proposed by Ponder & Lindberg (1997). For the reader not mainly interested in gastropod taxonomy, it can be mentioned that the old concept Archaeogastropoda corresponds to Patellogastropoda plus Vetigastropoda plus Cocculiniformia plus Neritimorpha. "Caenogastropoda" corresponds to the old concepts "Mesogastropoda" plus "Neogastropoda," and "Heterobranchia" corresponds to "Opistobranchia" plus "Pulmonata".

Subclass PATELLOGASTROPODA

Family NEOLEPETOPSIDAE McLean, 1990

Remarks: McLean (1990a) discussed deviations in radular characters compared with other Patellogastropoda and concluded that "Lepetopsina" (a "suborder" proposed for some fossils and the docoglossate limpets from hydrothermal vents) is a less modified group within the "Patellogastropoda" (= Docoglossa). Fretter (1990) described the anatomy of several species and believed the group to be more closely related to the Acmaeidae than to the Patellidae, which contradicts a position as a discrete "suborder" of the Patellogastropoda. McLean's (1990a) conclusions about the distinctness of the Lepetopsina were mainly based on the radular characters of the Recent species, and since we will here show that those characters are partly based on misinterpretations, we consider that Lepetopsina needs a more thorough reevaluation, beyond the intentions of the present report. For preparation of neolepetopsid and docoglossate radulae, see "Materials and Methods."

We have noticed a variation in radular development among the vent limpets (*Paralepetopsis, Neolepetopsis,* and *Eulepetopsis*). Some species are more similar to true limpets (*Patella,* etc.) in the development of mineralized cusps of the teeth. Examples of this are *Neolepetopsis densata* (Figure 2a), *N. gordensis* (Figure 2d), and *Paralepetopsis* ***ferrugivora*** (Figures 2e–f). They have defined apical cusps, although we have not investigated the presence of iron compounds. Other species like *Paralepetopsis* ***lepichoni*** (Figure 2c) and *Eulepetopsis vitrea* (Figures 2b, g) do not develop apical cusps. This difference, however, does not necessarily mean very much systematically since it corresponds to the maturation of the teeth along the radula. In *P.* ***ferrugivora,*** for example, about half the length of the radula, including the part in use, has well developed cusps (Figure 2e). Along the recently formed part, the teeth lack strengthened cusps (Figure 2f), and are very similar to those that never develop them. In this state they are also similar to the teeth of young, non-vent limpets (Patellidae and Lepetidae examined). Therefore we simply consider the radular differences from non-vent limpets a result of heterochrony.

Neolepetopsid limpets usually live on rocks and shells, more rarely vestimentiferan tubes. The gut is usually filled with reddish brown, granular masses. This seems to come from the ferrugineous crusts, which cover large parts of the hard substrates in the vents. These crusts harbor a fauna in which we noticed nematodes and ciliates to be common. Together with the bacteria that precipitate the iron oxides and hydroxides, these organisms seem to form the main food.

Neolepetopsis McLean, 1990

Neolepetopsis McLean, 1990a:492.

Type species: *N. gordensis* McLean, 1990; by original designation; Gorda Ridge, off northern California.

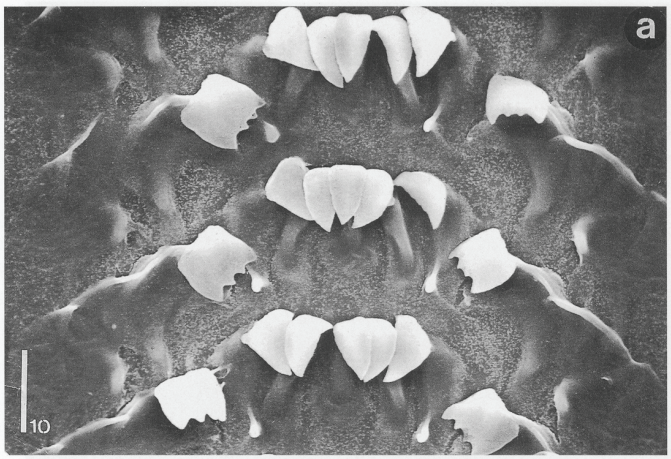
Neolepetopsis cf. *gordensis* McLean, 1990

(Figures 2d, 3f–g)

Neolepetopsis gordensis McLean, 1990a: 492, figs. Ia–h, IIa–g.

→

Figure 2. Neolepetopsidae, radulae. Numbers indicate sequential order of teeth with central tooth as 0. *a. Neolepetopsis densata,* EPR at 13°N. Partly damaged by KOH *b, g. Eulepetopsis vitrea,* EPR at 13°N, whole width and detail of central field. *c. Paralepetopsis* ***lepichoni*** Warén & Bouchet, sp. nov., holotype, old part. *d. Neolepetopsis gordensis,* Jalisco Block Seeps. *e, f. Paralepetopsis* ***ferrugivora*** Warén & Bouchet, sp. nov., MAR, Lucky Strike. *e.* Old part, treated with bleach (apical cusp broken off the center left pluricuspidate tooth). *f.* Newly formed part of radula. Scale bars in μm.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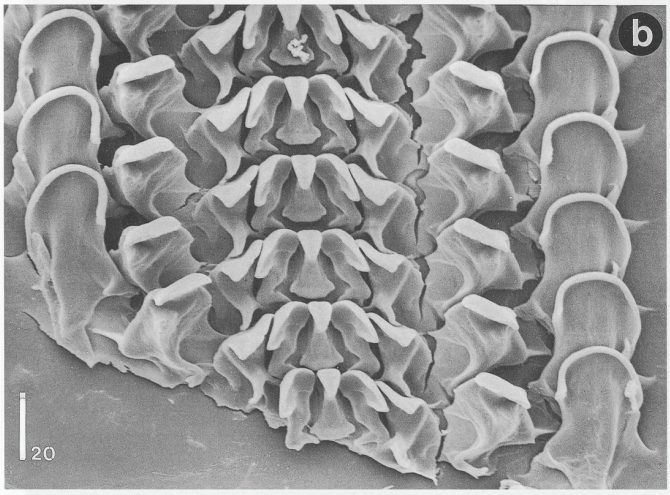
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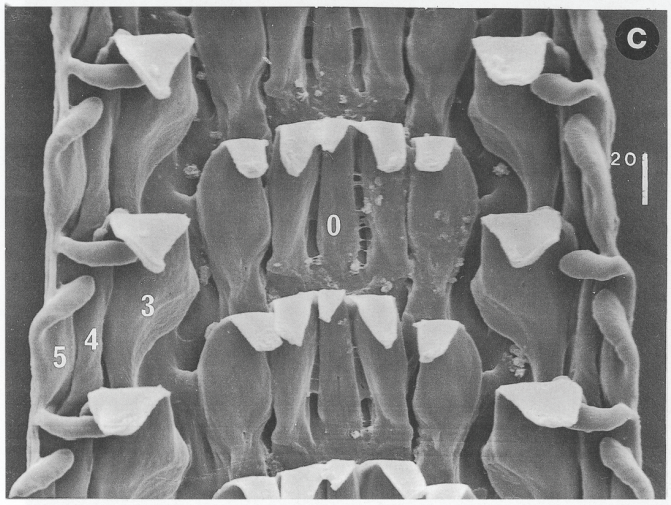
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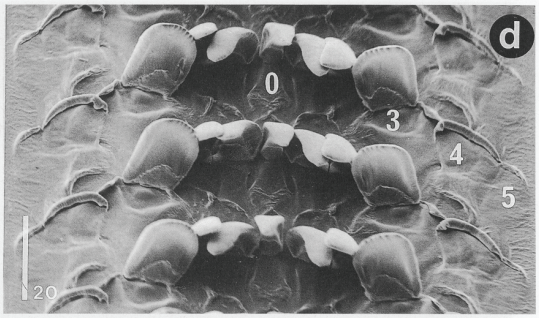
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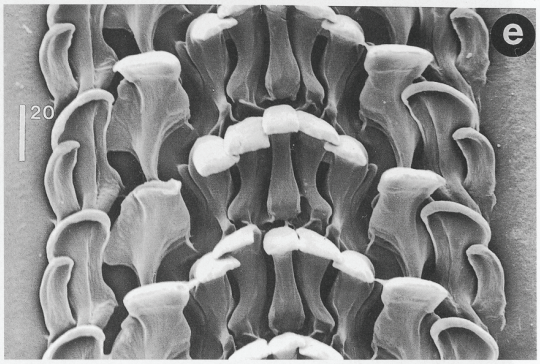
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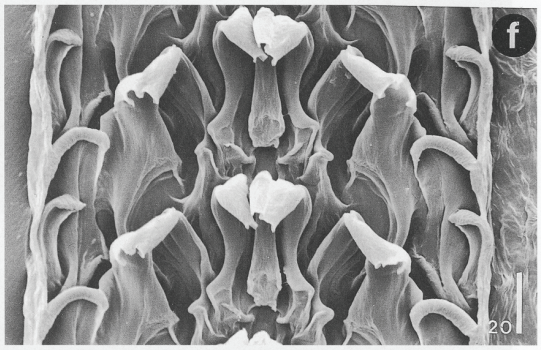
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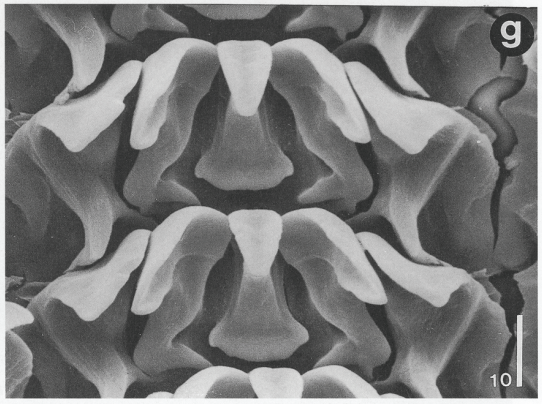
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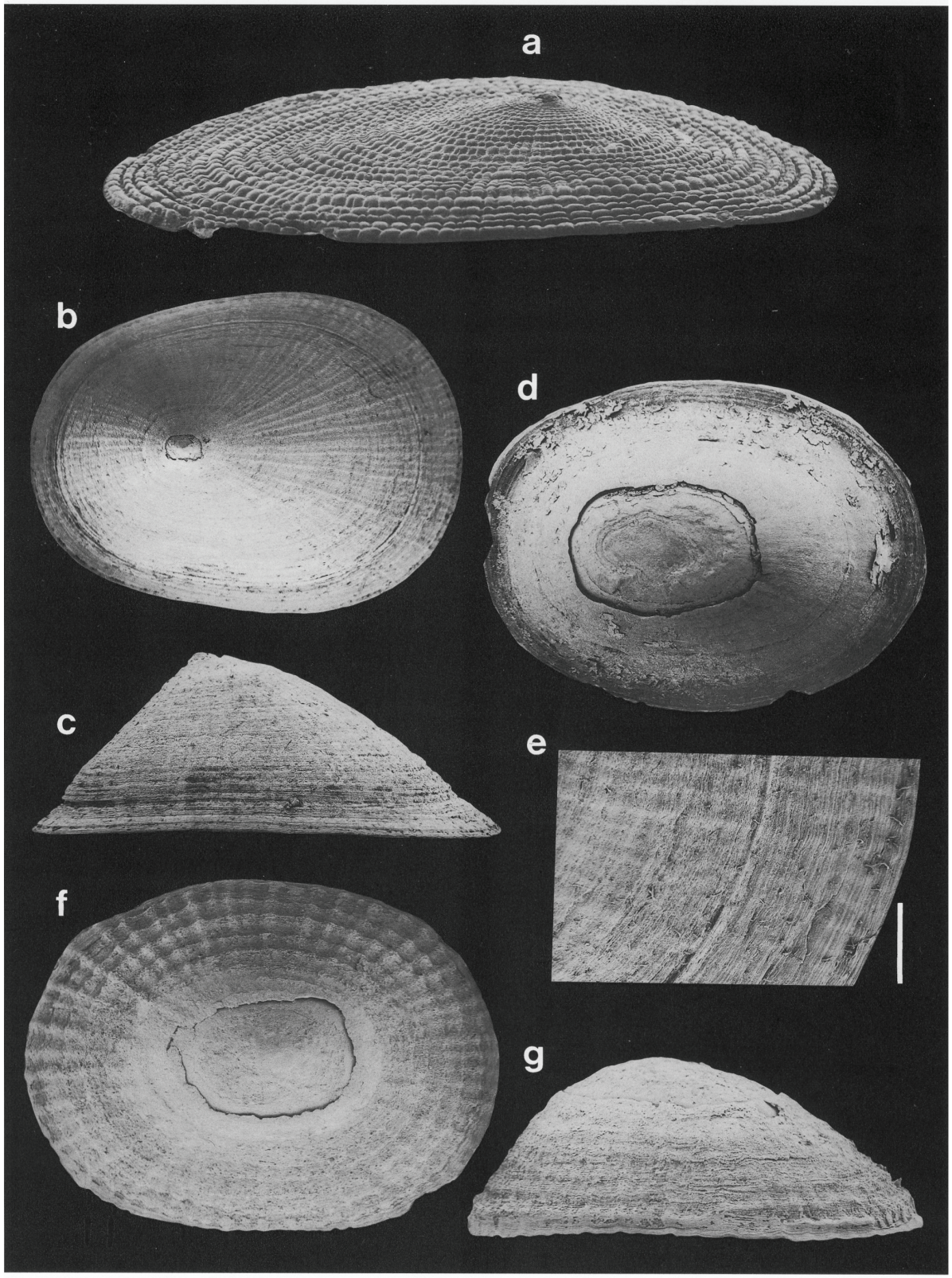
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Neolepetopsis sp.: Warén & Bouchet, 1993:88 (fauna list only).

New records: *Mid America Trench, Jalisco Block Seeps at 20°N:* - NAUTIMATE PL 10, 10 shs, 2 spms; - NAUTIMATE PL 16, 2 spms, on rocks. *Off Peru:* - NAUTIPERC PL01-4-13, 3 spms.

Distribution: From the Gorda Ridge, 41°00.4'N, 127°29.3'W, ca. 3200 m and south of Gulf of California, 20°01.79'N, 106°17.33'W, 3795 m, south to off Peru, 05°S, ca. 3500 m.

Remarks: Whether the three specimens from off Peru belong to *N. gordensis,* or not, is uncertain. McLean's material indicated high variability, the species is very featureless, all specimens are corroded, and our Peruvian specimens were found far away from the type locality. The records may belong to the same species, but our identification should, by no means, be used as an indication of faunal affinity between the localities.

We figure the shell (Figures 3f–g) and radula (Figure 2d) of specimens from the Jalisco Block Seeps, which are most probably conspecific with *N. gordensis.*

Neolepetopsis densata McLean, 1990

(Figures 2a, 3a, 15a–c)

Neolepetopsis densata McLean, 1990a: 496, figs. IIIa–g, IVa–d.

New records: *EPR at 13°N:* - HERO 91 PL 11, 1 spm; - HERO 91 PL 25, 13 spms; - HERO 92 dive 2522, 1 spm.

Distribution: Galapagos Rift (Gustafson & Lutz, 1994) and EPR at 13°N in 2630 m and 11°46'N, 103°47'W, 2725 m (from an inactive sulfide chimney).

Remarks: Our specimens agree closely with McLean's description and we feel confident in the identification. The species is characteristic with a very flat, transparent shell and small wart-shaped apex. We figure the protoconch (Figures 15a–c) which was damaged in McLean's specimens, and an adult shell (Figure 3a). Figure 2a shows a partly destroyed radula, but the shape of the cusps agrees with that shown by McLean (1990a).

Eulepetopsis McLean, 1990

Eulepetopsis McLean, 1990a:503.

Type species: *E. vitrea* McLean, 1990; by original designation; hydrothermal vents at EPR, 21°N.

Remarks: The genus *Eulepetopsis* remains monotypic.

Eulepetopsis vitrea McLean, 1990

(Figures 2b, g; 14c)

Eulepetopsis vitrea McLean, 1990a:503, figs VIIa–I, VIIIa–j, IXa–f.

New records: *EPR at 13°N:* - HERO 91 PL 12, 3 spms; - HERO 92 dive 2516, 1 spm; - dive 2517, 10 spms; - dive 2519, 1 spm; - dive 2523, 1 spm; - dive 2528, 12 spms. *EPR at 09°50'N:* - HERO 91 PL 07, 4 spms. *EPR at 17°S:* - NAUDUR PL 06, site Rehu, 27 spms; - NAUDUR PL18.4.8b, site Rehu, 2 spms.

Distribution. EPR from 21°N to 17°S, and the Galapagos Rift, in 2450–2630 m depth.

Remarks: We figure the radula and jaw (Figures 2b, g; 14c) since McLean's (1990a: fig. IX) preparations were somewhat damaged by KOH. The gut is usually filled with ferrugineous deposits.

Paralepetopsis McLean, 1990

Paralepetopsis McLean, 1990a:510.

Type species: *P. floridensis* McLean, 1990; by original designation; sulfide seeps at the Florida Escarpment.

Remarks: The differences between *Neolepetopsis* and *Paralepetopsis* are not very distinct. *Neolepetopsis densata, occulta,* and *verruca* all have a fairly similar, flat and partly transparent shell, while *N. gordensis,* the type species of *Neolepetopsis,* has a taller, opaque shell very similar to *Paralepetopsis floridensis,* the type species of *Paralepetopsis.* The radulae are not known in enough detail to allow comparison.

*Paralepetopsis **ferrugivora*** Warén & Bouchet, sp. nov.

(Figures 2e–f; 3b–e; 4a–b, e; 14a–b)

Type material: Holotype and one paratype in MNHN.

Type locality: MAR, Lucky Strike, 37°17.50'N, 32°17'W, 1665–1728 m.

Material examined: *MAR, Lucky Strike:* - DIVA 1 PL 17, 2 spms; - DIVA 1 PL 19, 2 spms; - DIVA 2 PL 03, 1 spm; - DIVA 2 PL 05, 1 sh; - DIVA 2 PL 09, suction sample among mussels and hydrothermal sediments, 1 spm; DIVA 2 PL 10, on a rock, 1 spm; retrieval box, 11 spms; - DIVA 2 PL 19, 1 spm; - ALVIN dive 2608 (Tour Eiffel), 1 spm; - LUSTRE Exp. (Tour Eiffel), on mussels, 1 spm; - MARVEL PL1194 (Tour Eiffel), retrieval box, 2 spms.

←

Figure 3. Neolepetopsidae, shells. *a. Neolepetopsis densata,* EPR at 13°N, 8.1 mm maximum diameter *b–e. Paralepetopsis **ferrugivora*** Warén & Bouchet, sp. nov. *b, c, e.* Holotype, 8.0 mm diameter. *e.* Detail of sculpture, scale bar 0.5 mm. *d.* Large corroded specimen, 9.4 mm. *f, g. Neolepetopsis gordensis,* Jalisco Block Seeps, maximum diameter 4.9 and 4.3 mm.

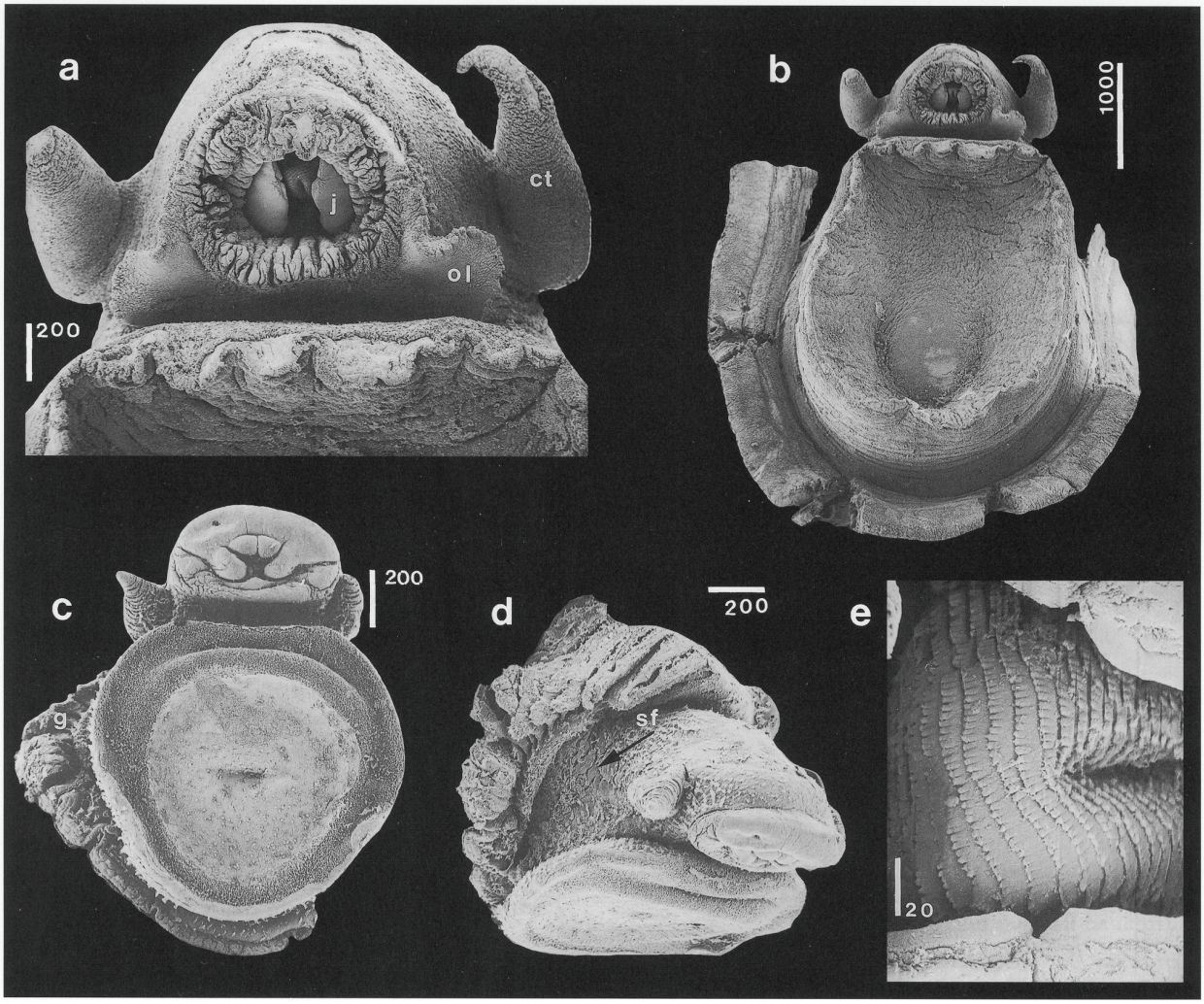


Figure 4. *a, b, e. Paralepetopsis* ***ferrugivora*** Warén & Bouchet, sp. nov., soft parts. *a.* Anterior part of head-foot *b.* Body, ventral view, anterior part of pallial skirt removed. *e.* Detail of licker. *c, d. Pyropelta corymba,* Oregon Margin. *c.* Ventral view of head-foot. *d.* Anterolateral view to show gill, pallial skirt folded backward. ct - cephalic tentacle; g - gill; ol - oral lappet; sf - seminal furrow. Scale bars in μm.

Distribution: Only known from the Mid-Atlantic Ridge at Lucky Strike, about 1700 m depth.

Etymology: From "ferrugo" and "voro," Latin, meaning rust and to eat.

Description: *Shell (Figures 3b–e).* Of normal size for the genus, sturdy, depressed, and with a rough surface. Juvenile specimens and the protoconch are not known. The apex is situated at the anterior ⅓ and worn in all specimens we have seen. The anterior surface of the shell is straight in profile, the posterior one weakly convex. The periostracum is thin and colorless, hardly noticeable. The outer layer of the shell is semitransparent, slightly brownish or colorless, and rough. A thick medium layer is perfectly transparent, giving an impression of "empty space." It is followed by an inner, white, chalky and thin layer with concentric pattern, which easily peels off. The sculpture consists of numerous radial ribs.

Dimensions. Maximum diameter of holotype 8.0 mm, height 2.7 mm, maximum diameter seen, 9.2 mm.

Soft parts (Figures 4a, b, e). The external morphology agrees well with the original description of the genus and Fretter's (1990) more detailed account. It can be added that the licker (*sensu* Fretter 1990:532) has transverse, regularly crenulate folds all over its surface (Figure 4e).

Radula (Figures 2e–f). The part in use and half the length backward has well developed and strengthened cusps on the central tooth and the three inner teeth at

each side (Figure 2e). The more recently formed part lacks reinforcement and its teeth are soft (Figure 2f). The central tooth has a simple, straight cutting edge like a chisel and a more slender shaft which basally is flattened and carries a small antero-lateral ridge at each side. The first lateral tooth is of similar shape, is slightly broader, and has a single lateral, more sturdy and curved lateral ridge. The second lateral resembles the first, but the base is tapering and the basal ridge central, and forms an articulation toward the center. The third lateral tooth ("pluricuspid tooth") has a cutting edge twice as broad as number 2, is larger and more sturdy, and its cutting edge has two to three low and blunt tubercles. Its base is broad, and the centrally placed ridge is drawn out anteriorly. The two outer teeth are simple and scooplike; the outer one is half the size of the inner one.

Remarks: *Paralepetopsis* ***ferrugivora*** differs from *P. floridensis* in having square instead of triangular cusps on the central and lateral radular teeth, by having more distinct radial sculpture on the shell, and by lacking papillae on the pallial margin. There are two different color forms of *P.* ***ferrugivora:*** the shell is either white or slightly orange-brown, but we have seen no intermediate variations.

The intestine is always full of orange-brown matter with a granular structure with many nematode and ciliate fragments. This seems to be the bacterially precipitated "rust deposit" of most hard surfaces that are scratched off together with its inhabitants.

Paralepetopsis ***lepichoni*** Warén & Bouchet, sp. nov.

(Figures 2c, 5a–f)

Type material: Holotype in MNHN.

Type locality: Off south-eastern Honshu, Nankai Trench seeps, KAIKO-NANKAI 14, 33°49.40'N, 137°55.20'E, 2140 m.

Material examined: Only known from the holotype.

Distribution: Only known from the type locality.

Etymology: Named after Xavier Le Pichon, leader of the expedition that retrieved the specimen.

Description: *Shell (Figures 5a–f).* Greyish white, slightly discolored by very thin, brown ferrugineous deposits, rather thick and sturdy, ovate, depressed, with anteriorly situated apex. The protoconch is not known. The anterior surface is straight; the posterior one distinctly convex. The shell is sculptured by numerous, fine and sharp radiating with small scalelike tubercles (Figures 5b, d).

Dimensions. Maximum diameter of holotype 9.8 mm, height 2.8 mm.

Soft parts. Not examined, specimen dried.

Radula (Figure 2c). Apical cusps of teeth not strengthened. The central tooth is slender with a bluntly pointed apical cusp. The first and second lateral tooth are quite similar to each other, the inner one slightly more slender. The third lateral tooth is twice as broad as these and its basal ridge is turned away from the center. The two outer teeth are not well visible in the preparations, but it can be seen that the outer one is considerably smaller.

Remarks: The gut was filled with sediment in the holotype, not ferrugineous crusts as is usually the case in the family.

Subclass Cocculiniformia

Family Pyropeltidae McLean & Haszprunar, 1987

Pyropelta McLean & Haszprunar, 1987

Pyropelta McLean & Haszprunar, 1987:197.

Type species: *P. musaica* McLean & Haszprunar, 1987; by original designation; hydrothermal vents, JdF.

Pyropelta cf. *musaica* McLean & Haszprunar, 1987

(Figures 6a–b, 7c)

Pyropelta musaica McLean & Haszprunar, 1987:198, figs. 1–8, 9A.
Pyropelta musaica: McLean, 1992b:406, figs. 9–16.

New records: *JdF, Axial Seamount,* Ashes vent field: - ROPOS R406, 5 spms (FMNH 280892). *Mid America Trench, Jalisco Block Seeps at 20°N:* - NAUTIMATE PL 10, 2 shs; - NAUTIMATE PL 16, on rocks, 4 spms.

Distribution: JdF, Axial Seamount, 1575 m, at vents, and on whale skeletons, several localities off California, 33–36°N, 940–1400 m. Possibly also south to the Jalisco Block Seeps at 20°N, 3000–3775 m.

Remarks: The radula of one of the specimens from the Jalisco Block seeps (Figure 7c) was compared with McLean & Haszprunar (1987) and McLean's (1992b) illustrations and no differences were found. All specimens of "this species," ours and McLean's, have lost the primary shell surface by corrosion (Figures 6a, b), and we find it impossible to be certain that they belong to the same species.

Pyropelta corymba McLean & Haszprunar, 1987

(Figures 4c–d, 6c–f, 7a–b)

Pyropelta corymba McLean & Haszprunar, 1987:200, figs. 9–11.
Pyropelta corymba: McLean, 1992b:409, figs. 17–24.

New records: *Oregon Margin:* - ROPOS #339, Pete Vent

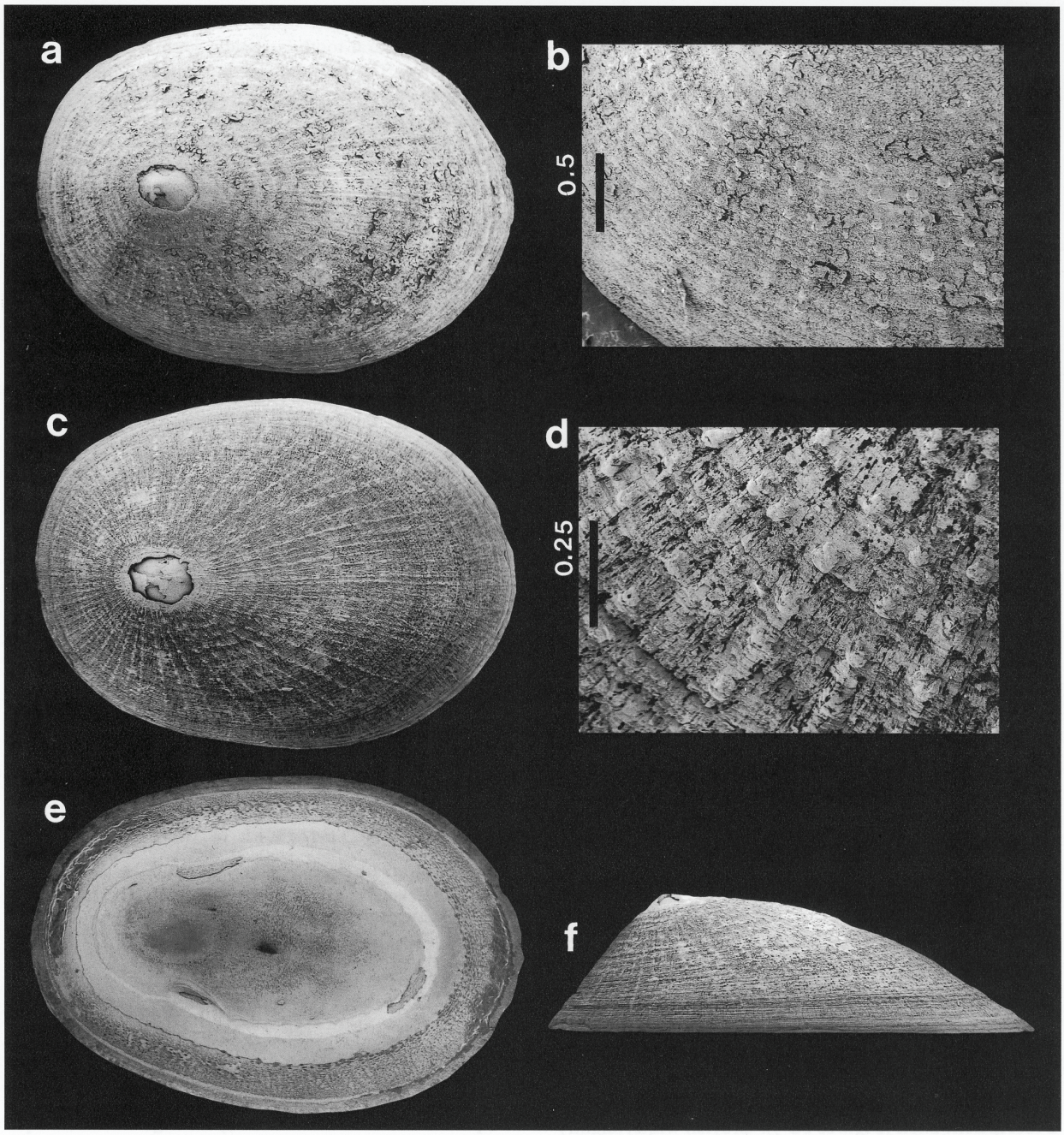


Figure 5. *Paralepetopsis* ***lepichoni*** Warén & Bouchet, sp. nov., holotype, maximum diameter 9.8 mm. *a, b.* Shell *c, d.* Shell cleaned with bleach. *e.* Inside of shell. *f.* Lateral view.

Field, 3 spms on shell of live *Provanna laevis* (SMF 311990); - TVG 11, 1 spm on shell of live *Provanna laevis.*

Distribution: Hydrothermal seeps in the Guaymas Basin to seeps at the Oregon Margin, 2022–524 m, also on whale bone (McLean, 1992b).

Remarks: We figure a critical-point dried specimen, shell and radula to facilitate future identification. The differ-

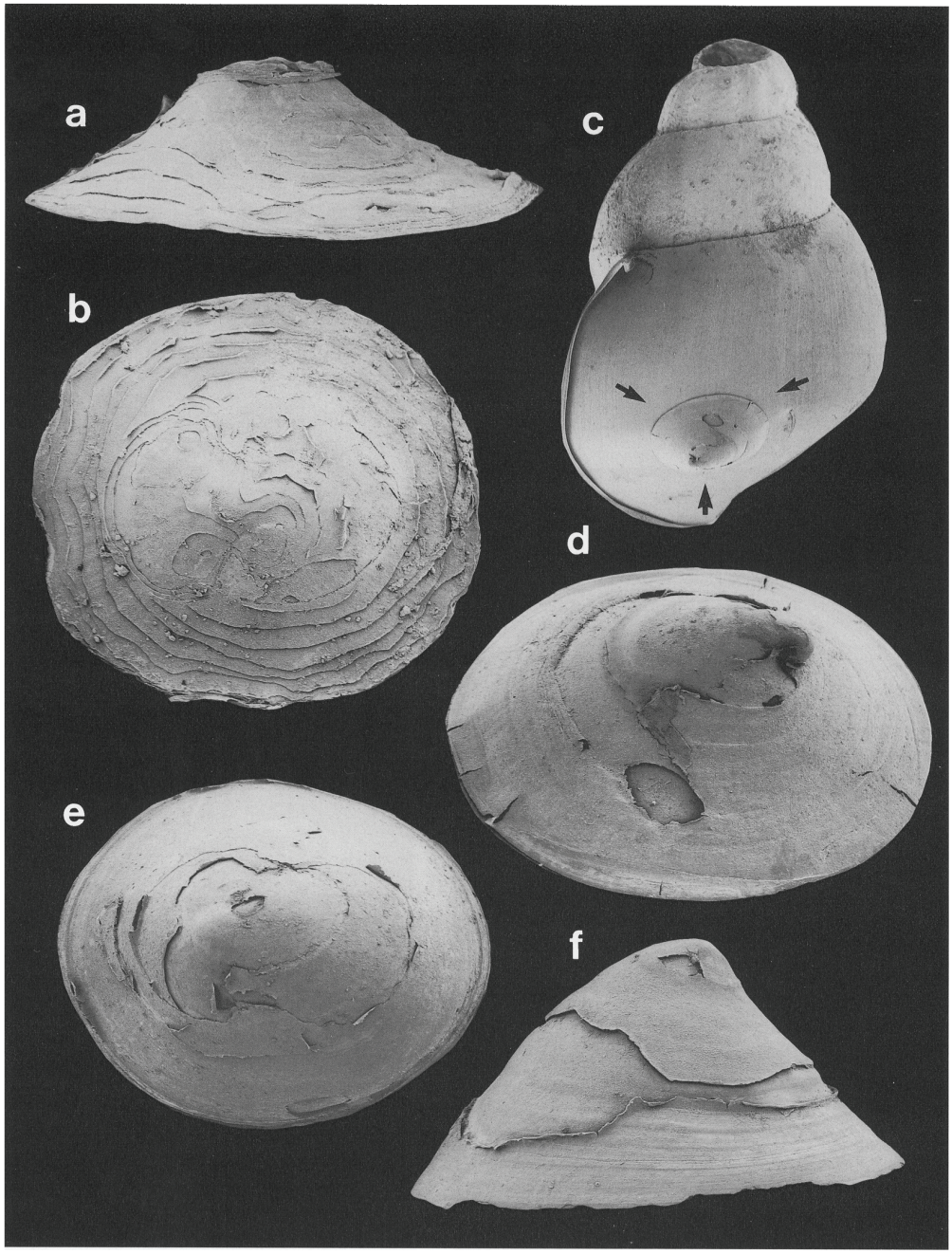
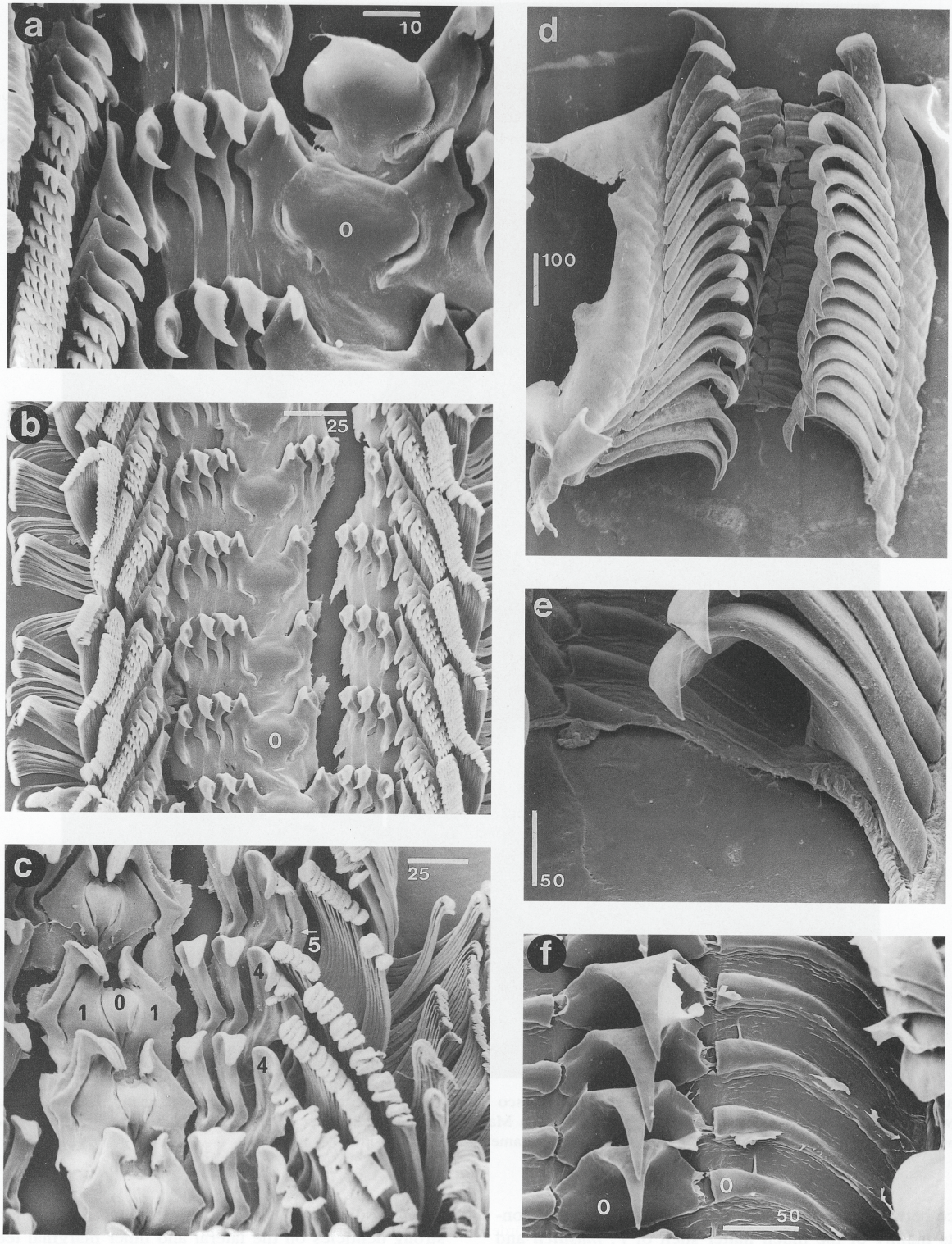


Figure 6. *Pyropelta* spp., shells. *a, b. P.* cf. *musaica,* Jalisco Block Seeps. *a.* Lateral view, maximum diameter 3.4 mm. *b.* Apical view, maximum diameter 4.6 mm. *c–f. P. corymba*, Oregon Margin. *c. In situ*, diameter 1.9 mm, on a living specimen of *Provanna laevis. d.* Same specimen removed. *e, f.* Adult specimens, diameter 2.8 and 2.5 mm.

ence between the three known species of *Pyropelta,* consists mainly of the much flatter shell of *P. musaica* and *P. craigsmithi* (McLean, 1992) and we do not know if there may be additional species hidden. The radula of *P. corymba* differs considerably from *P. musaica* in having strong denticles on the lateral and inner marginal teeth.

McLean (1992b) completed the original description with several figures of the radula. We do believe there is


a
10
0
b
25
0
c
25
5
4
4
1 0 1
d
100
e
50
f
0
0
50

a good possibility that our identification is correct since *P. corymba* was described from the same seep system as *Provanna laevis,* and our present records indicate an association between the two species.

The shell muscle is semicircular, anteriorly broader, its left side has an indistinct "hook." The gill is restricted to the right part of the pallial cavity and enters the right pallial furrow. There is a conspicuous seminal furrow from the right part of the pallial cavity to the right cephalic tentacle.

Subclass VETIGASTROPODA

Family Uncertain

Sahlingia Warén & Bouchet, gen. nov.

Type species: ***Sahlingia xandaros,*** sp. nov.

Diagnosis: "Vetigastropods" with a small to medium size, simple, fragile shell with slightly curved incremental lines. Pallial cavity unusually deep, with single, monopectinate left gill far over to right side. Cephalic tentacles triangular, short, and flat with unusually long sensory papillae along sides. Eye-lobe and eye absent. Right necklobe triangular; left one absent. A single epipodial tentacle under operculum. Radula 1 - 1 - 1; radular sac bilobed. Rhachidian tooth extremely low and broad, with single cusp and small triangular central body. "Marginal teeth" hooklike with simple, sturdy, and flattened base.

Etymology: Named after Heiko Sahling, Kiel, who collected the type species.

Remarks: ***Sahlingia*** is still one more example of a vetigastropod that can not easily be placed in a family level or higher taxon. The position in the Vetigastropoda is supported by the presence of sensory papillae and bilobed radular sac, but the external morphology of the soft parts and shell is too simple and plesiomorphic to allow inferences. The radula is too simplified and specialized to be of any use except its presence and as a synapomorphy of the members of the genus.

We have earlier encountered two undescribed species, in normal deep-sea environment, which can be classified in ***Sahlingia.*** One was found at 2000 m depth at the Lord Howe Rise (between Australia and New Zealand), the other from 4000 m depth in the Bay of Biscay, each represented by a single specimen. They both have conspicuously yellow soft parts. The radula was prepared of the one from the Bay of Biscay and proved to differ only by having the cusps of the "marginal" teeth finely serrated.

It seems quite probable that *Thalassonerita eocenica* Squires & Goedert, 1996, described from Middle-Eocene cold-seeps in the Humptulips Formation in Washington, belongs to this new genus. The size, shape, and sculpture are similar, but no protoconchs are known. It was described in Neritidae (?), but its shell is thin and has an umbilicus which is contradictory to a position in Neritidae.

Sahlingia xandaros Warén & Bouchet, sp. nov.

(Figures 7d–f, 8a–b, 9a–d, 15d, 16h)

Type material: Holotype SMF311980 and 1 paratype SMF311981, 1 paratype SMNH5082, 1 paratype (TVG 43) in MNHN.

Type locality: Aleutian Trench Seeps, Edge site, TVGKG 24, 57°27.394'N, 148°00.013'W, 4890 m - 3 spms.

Material examined: The types and: *Aleutian Trench:* - TVG 43, 2 spms.

Distribution: Only known from the material above. Aleutian Trench Seeps at about 4800–4900 m depth.

Etymology: From "*xandaros*" (Greek), clear, distinct; from its deviating appearance.

Description: *Shell (Figures 8a, b).* Of medium size, rounded with depressed spire, colorless, with very thin brownish transparent periostracum and deep umbilicus. The protoconch (Figure 15d) is pale brownish and has slightly more than half a whorl, diameter 390 μm; the sculpture is not known (covered by deposits that had corroded its surface). The teleoconch has up to 2.7 whorls of rapidly increasing diameter and is sculptured with numerous sharp, incremental lines, and scattered, very indistinct spiral lines. In addition to the incremental lines, there are also a few axial lines that differ in curvature and probably represent longer periods of absence of growth. The outer lip is thin and fragile, not noticeably thickened, and very slightly expanded. The umbilicus is not surrounded by a keel and there are no ribs on the reflected inner lip. The peristome is large, more tangential than radial, prosocline, almost round, slightly indented by the preceding whorl. The outer lip is shallowly sinuated at the mid-point of its height.

Dimensions. Diameter of holotype, 5.6 mm, maximum diameter 9.7 mm.

←

Figure 7. Radulae. Numbers indicate sequential order of teeth with central tooth as 0. *a,b. Pyropelta corymba,* Oregon Margin. *a.* Detail of central part. *b.* Whole width. *c. P.* cf. *musaica,* Jalisco Block Seeps. *d–f.* ***Sahlingia xandaros*** Warén & Bouchet, gen. & sp. nov., Aleutian Seeps, Edge site. *d.* Half the length of the radula. *e.* Detail of central part showing the basal part of the lateral tooth. *f.* Central teeth. Scale bars in μm.

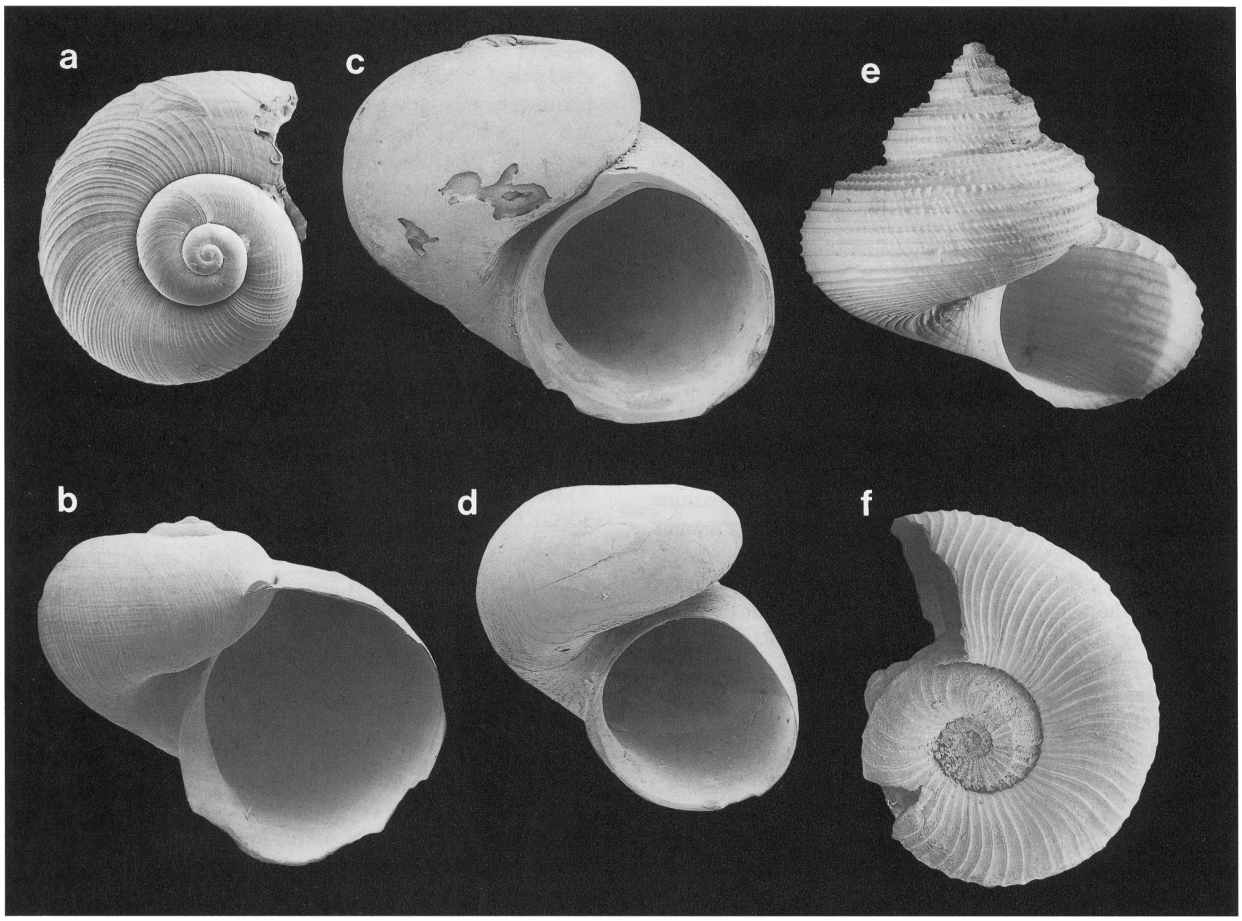


Figure 8. Shells. *a,b.* ***Sahlingia xandaros*** Warén & Bouchet, gen. & sp. nov. *a.* Paratype, apical view, diameter 5.8 mm. *b.* Holotype, diameter 5.6 mm. *c. Fucaria* ***mystax*** Warén & Bouchet, sp. nov., apical whorls lost, Aleutian Seeps, Shumagin site, diameter 2.4 mm. *e. Falsimargarita* ***nauduri*** Warén & Bouchet, sp. nov., holotype, height 18.6 mm. *f. Adeuomphalus* ***trochanter*** Warén & Bouchet, sp. nov., holotype, diameter 2.7 mm.

Soft parts (Figures 9a–d). The milky white soft parts are retracted only very shallowly into the shell and seem not to be able to withdraw farther. The pallial cavity reaches almost one whorl backward, and the monopectinate gill can be seen by transparency along the right(!) side of pallial cavity. It is very long, ca. 40 leaflets, of mainly even width, corresponding to ⅓ of the width of the pallial cavity. There is a conspicuous efferent axis along its left side. The leaflets are tall, and bursicles are probably not present. The foot is large, flat, posteriorly rounded, anteriorly drawn out to unusually long lateral corner tentacles. There is one little, wartlike epipodial "tentacle" under the anterior part of operculum. At the ventral, left side of the neck, a small "wart" (a sensory papilla?) is connected to the corresponding epipodial tentacle by an indistinct ridge. At the right side of the neck is a flat tentacle, below and partly covered by the cephalic tentacle, perhaps a neck-lobe derivative. The snout is long and broad with the triangular, unusually flat cephalic tentacles attached far back. Eyes are absent. The sides of the cephalic tentacles are richly equipped with sensory papillae.

Operculum (Figure 16h). Transparent, yellowish at the zone of attachment, multispiral with central nucleus and short growth zone.

Radula (Figures 7d–f). 1 - 1 - 1, short and broad with ca. 39 transverse rows. The central tooth is very low and broad with a triangular central part and a long lateral process at each side. The point of the central triangle is curved backward and free from secondary denticles. The lateral processes are broken both in the standard preparation and in a specimen which was critical-point dried with everted buccal mass. The lateral tooth is flattened, claw-shaped, with a simple apical cusp. Before being dried, the radula was bluish violet. The radular sac is bilobed at its posterior end.

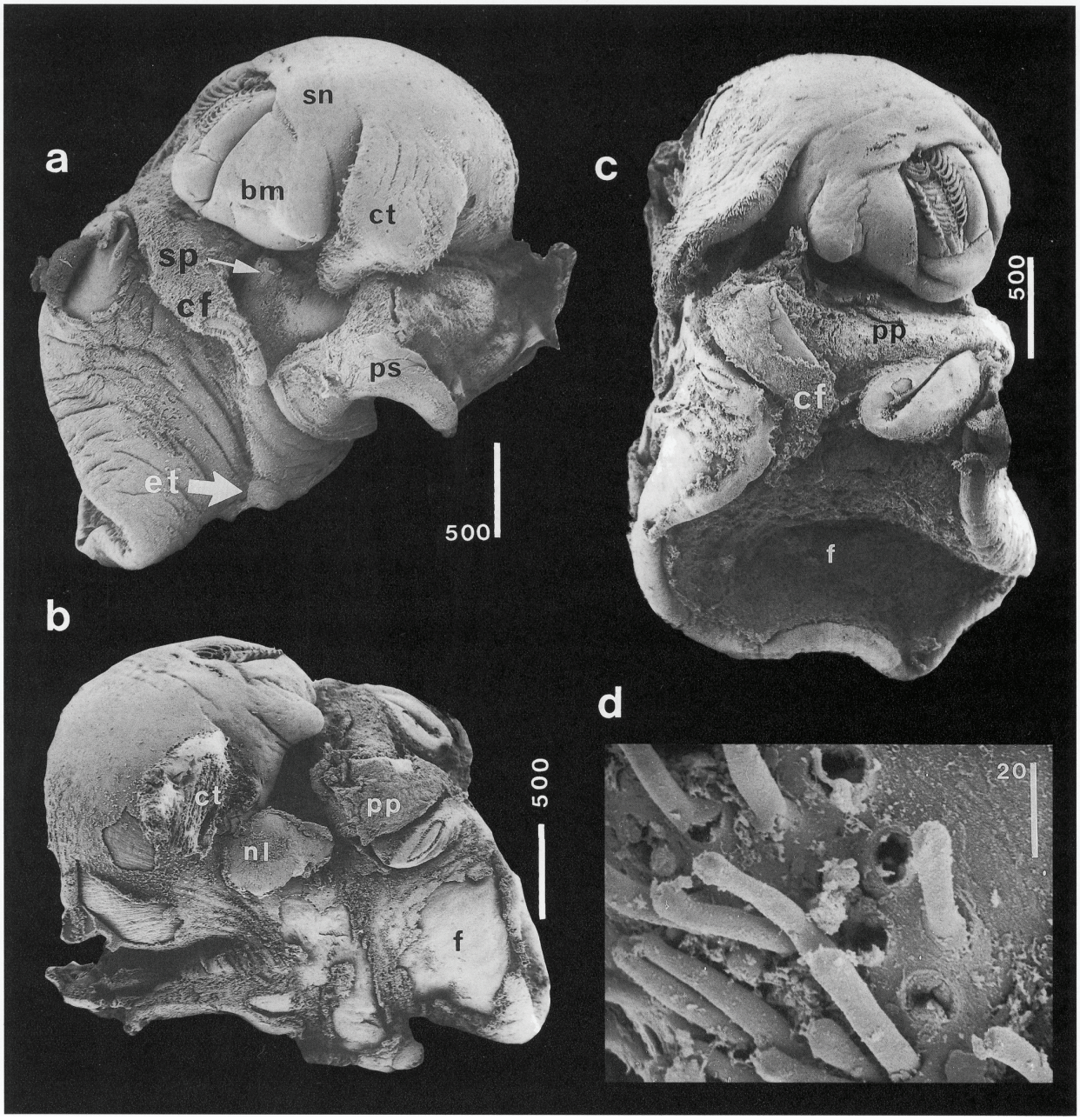


Figure 9. ***Sahlingia xandaros*** Warén & Bouchet, gen. & sp. nov., critical-point dried. *a.* Head-foot, left side. *b.* Head-foot, right side, cephalic tentacle bent to show triangular neck-lobe. *c.* Head-foot, front view. *d.* Detail of sensory papillae from cephalic tentacle. bm - buccal mass; cf - corner of foot; ct - cephalic tentacle; et - epipodial tentacle; nl - neck-lobe; pp - propodium; ps - pallial skirt; sn - snout; sp - sensory papilla. Scale bars in μm.

Remarks: We are not aware of any species that invite confusion; ***S. xandaros*** is unusually large for being a "skeneimorph" and is more likely to be confused with a specimen of the capulid genus *Torellia* Jeffreys, 1867 (Neotaenioglossa).

Adeuomphalus Seguenza, 1876

Adeuomphalus Seguenza, 1876:10.

Type species: *A. ammoniformis* Seguenza, 1876; by monotypy; Plio-Pleistocene deep water fossil, southern Italy.

Remarks: The genus was discussed by Warén (1991:74), who pointed out the similarity to *Eudaronia* Cotton, 1945, a vetigastropod genus of uncertain position, from deep water off South Australia. Warén has afterward examined a couple of species of *Adeuomphalus* which turned out to lack a radula, among them, the type species. This lack of a radula was confirmed also in the new species described here, but serial sectioning of the paratype confirmed that it is a vetigastropod, by the presence of sensory papillae on the cephalic tentacles.

Adeuomphalus ***trochanter*** Warén & Bouchet, sp. nov.

(Figures 8f, 151, 16d)

Type material: Holotype (MNHN) and one paratype (SMNH5083), serially sectioned.

Type locality: JdF, CoAxial Segment: Beard Chimney Source site, 46°09.3'N, 129°48.4'W, 2060 m, both specimens found in a running shoe, caught by a grab.

Material examined: Only known from the type material.

Etymology: From "trochanter," a torture wheel (Latin), referring to the superficial appearance of the shell.

Description: *Shell (Figure 8f).* Small, fragile, colorless, planispiral, with evenly rounded whorls and sigmoid axial riblets. The protoconch (Figure 151) has a diameter of 190 μm, consists of ⅔ of a whorl, and is sculptured by an irregular net demarcating pits of highly irregular shape and size. The teleoconch is demarcated by a small but distinct rib. The first 1.5 teleoconch whorls are distinctly keeled halfway between the two sutures, at both sides of the shell. Where this keel disappears the axial riblets become slightly flexuous instead of radial and straight. The holotype is slightly broken (the paratype more so), but seems to have had 2.0 whorls. The peristome is circular except for an indentation by the preceding whorl.

Dimensions. Diameter of holotype 2.7 mm, height 1.2 mm; paratype diameter 2.2 mm.

Operculum (Figure 16d). Same diameter as peristome, multispiral with central nucleus, transparent but quite sturdy.

Radula. Absent.

Soft parts. The anterior end of the foot is bifurcated, the corners drawn out to tentaclelike formations. The anterior pedal gland is large and conspicuously white in a rehydrated specimen. Epipodial tentacles are present, but no detail could be discerned. The cephalic tentacles are blunt, cylindrical, slightly longer than the large, broad, apically expanded snout, and lack eyes. A right neck-lobe is present; a left one was not detected. The gill is small, monopectinate with 10 leaflets; the outline of the whole gill is semi-circular with the diameter corresponding to the axis and directed straight backward. From what could be detected by transparency of the soft parts, the visceral mass is mainly occupied by the gonad.

Remarks: Examination of the serial sections confirmed *Adeuomphalus* to be a vetigastropod, but few other details. It is a simultaneous hermaphrodite; its buccal mass, esophagus, and stomach are much simplified and did not contain identifiable material. The gill is monopectinate. The holotype had an arenaceous foram attached to the right side of the shell.

Superfamily TROCHOIDEA Rafinesque, 1815

Family TURBINIDAE Rafinesque, 1815

Cantrainea Jeffreys, 1883

Cantrainea Jeffreys, 1883:109.

Type species: *Turbo peloritanus* Cantraine, 1840; by monotypy; Plio-Pleistocene fossil, Sicily.

Remarks: The type species also occurs living in depths between 100 and 1000 m off southern and western Europe. The genus comprises several bathyal species, worldwide, except in polar areas.

Cantrainea macleani Warén & Bouchet, 1993

Cantrainea macleani Warén & Bouchet, 1993:8, figs. 4A–C, 5B, F–G, 6A.

New records: *Off Louisiana:* - Johnson Sealink dive 3129, 3 spms (2 with neritid egg capsules on shell).

Distribution: Only known from off Louisiana, Bush Hill Seep, ca. 540 m.

Family TROCHIDAE Rafinesque, 1815

Remarks: We have largely followed Hickman & McLean (1990) in the classification of the family.

Bathymargarites Warén & Bouchet, 1989

Bathymargarites Warén & Bouchet, 1989:87.

Type species: *B. symplector* Warén & Bouchet, 1989; by original designation; hydrothermal vents at the EPR.

Bathymargarites symplector Warén & Bouchet, 1989

Bathymargarites symplector Warén & Bouchet, 1989:91, figs. 92–95, 100–101, 104–107, 110.
Bathymargarites symplector: Warén & Bouchet, 1993:11, figs. 10A–E, 11A–B.

New records: *EPR at 13°N:* - HERO 91 PL 09, 11 spms; - HERO 91 PL 11 (Genesis), 20 spms; - HERO 91 PL 12, 1 spm; - HERO 91 PL 14 (Elsa), 2 spms; - HERO 92 dive 2520, 1 sh. *09°50'N:* - HERO 91 PL 07, 2 spms; - HERO 91 PL 08, 1 spm; - HERO 91 PL 09, 2 spms.

17°S: - NAUDUR PL 06, 34 spms; - NAUDUR PL 18, 5 spms.

Distribution: EPR from 21°N to 17°S. Depth range 2500–2600 m.

Remarks: The new records enlarge the distribution considerably.

Cataegis McLean & Quinn, 1987

Cataegis McLean & Quinn, 1987:113.

Type species: *C. toreuta* McLean & Quinn, 1987 [31 July] (= *Homalopoma finkli* Petuch, 1987 [not dated, hence deemed to be 31 December]); by original designation; deep water off Colombia.

Cataegis meroglypta McLean & Quinn, 1987

Cataegis meroglypta McLean & Quinn, 1987:115, figs. 3, 4, 7, 8.
Cataegis meroglypta: Warén & Bouchet, 1993:19, figs. 14A–G, 15A–B.

New records: *Off Louisiana:* - Johnson Sealink dive 3129, 35 spms. *Off Barbados (El Pilar Sector):* - DIAPISUB 15-4, 11 spms; - DIAPISUB 16-3, 11 spms.

Distribution: Off Louisiana and Barbados, 540–1135 m.

Remarks: Several specimens from the Bush Hill Seep had the shell tunnelled by polychaetes of the subfamily Polydorinae, in one case so wide a tunnel that both the in- and outside of the shell had been broken through. Usually the tubes were restricted to the umbilicus of the shell.

Falsimargarita Powell, 1951

Falsimargarita Powell, 1951:93.

Type species: *Margarites gemma* Smith, 1915; by original designation; Antarctic, bathyal.

Remarks: The genus *Falsimargarita* comprises a few species of mainly Antarctic distribution, in depths between 300 and 3500 m (Dell, 1990:93). We have seen a couple of similar species from deep-sea dredgings around New Caledonia (25°S), but nothing more northern.

The species of *Falsimargarita* have a fragile shell with mainly spiral sculpture. The internal nacreous layer, visible through the surface of the shell, is of a greenish iridescent hue. The protoconch of *Falsimargarita* is finely tuberculate.

The protoconch of species of Calliostomatinae has a diagnostic honey-comb sculpture (Marshall, 1995), but the radula and soft parts are very similar to shallow water species and we consider the placement in Calliostomatinae (Powell, 1951, Marshall, 1995) correct.

Falsimargarita ***nauduri*** Warén & Bouchet sp. nov.

(Figures 8e, 10a–d, 11a, b, 14e, 16c)

Type material: Holotype in MNHN.

Type locality: EPR at 17°25'S, NAUDUR PL 04-8-4, site Rehu, 17°24.85'S, 113°12.15'W, 2578 m.

Material examined: The holotype.

Distribution: Only known from the type locality.

Etymology: Named after the expedition that found the species.

Description: *Shell (Figure 8e).* Large, fragile, slightly greenish iridescent, conical with strongly convex whorls. The protoconch is large and inflated, diameter 1.2 mm, with less than half a whorl and almost no suture. Its surface is finely tuberculate. The teleoconch has 4.25 strongly convex whorls. The first whorl is sculptured with three sharp keels, starting directly after the protoconch, of which the adapical one remains close to the suture, the median one becomes number 5, and the abapical one becomes number 8 on the body whorl at the peristome. The total number of major keels at the peristome is 33 plus three recently added minor ones. The axial sculpture starts after ¼ of a whorl, with ribs of similar strength as the spirals, 38 in number on the first ribbed whorl. The axial ribs form tubercles at the intersection with the spines, and on the later whorls they become much less obvious between the spiral ribs, and not much stronger than on the first whorl. The interior of the whorls is covered by a thin nacreous layer and has broad, shallow furrows corresponding to the spiral ribs and low axial ribs reflecting the axial ones of the exterior. Umbilicus deep and narrow.

Dimensions. Height 18.6 mm, diameter 18.7 mm.

Soft parts (Figures 10a–d). The foot is long and slender, laterally covered by small papillae below the epipodial membrane (Figure 10c), smooth above it, posteriorly pointed, anteriorly truncate, slightly bilobed and drawn out to short corner tentacles, paralleled by the propodium. Each side of the foot has an epipodial membrane with smooth dorsal surface and richly covered by papillae similar to those of the sides of the foot but two to three times higher and more pointed, on its ventral side. Halfway backward under the operculum the membrane becomes lower and continues posteriorly as a low papillose ridge. The membrane has six tentacles evenly spaced between the operculum and the neck-lobe. The left neck-lobe starts below the eye-lobe and forms a smooth undulating membrane, continuous with the epipodial membrane. The right neck-lobe is similar, but has a small membrane, drawn out ventrally and entering the right part of the space between the head and foot and connects to the mouth. The

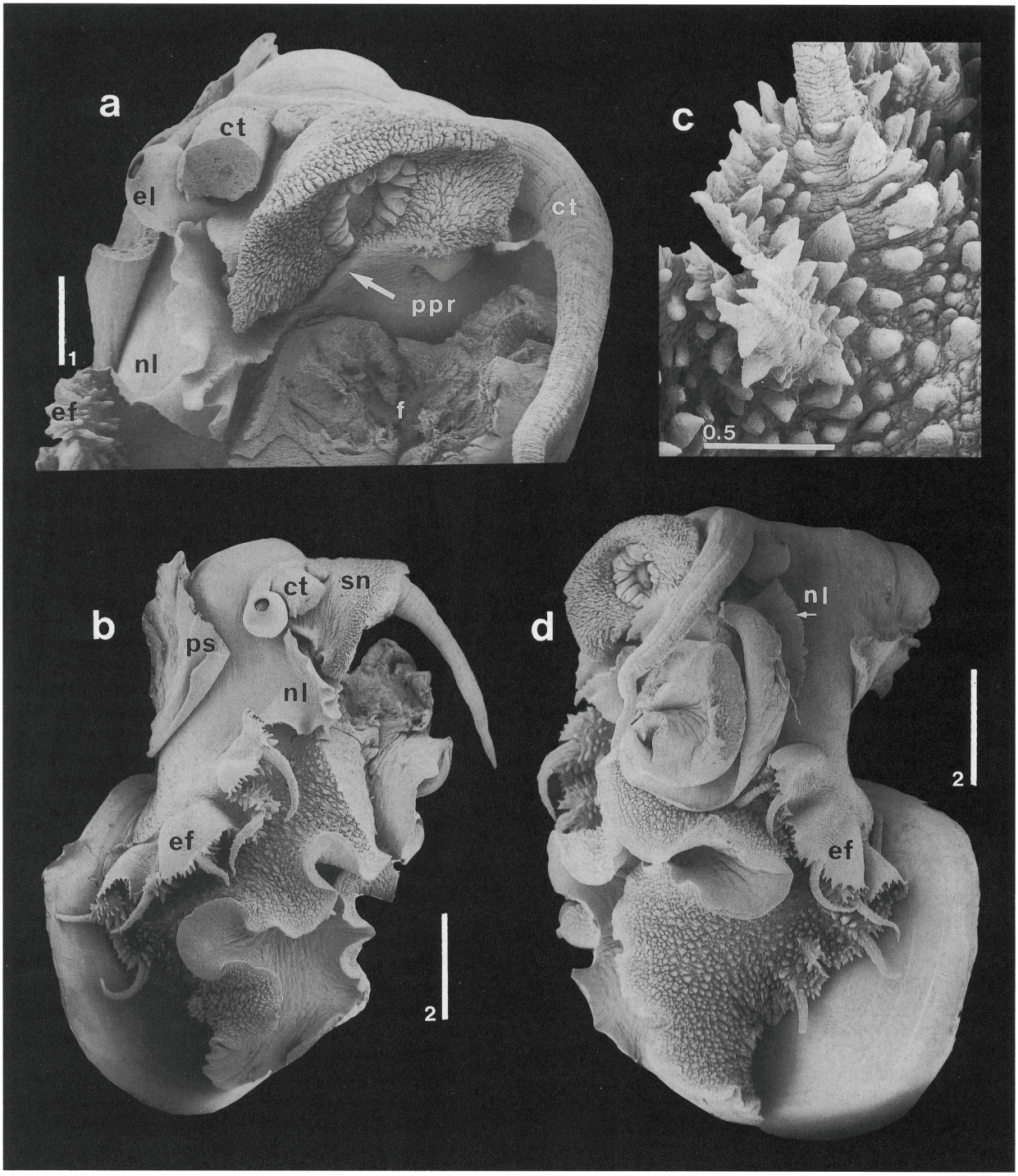
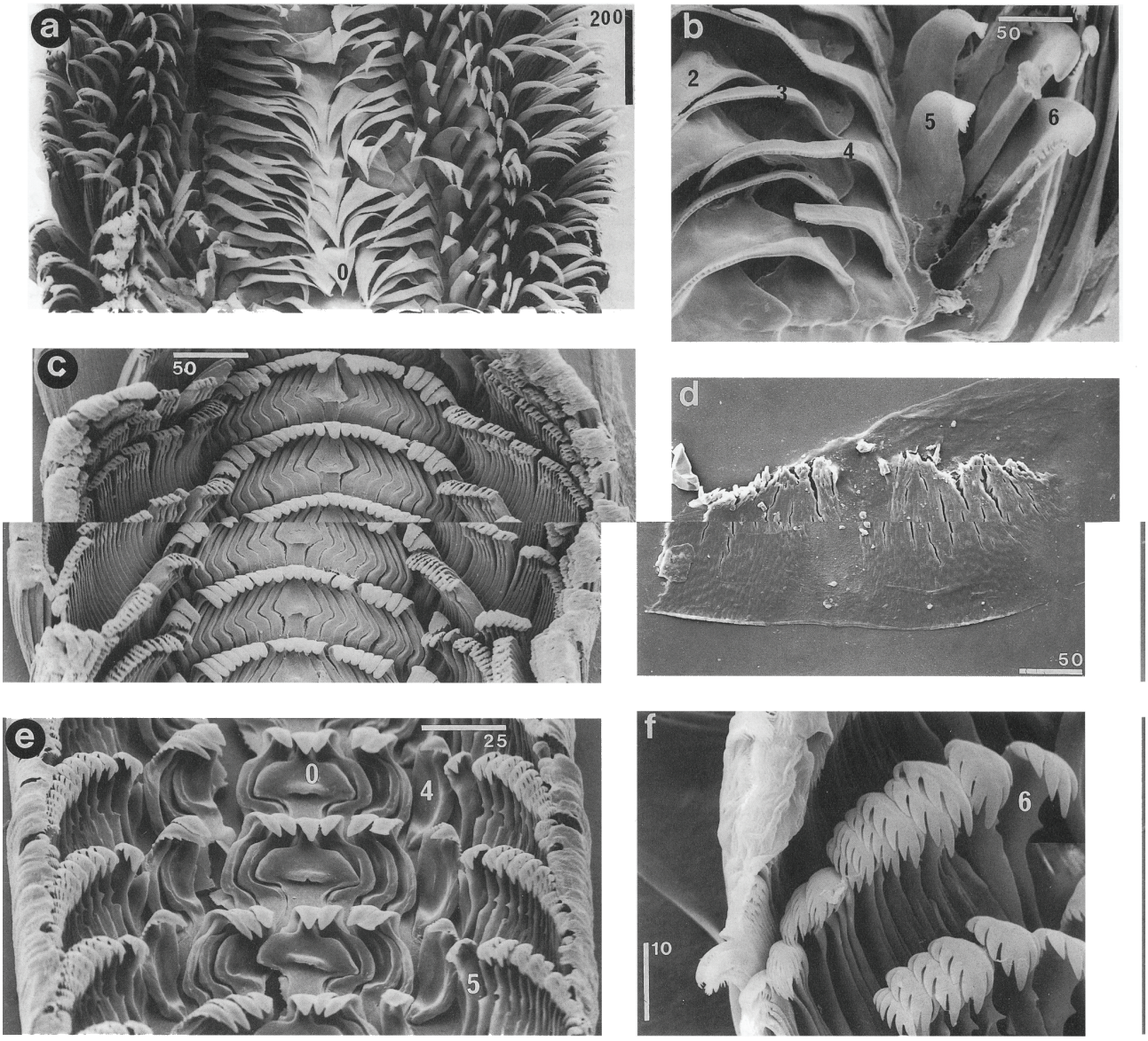


Figure 10. *Falsimargarita* ***nauduri*** Warén & Bouchet, sp. nov., holotype, critical-point dried. Right cephalic tentacle and right anterior part of foot removed to show details. *a.* Snout, ventral view. *b.* Head-foot, right side. *c.* Detail of ventral surface of epipodial fringe. *d.* Head-foot, left side. ct - cephalic tentacle; ef - epipodial fringe; el - eye-lobe; f - foot (partly cut off); nl - neck-lobe; ppr - pseudoproboscis; ps - pallial skirt; sn - snout. Scale bars in mm.



igure 11. Radulae and jaw. Numbers indicate sequential order of teeth with central tooth as 0. *a, b. Falsimargarita* ***nauduri*** Warén
: Bouchet, sp. nov., holotype. *a.* Whole width. *b.* Detail of outermost lateral and innermost marginal teeth. *c. Fucaria* ***mystax*** Warén
: Bouchet, sp. nov., holotype. *d–f. Bruceiella* ***athlia*** Warén & Bouchet, sp. nov., Aleutian Seeps, Shumagin site. *d.* Jaw. *e.* Whole
/idth of radula. *f.* Detail of marginals.

ephalic tentacles are long and slender with longitudinal urrows. At their anterior, central and basal part is a small ephalic lappet. The eye-lobes are five times as long as he basal diameter and apically inflated to twice the basal iameter, to contain the large, black eye. The snout is hort, apically broader, and flattened. Its anterior face is overed by small papillae and sharply demarcated from he oral disc surrounding the mouth. The mouth is surounded by a zone of large folds; more peripherally these are abruptly replaced by much smaller papillae. At the ventral mid-point of the mouth, the snout is drawn out into a narrow fold ("pseudoproboscis") connecting to the right neck-lobe. On the ventral part of the neck, just behind the left part of the oral disc is a (sensory?) tubercle. Along the right side of the snout runs a low membrane, from the central side of the eye-lobe, to the right ventral corner of the oral disc. The gill was poorly preserved, but is long and bipectinate with osphradium on the ventral

face of the efferent membrane. There are no pallial margin tentacles or other appendages.

Operculum (Figure 16c). Brownish, multispiral, with central nucleus.

Radula (Figures 11a, b). n - 5 - 1 - 5 - n [n = 25–50, difficult to count], typical for the subfamily. The central and four inner lateral teeth are membranous, their apical half finely serrated. The outer lateral tooth, number 5, is more sturdily built and slightly smaller. The inner marginal tooth is sturdy and broad with about 10 small denticles along its apical third. The second marginal tooth is much more slender and slightly smaller; the third one and outward are simple and clawlike.

Jaw (Figure 14e). Rather thin and fragile, composed of numerous rodlets, dorsally and anteriorly deeply notched.

Remarks: Since no other species of *Falsimargarita* is known to be associated with hydrothermal vents or seeps, *F.* ***nauduri*** may be an occasional intruder. *Falsimargarita* ***nauduri*** resembles *F. georgiana* Dell, 1990 and *F. benthicola* Dell, 1990, but is proportionally taller and has a more circular cross section of the whorls.

Nothing is known about the biology of any species of *Falsimargarita,* and we were not able to find any stomach contents.

Fucaria Warén & Bouchet, 1993

Fucaria Warén & Bouchet, 1993:15.

Type species: *F. striata* Warén & Bouchet, 1993; by original designation; hydrothermal vents, JdF.

Remarks: Warén & Bouchet (1993) classified *Fucaria* in the subfamily Halistylinae, but we now consider this uncertain.

The snout with its coat of sensory papillae may draw attention to the Solariellinae and Lirulariinae (cf. Hickman & McLean, 1990, fig. 79D, E), but in these groups the tentacles on the snout are much larger and true tentacles, with no apical tuft of sensory cilia. This is obvious in Hickman & McLean's (1990) fig. 79E, where the sensory papillae on the tentacles can be compared. We have not seen any comparably equipped snout among other "vetigastropods," and the character is a good apomorphy for *Fucaria.*

The new species below is quite similar to the type species and differs mainly in having a smooth shell. This is the third species of the genus, which now is known from the JdF, Florida Escarpment, and the south-western Pacific. (Inquiries about the whereabouts of the material from the Florida Escarpment have remained unanswered and the species therefore remains undescribed.)

Fucaria striata Warén & Bouchet, 1993

Fucaria striata Warén & Bouchet, 1993:16, figs. 9e–h, 12a–c, 13a–c, 38c.

New records: *JdF,* Middle Valley vent field: - ALVIN dive 3146, 10 spms (FMNH 280955).

Fucaria ***mystax*** Warén & Bouchet, sp. nov.

(Figures 8c, 11c, 12a–d, 16e)

Type material: Holotype and 2 paratypes in MNHN, 2 paratypes in V. Tunnicliffe reference collection.

Type locality: Off northeastern side of Papua New Guinea, 3 miles south of Lihir Island, Edison Seamount, 03°01.185'S, 152°03.492'E, 1483 m, 30-GTVA.

Material examined: Only known from the type material.

Distribution: Only known from the type locality.

Etymology: "Mystax," Greek, moustache, alluding to the coat of sensory papillae on the snout.

Description: *Shell (Figure 8c).* Rounded, skeneiform, sturdy, with thin, pale beige periostracum. The protoconch and apical whorls are lost by corrosion in all specimens. The teleoconch has more than 1.5 whorls, estimated to ca. 2.5 whorls. There is no sculpture, not even growth lines, except occasional scars from earlier damage to the outer lip. The periostracum is smooth and very thin. The peristome is not thickened in any specimen, almost round, not indented by the preceding whorl, more tangential than radial and prosocline. The umbilicus is deep and narrow, barely visible in a basal view.

Dimensions. Maximum diameter 5.8 mm.

Soft parts (Figures 12a–d). The foot is large and flat with well demarcated propodium, truncate anteriorly with the corners drawn out to small tentacles and paralleled by the propodium. Each side of the foot has more than three epipodial tentacles. The head is quite large, the snout cylindrical with the apical part demarcated by a rounded swelling. The mouth is centrally situated in the flat extremity of the snout. The cephalic tentacles are rather short, of similar length as the snout, and encircled, except antero-ventrally, by a ridge, perhaps a modified combination of cephalic lappet and eye-lobe. Eyes not seen. The right neck-lobe consists of two flat tentacles, the left one probably a single large one which apically is split in two or three parts. The cephalic tentacles are anteriorly (Figure 12d) and posteriorly covered by a dense coat of sensory papillae, up to 100 μm long, as is the apical part of the snout. The gill is monopectinate, attached in its whole length, and has sensory bursicles.

Operculum (Figure 16e). It is yellowish, rather stiff, multispiral with about 10 whorls, it has a central nucleus, short growth zone, and indistinct sculpture of growth lines. There is a slight overlap of the edge of the preceding whorl.

Radula (Figure 11c). n - 11 - 1 - 11 - n. The central tooth is short with a drawn out, narrow anterior support,

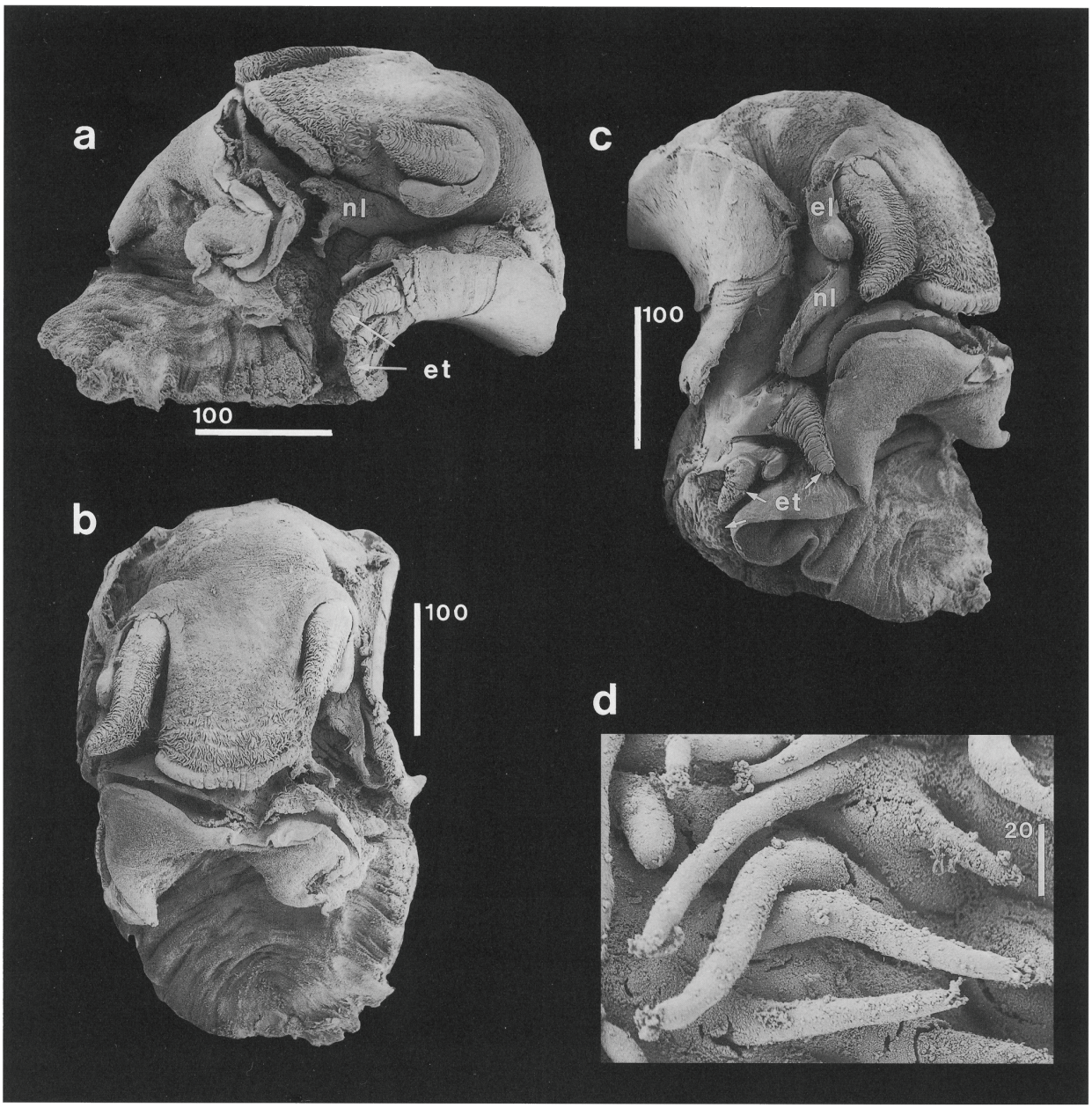


Figure 12. *Fucaria* ***mystax*** Warén & Bouchet, sp. nov., holotype, critical-point dried. *a.* Head-foot, left side. *b.* Head-foot, front view. *c.* Head-foot, right side. *d.* Sensory papillae from snout. el - eye-lobe; et - epipodial tentacle; nl - neck-lobe. Scale bars in μm.

sturdy shaft, and smooth edge of the apical plate. The lateral teeth are tightly packed, interlocking along most of their length, and only the outermost two teeth have a denticulate apical plate. The marginals form an almost unbroken continuation of the laterals but differ in having a strong tubercle below the denticulate apical plate.

Remarks: The few specimens had been preserved in a mixture of methanol and vodka (Tunnicliffe, 1994), but some detail can be seen from the critical-point dried body. The neck-lobes may be broken or deeply split, this could not be decided because their epithelium was peeling badly.

Family SKENEIDAE Clark, 1851

Protolira Warén & Bouchet, 1993

Protolira Warén & Bouchet, 1993: 22.

Type species: *P. valvatoides* Warén & Bouchet, 1993; by original designation; hydrothermal vents, MAR, Snake Pit.

Remarks: A second species, *P. thorvaldssoni* Warén, 1996, was recently described from decaying whale bone off south-western Iceland, and turned out to be very common at Lucky Strike. The two species are quite similar, and the poor condition of most adult specimens makes it more difficult to separate them. *Protolira valvatoides* does, however, have a thick, tough, shiny, and dark olive green periostracum, the shell has a slightly more depressed shape, and a narrow, brown line parallels the pallial margin, about 0.1 mm behind it. This line is missing in *P. thorvaldssoni.*

Warén & Bouchet (1993: fig. 18D) figured what they assumed to be the protoconch of *Protolira valvatoides,* but that was a very young specimen of what we here describe as *Lirapex* ***costellata*** (not known then), a mistake we realized only after finishing this manuscript, when some very young specimens became available from particle traps. The protoconch of *Protolira* actually is similar to that of *Bruciella* (Figure 15E), with the same kind of spiral sculpture and sharp incremental line after 1/20 of a teleoconch whorl.

Protolira valvatoides Warén & Bouchet, 1993

Protolira valvatoides Warén & Bouchet, 1993: 20, figs. 17A–B, 18D, G, 19A–C, 20A–F.

New records: *MAR, Menez Gwen:* DIVA, 1.13 on an active chimney, 19 spms; - DIVA 1 PL 14, on sulfide rock with Hydrozoa, 36 spms; - DIVA 1 PL 16, on base of a black smoker, 1 young; - DIVA 2 PL 11, 12 spms; on mussels, 11 spms; on rocks, 131 spms; suction sample among mussels, 3 spms; - DIVA 2 PL 12, 524 spms; suction sample among mussels, 8 spms; - DIVA 2 PL 13, 2 suction samples among mussels, 5 and 7 spms; - DIVA 2 PL 14, 6 spms; - DIVA 2 PL 16, 77 spms; - MARVEL PL1201, 850 m, 3700 spms; - MARVEL PL1202, 850 m, suction sample, 50 spms; among mussels, 1637 spms; retrieval box, 1130 spms; - MARVEL PL1203, 850 m, retrieval box, 895 spms; - MARVEL PL1208, 850 m, retrieval box, 17 spms; - MARVEL PP10, particle trap, 15 spms, 3 protoconchs; - MARVEL PP49, particle trap, 4 spms; - MARVEL PP50, particle trap, 6 spms, 3 protoconchs; - MARVEL PPS 20, particle trap, 13 spms, 3 protoconchs. *Lucky Strike:* DIVA 1 PL 18, among mussels, 1 spm; - DIVA 2 PL 02, 3 spms; - DIVA 2 PL 03, 1 spm; DIVA 2 PL 07, 3 spms; - DIVA 2 PL 19, 7 spms; - DIVA 2 PL 20, 4 spms; - ALVIN dive 2606, 5 spms; - LUSTRE Exp., Tour Eiffel, on mussels, 2 spms; - MARVEL PL1191, Bairro Alto, retrieval box, 1 spm; 2 suction samples, 1 spm each; - MARVEL PL1193, Bairro Alto, 1585 m, retrieval box, 8 spms; - MARVEL PL1194, Tour Eiffel, retrieval box, 4 spms; - MARVEL PL1195, Tour Eiffel, 1685 m, retrieval box, 3 spms; - MARVEL PL1200, Bairro Alto, 0.25 m^2 rock surface close to edifice, 4 spms; - MARVEL PL1205, Bairro Alto + Tour Eiffel (mixed), 1700 m, 5 spms.

Distribution: MAR from Menez Gwen to Lucky Strike, in ca. 850–1800 m depth, living among mussels, in sediment and on rocks.

Remarks: *Protolira valvatoides* is one of the most common gastropods at Menez Gwen. It reaches a maximum size of 3.5 mm. Most of the spire is usually corroded away, and in extreme cases the body may consist of half a whorl with the digestive gland and gonad remaining as a very short $1/_{10}$ of a whorl. The gut contains mixed sediment.

When we originally described *P. valvatoides,* we had two complete and several decalcified specimens. We are therefore not certain that the original illustrations of the radula and soft parts are based on *P. valvatoides.* We have now examined radulae and critical point dried specimens of both *valvatoides* and *thorvaldssoni* and have found no differences in the external morphology of the soft parts, except that *P. valvatoides* has a sharp reddish brown line paralleling the pallial margin. There is a tendency that *P. thorvaldssoni* has a more well demarcated unpaired cusp on the central radular tooth, but this was not always the case when we examined 15 radulae of each species. Some specimens of *thorvaldssoni* had a poorly defined cusp, while no specimen of *valvatoides* had a well defined one. Our (1993: fig. 19A–B) therefore is probably based on *P. thorvaldssoni.*

Protolira thorvaldssoni Warén, 1996

Protolira thorvaldsoni Warén, 1996: 201, figs. 3E–F, 4A–D (incorrect original spelling).

New records: *Menez Gwen:* DIVA 1 PL 13 on an active chimney, 2 spms; - DIVA 1 PL 14, on sulfide rock with Hydrozoa, 6 spms; - MARVEL PL1201, 850 m, 3 spms; - MARVEL PL1203, 850 m, retrieval box, 9 spms. *Lucky Strike:* DIVA 1 PL 01, among mussels, 1 spm; - DIVA 1 PL03(1), 7 spms; - DIVA 1 PL 04, in baited trap, 4 spms; on inactive chimney among Hydrozoa and sponge *Cladorhiza,* 39 spms; - DIVA 1 PL 17, among mussels, 6 spms; - DIVA 1 PL 19, among mussels, 6 spms; DIVA 2 PL 02, 34 spms; on chimney, 3 spms; - DIVA 2 PL 03, 52 spms; - DIVA 2 PL 04, 58 spms; 2 suction samples among mussels in shimmering water, 12 and 39 spms; - DIVA 2 PL 05, 9 spms; - DIVA 2 PL 06, 2 spms; - DIVA 2 PL 07, 84 spms; 3 suction samples among mussels and hydrothermal sediments, 9, 3, and 12 spms; - DIVA 2 PL 08, in retrieval box, 16 spms; 2 suction samples among

mussels and hydrothermal sediments, 2 and 7 spms; - DIVA 2 PL 09, 8 spms; suction sample among mussels and hydrothermal sediments, 1 spm; - DIVA 2 PL 10, 104 spms; on rocks, 5 spms; 2 suction sample among mussels and hydrothermal sediments, 5 and 14 spms; in retrieval box, 1750 spms; - DIVA 2 PL 17, 6 spms; - DIVA 2 PL 19, 17 spms; - DIVA 2 PL 20, 562 spms; - DIVA 2 PL 21, 30 spms; - DIVA 2 PL 25, 66 spms; - DIVA 2 PL 26, 72 spms; Sintra site, 1 spm; - DIVA 2, in particle trap, 1 spm; - ALVIN dive 2606, 20 spms; - ALVIN dive 2607, 187 spms; - LUSTRE Exp., Sintra site, on mussels, 51 spms; - MARVEL PL1191, Bairro Alto, retrieval box, 28 spms; 1 suction sample, 1 spm; - MARVEL PL1192, Bairro Alto, retrieval box, 1630 m, 5 spms; - MARVEL PL1193, Bairro Alto, 1585 m, retrieval box, 44 spms; - MARVEL PL1194, Tour Eiffel, retrieval box, 98 spms; - MARVEL PL1195, Tour Eiffel, 1685 m, retrieval box, 141 spms; - MARVEL PL1200, Bairro Alto, 0.25 m^2 rock surface close to edifice, 90 spms; - MARVEL PL1205, Bairro Alto, retrieval box, 23 spms; Bairro Alto + Tour Eiffel (mixed), 1700 m, 59 spms; - MARVEL PP49, particle trap, 2 spms. *Rainbow:* MARVEL PL1196, among mussels, 2300 m, 13 spms. *Snake Pit:* ALVIN dive 2615, 6 spms; - ALVIN dive 2617, 5 spms; - ALVIN dive 2619, 15 spms; - ALVIN dive 2622, 1 spm.

Distribution: MAR from Menez Gwen to Snake Pit, in ca. 850–3700 m depth, living among mussels, in sediment and on rocks; also off south-western Iceland, ca. 63°N, in a few hundred meters depth, on whale bone.

Remarks: *Protolira thorvaldssoni* is very common at Lucky Strike, much more so than *P. valvatoides*. It attains a maximum shell diameter of 4.2 mm. Some specimens from Lucky Strike had a small syllid polychaete in the umbilicus. The gut contains mixed sediment.

The spire is usually partly corroded away, but less so than in *P. valvatoides*. This may be the result of a slight difference in preferred micro habitat, since *P. valvatoides* has a thicker and presumably more protective periostracum.

Protolira thorvaldssoni is one of the few species known both in hydrothermal vents and outside them, and it is significant that it was described from a biogenic substrate. The two specimens that formed the base for the original description were not very well preserved, and the identification may be questioned, but they are more similar to each other than to two more species of the same group (undescribed) from off western Europe, with a radula with a more normal skeneid type central field.

In the original description, the specific epithet was spelled *thorvaldsoni* but the species was said to be named after Mr Jón Thorvaldsson. This is an incorrect original spelling in the sense of Art. 32.5 of the Code, and the spelling *thorvaldssoni* is a justified emendation.

Bruceiella Warén & Bouchet, 1993

Bruceiella Warén & Bouchet, 1993:26.

Type species: *B. globulus* Warén & Bouchet, 1993; by original designation; vents in the North Fiji Basin.

*Bruceiella **athlia*** Warén & Bouchet, sp. nov.

(Figures 8d, 11d–f, 13a–d, 15e, 16j)

Type material: Holotype SMF 311982 and 50+ paratypes SMF311983; 50+ paratypes in MNHN.

Type locality: Aleutian Trench, Shumagin site, 54°18'N, 157°12'W, 4808 m (TVGKG 40), 180 spms and shs.

Material examined: The types and: *Aleutian Trench:* - TVGKG 49, 16 shs and spms.

Distribution: Only known from the Aleutian seeps, Shumagin site, at about 4800 m.

Etymology: "*athlios, -a,*" Greek, miserable, referring to the sad condition of all adult specimens.

Description: *Shell (Figure 8d).* Fairly sturdy, opaque greyish, tall skeneiform, always badly corroded and only in juvenile specimens, more than half an intact whorl. The protoconch (Figure 15e) has about ⅔ of a whorl, a diameter of 450 μm, and its initial part is sculptured by a system of low, raised ridges forming an irregular net. More distally these ridges get a mainly spiral orientation and finally they fade out, well before the end of the protoconch. The transition to the protoconch is marked by a sharp and narrow furrow, followed by a short, smooth area and a varix. The teleoconch is almost smooth, except irregular and indistinct incremental lines. The shape of the shell is difficult to reconstruct, but without interference of corrosion it may have been more tall spired than the type species. The peristome is prosocline, more tangential than radial, round, and not indented by the preceding whorl. An umbilicus is probably present in undamaged specimens but it is probably narrow.

Dimensions. Maximum diameter 2.3 mm.

Soft parts (Figures 13a–d). The pallial cavity comprises almost half a whorl, and its margin is smooth. The single gill is monopectinate, has ca. 20–25 leaflets and is situated in the left half. The presence of sensory bursicles could not be verified, because of problems with mucus. The head-foot is well developed, with a slightly tapering snout and a mainly ventrally situated mouth. The cephalic tentacles are distinctly shorter than the snout when contracted, laterally richly beset with sensory papillae (Figure 13c), have an indistinct basal ventral sheath, and lack eyes. Behind the right cephalic tentacle follows a smooth, claviform and a larger, irregularly shaped, laterally ciliated, fingerlike appendage ("neck tentacles"). Ventrally to the left cephalic tentacle is a large, partly ciliated appendage. The foot is large and flat, posteriorly rounded,

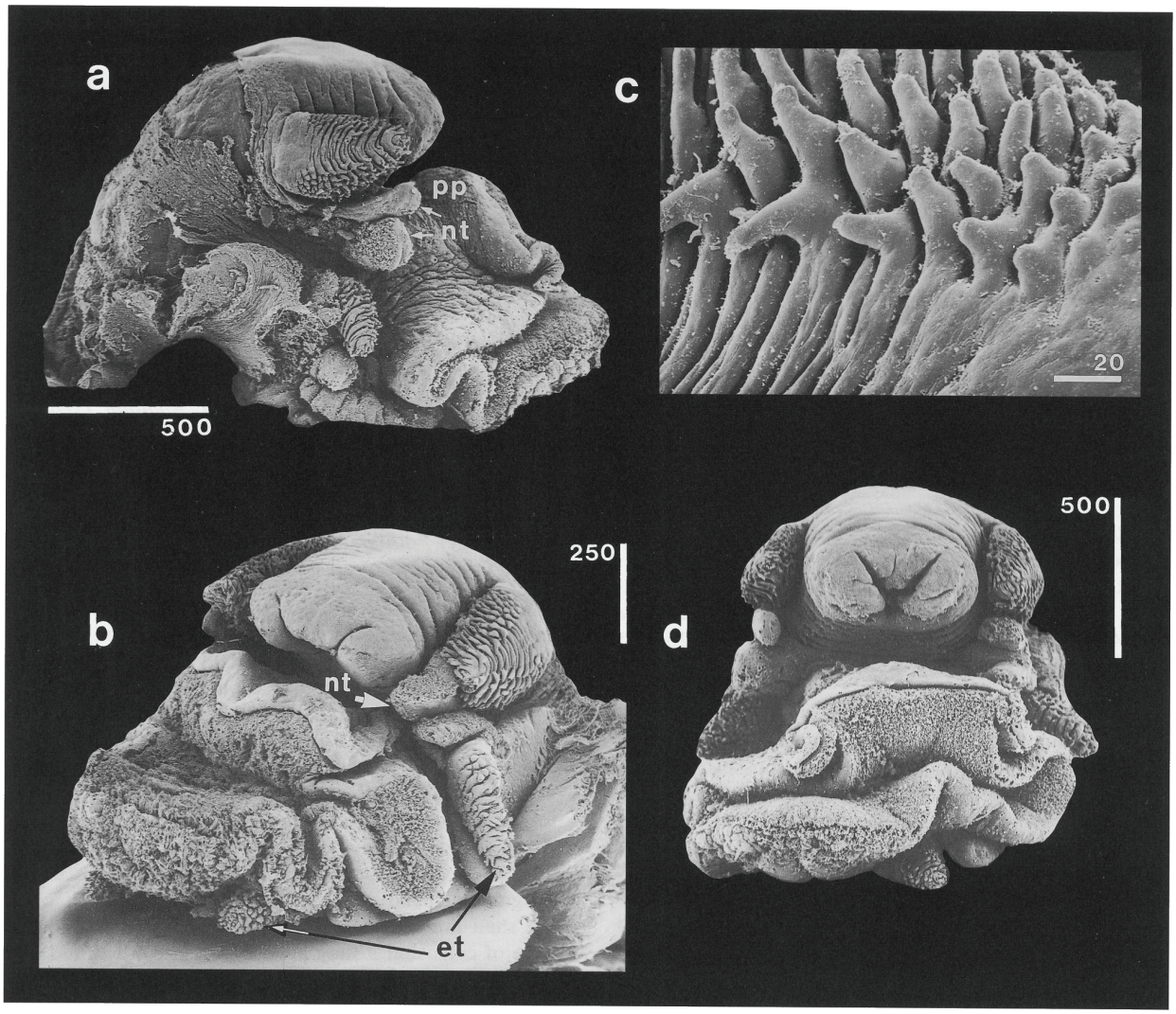


Figure 13. *Bruceiella* ***athlia*** Warén & Bouchet, sp. nov., critical-point dried, Aleutian Seeps, Shumagin site. *a.* right side of head-foot. *b.* Anterolateral view, left side, of head-foot. *c.* Detail of cephalic tentacle. *d.* Head-foot, front view. et - epipodial tentacle; nt - neck tentacle; pp - propodium. Scale bars in μm.

anteriorly truncate, and its corners are drawn out to short tentacles, paralleled by the propodium. The right epipodial arrangement consists of at least four tentacles; the left one seems to have one tentacle less.

Operculum (Figure 16j). Highly multispiral, dull, and opaque with central nucleus.

Radula (Figures 11e, f). n - 4 - 1 - 4 - n, long and slender; sac with bilobed end. The central tooth has a smooth, triangular apical plate; broad, winglike laterobasal processes; and a central projecting ridge. The four laterals are uniformly shaped, with a distinct, basal "elbow" and a weakly serrate, apical triangular plate. The innermost marginal has a lateromarginal plate demarcating its field; the tooth is slender, has a laterally flattened shaft and a notch below the hand-shaped, "7-fingered" apical plate. The second to eighth marginals (Figure 11f, number 6) resemble the first; farther laterally the marginals become more slender with finer and more numerous denticles, a less defined apical plate, and end up as simple membranous "ribbons."

Remarks: *Bruceiella* ***athlia*** closely resembles *B. globulus,* but is larger and has a much broader central tooth in the radula. The central tooth of *B. globulus* also lacks the transverse basal ridge. The outermost whorl of the operculum corresponds to 6% of the diameter in *B.* ***athlia,*** 10% in *B. globulus,* which means that it is almost twice as tightly coiled.

Entoprocts are often attached along the edge of operculum. The gut was filled by detritus.

Superfamily LEPETODRILOIDEA McLean, 1988

Remarks: The systematic position of the lepetodriloids has varied in the literature (McLean, 1988; Haszprunar, 1988; Ponder & Lindberg, 1997; Warén, in press). We follow the classification proposed by Warén (in press), to which we refer for more detailed information.

Family SUTILIZONIDAE McLean, 1989

Remarks: Warén (in press) raised Sutilizoninae to family level to make it equivalent with its assumed sister taxon Lepetodrilidae. At the same time *Temnocinclis* and *Temnozaga* were placed in Sutilizonidae, without any subfamily grouping because of lack of information on some characters.

Sutilizona McLean, 1990

Sutilizona McLean, 1989a:14.

Type species: *S. theca* McLean, 1989; by original designation; EPR, on sulfide mounds near 12°N.

Remarks: *Sutilizona* is now known from the three species below, from the EPR, the JdF, and the MAR. They all share the same shell shape, radular morphology, and protoconch.

Sutilizona theca McLean, 1989

(Figures 17f, i)

Sutilizona theca McLean, 1989a: 15, figs. 3A–C, 4D–F, 5E–F.

New records: *EPR at 13°N:* - HERO 92 dive 2522, 5 spms.

Distribution: EPR, 12–13°N, 2500–2700 m.

Remarks: The largest of the new specimens has a maximum diameter of 2.4 mm; previously recorded maximum size was 1.3 mm. The sculpture varies considerably (Figures 17f, i); some have a much finer sculpture, but the largest specimen, which regrettably was broken, starts out with a coarse sculpture and changes to much finer. *Sutilizona* ***tunnicliffae*** differs from *S. theca* in having weaker axial sculpture and distinct spiral sculpture.

Sutilizona ***pterodon*** Warén & Bouchet, sp. nov.

(Figures 15g; 17c, e, g, h; 18a, f)

Type material: Holotype and 5 paratypes in MNHN.

Type locality: MAR, Snake Pit, Ruches or Elan, ALVIN dive 2619, 23°22.13'N, 44°57.13'W, 3490–3520 m.

Material examined: The types and: *MAR at Snake Pit:* - ALVIN dive 2613, 2 spms; - ALVIN dive 2617, 4 spms; HYDROSNAKE PL 10, retrieval box, 6 spms (shells dissolved).

Distribution: Only known from the MAR, Snake Pit, depth 3470–3520 m.

Etymology: From Greek "pteros" wing and "odous" teeth, referring to the winglike outer marginal teeth.

Description: *Shell (Figures 17c, e, g, h).* Fragile, white with a thin periostracum and covered by thick deposits of bacterially precipitated iron and manganese oxides. The protoconch (Figure 15g) consists of about half a whorl with poorly defined coiling sculptured with strong pits of a diameter of 1–4 μm and to some extent arranged to form a spiral pattern. The diameter is 200 μm, and the protoconch is conspicuously protruding in an apertural view (Figure 15g), although it usually is completely concealed by the deposits. The teleoconch consists of up to 1.2 whorls of rapidly increasing diameter. Initially it is sculptured only by coarse and irregular growth lines; at the beginning of the slit, after ca. ½ a whorl; also some spiral ribs of varying size develop and form an indistinct and irregular network on the last half whorl. Frequently the intersections of the spiral and axial sculpture form small, almost spinelike tubercles. The basal surface of the shell is demarcated by an indistinct keel. The slit is open for a length of about ⅓ of the shell, its earlier part is filled by small scalelike incremental lamellae. The umbilicus is deep and widely open.

Dimensions. Maximum diameter of shell 2.0 mm (holotype).

Operculum extremely thin, membranous, transparent, multispiral with central nucleus and kept folded double in crawling position.

Radula (Figures 18a, f). Similar to *S. theca,* but the central tooth is more narrow. The lateral and marginal fields can hardly be distinguished, but the two fields form a continuous series of laterally more slender and simplified teeth. The outermost marginal tooth is conspicuous in successful preparations, broadly fan-shaped, and with an inner fused tooth looking like a shepherd's crook.

Soft parts. The foot is thick and muscular, simple, anteriorly bluntly rounded, posteriorly more pointed; propodium not visibly set off. The foot has one pair of epipodial tentacles, placed just behind the anterior margin of the operculum. The head is large, with a pair of slender, tapering cephalic tentacles, posteriorly directly followed by an inconspicuous eye-lobe (without eye); no other appendages. The snout is short, slightly tapering, with ventral mouth. The left gill is small, monopectinate with seven leaflets; the right gill is reduced to a group of five small appendages at the extreme part of the corner formed between the slit and the adjoining pallial margin. The length of the gill slit corresponds to ⅓ of the depth

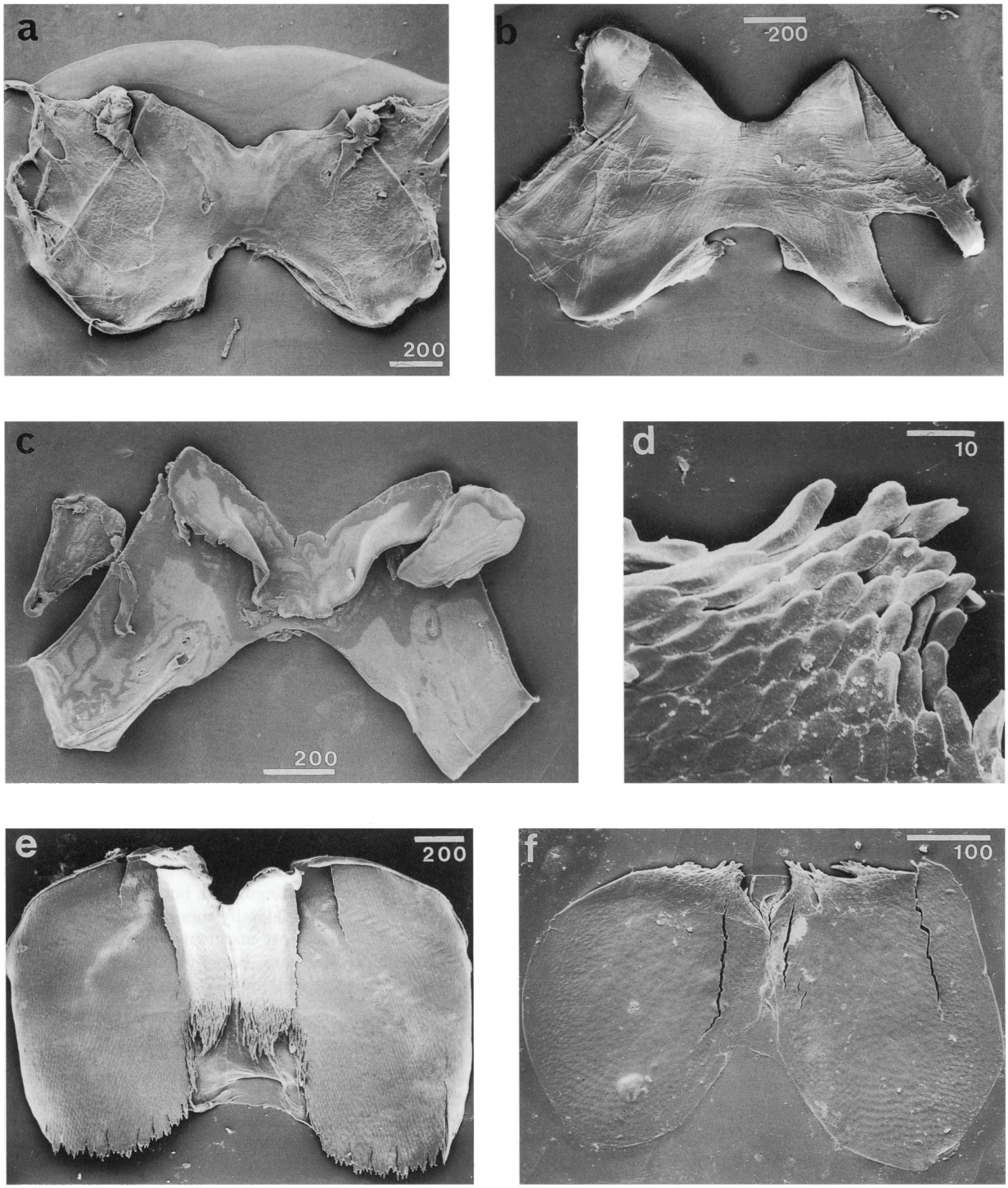


Figure 14. Jaws. *a, b. Neolepetopsis* ***ferrugivora*** Warén & Bouchet, sp. nov., MAR, Lucky Strike. *a.* Inside. *b.* Outside. *c. Eulepetopsis vitrea,* EPR, 13°N, inside. *d, f. Lepetodrilus* ***atlanticus*** Warén & Bouchet, sp. nov., MAR, Lucky Strike. *e. Falsimargarita* ***nauduri*** Warén & Bouchet, sp. nov., holotype. Scale bars in μm.

of the pallial cavity; its sides are furnished with two or three broad and low papillae, basally in the slit is a longer, cylindrical tentacle. There are no sensory papillae anywhere on the body, and the presence of ctenidial bursicles could not be verified.

Remarks: *Sutilizona* ***pterodon*** differs from *S. theca* and *S.* ***tunnicliffae*** in never closing the slit (if our specimens are adult), in having weaker sculpture and in not developing the distinct corner of the teleoconch at the slit. It differs also in its peculiar outer marginal radular teeth. *Sutilizona* ***tunnicliffae*** instead has its outermost four to five marginals much broader and simpler than usual (Figure 18g). The fan-shaped outer marginal can therefore hardly be considered more than a specific apomorphy.

Sutilizona ***tunnicliffae*** Warén & Bouchet, sp. nov.

(Figures 15f; 17d; 18b, d, g)

Type material: Holotype destroyed during examination.

Type locality: JdF, Endeavour Segment: - ROPOS #278, fissure at Main Field, 47°56.9'N, 129°06.9'W, 2202 m.

Material examined: Only known from the type locality.

Distribution: Only known from the type locality.

Etymology: Named after Verena Tunnicliffe.

Description: *Shell (Figure 17d).* Fragile, white with a thin periostracum and covered by thin deposits of iron oxides. The protoconch (Figure 15f) consists of about half a whorl with poorly defined coiling sculptured with strong pits of a diameter of 1–4 μm and to some extent arranged to form a spiral pattern. The diameter is uncertain because of corrosion but has been within the range 165–220 μm. The protoconch is conspicuously protruding in an apertural view. The teleoconch consists of up to 1.1–1.3 whorls of rapidly increasing diameter. Initially it is sculptured only by coarse and irregular growth lines; at the beginning of the slit, after ca. ¼ of a whorl, also some spiral ribs of varying size develop and form an indistinct and irregular network on the last half whorl. The slit is open for a length of about ⅓ of the shell, its earlier part is filled by small scalelike incremental lamellae. The umbilicus is deep and widely open.

Dimensions. Maximum diameter of shell 2.2 mm (holotype).

Operculum extremely thin, membranous, transparent, with central nucleus.

Radula (Figures 18b, d, g). Similar to *S. theca,* but the lateral field is more demarcated. The outermost marginals (Figure 18g) consist of a series of simple and flat teeth with a weak apical crenulation and small basal angle. The demarcation between the lateral and marginal field is unclear, but there are at least two unquestionable lateral teeth. The central tooth is low and broad with three denticles at each side of the main cusp.

Remarks: We have only seen a single, slightly damaged specimen of this species and would probably not have described it, if it did not so nicely show the scissurellid affinities in radular characters. Regrettably the specimen was badly broken when dismounted from the stub.

Temnocinclis McLean, 1989

Temnocinclis McLean, 1989:5.

Type species: *T. euripes* McLean, 1989; by original designation; hydrothermal vents at JdF.

Temnocinclis euripes McLean, 1989

Temnocinclis euripes McLean, 1989a: 7, figs. 1A–H, 4A, 5A–B.

Temnocinclis euripes: Haszprunar, 1989b: 3, fig. 1; Warén, in press.

New records: *JdF,* Explorer Ridge: - ROPOS 284, on a chimney top, 5 spms (Tunnicliffe ref. coll., 1 in MNHN). Megaplume South: - ALVIN dive 2078, 6 spms (Tunnicliffe ref. coll., 3 in MNHN).

Distribution: JdF, at ca. 44–50°N, in ca. 1500–2300 m.

Remarks: There are still some problems with the systematic position of this species (Warén in press), due to lack of well fixed specimens.

Family Lepetodrilidae McLean, 1988

Lepetodrilus McLean, 1988

Lepetodrilus McLean, 1988:6.

Type species: *L. pustulosus* McLean, 1988; by original designation; vents at the EPR.

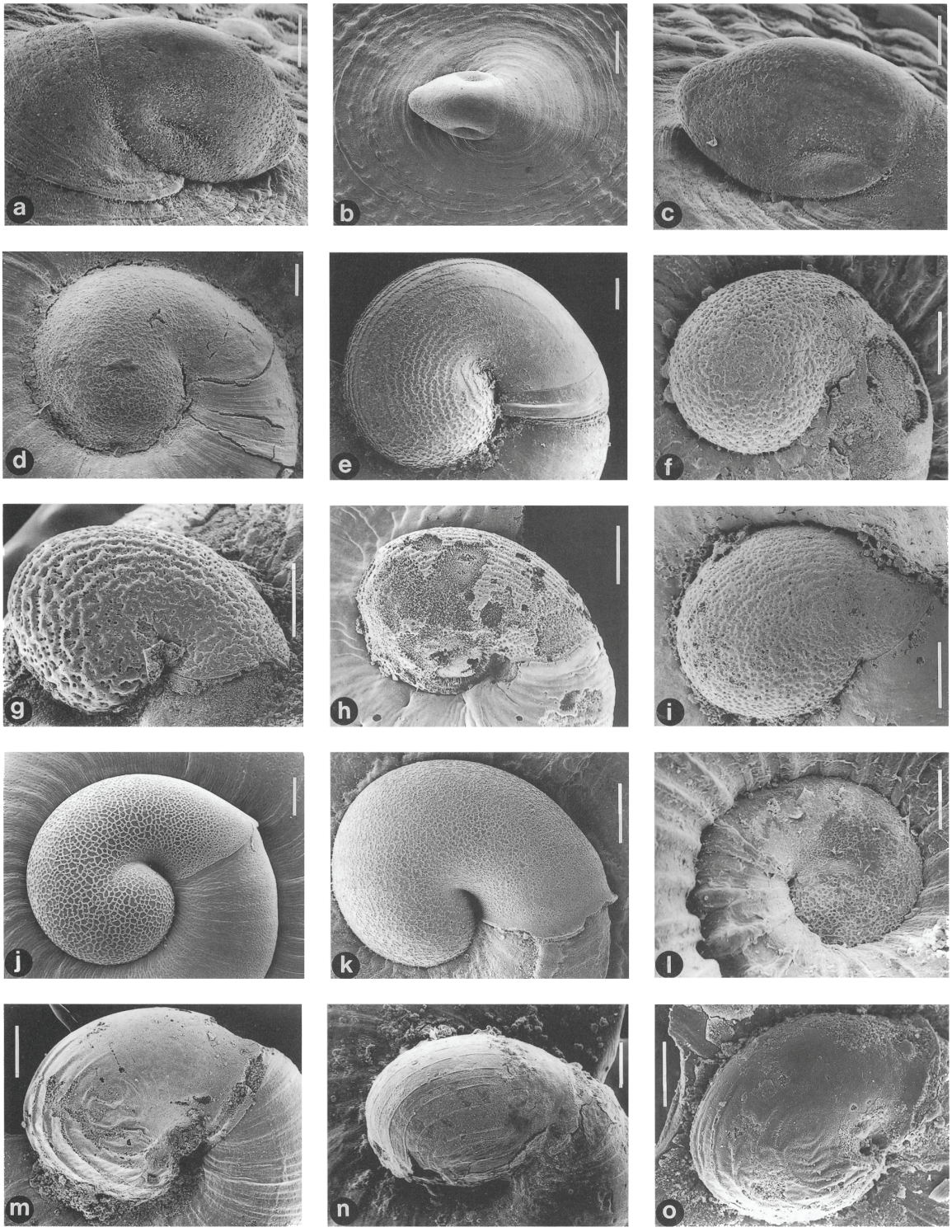
Remarks: The species of *Lepetodrilus* form a morphologically uniform group with only slight variation in shell and gill morphology. Some are difficult to identify as young at the EPR where there may be up to four sympatric species, and we figure a set of young specimens (Figures 22a–e) of the size when they give rise to problems. The species of *Lepetodrilus* often totally dominate the gastropod fauna of the vents at the EPR and MAR. A large sampling at 13°N contained the four species, of which *L. elevatus* formed 91% and the four together 93% of 176.000 specimens.

Lepetodrilus ***atlanticus*** Warén & Bouchet, sp. nov.

(Figures 14d, f, 15i, 19a–f, 20a–d, 21a, b)

Type material: Holotype and ca. 9500 paratypes in MNHN.

Type locality: MAR, Menez Gwen, DIVA 2 PL 16, 37°50.54'N, 31°31.30'W, 860–870 m.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Material examined: The type material and: *MAR, Menez Gwen:* - DIVA 1 PL 13, 1 spm; on active chimney, 38 spms; - DIVA 1 PL 14, on sulfide rock with Hydrozoa, 14 spms; - DIVA 1 PL 16, on base of a black smoker, 19 young; - DIVA 2 PL 11, on mussels, 606 spms; on blocks, 349 spms; suction sample among mussels, 10 spms; - DIVA 2 PL 12, 312 spms; 3 suction samples among mussels, 114, 127, and 149 spms; - DIVA 2 PL 14, 22 spms; suction sample among mussels, 43 spms; on mussels, 78 spms; - MARVEL PL1201, 850 m, 23,950 spms; - MARVEL PL1202, 850 m, suction sample, 722 spms; among mussels, 1700 spms; retrieval box, 1374 spms; - MARVEL PL1203, 850 m, retrieval box, 1804 spms; - MARVEL PL1208, 850 m, retrieval box, 33 spms; - MARVEL PP49, particle trap, 4 spms. *Lucky Strike:* - DIVA 1 PL 01 among mussels, 6 spms; - DIVA 1 PL 03, 8 spms; - DIVA 1 PL 04, on inactive chimney among Hydrozoa and the sponge *Cladorhiza,* 11 spms; - DIVA 1 PL 09, 21 spms; - DIVA 1 PL 17, among mussels, 90 spms; - DIVA 1 PL 18, among mussels, 1 spm; - DIVA 1 PL 19, among mussels, 10 spms; - DIVA 2 PL 01, 3 spms; - DIVA 2 PL 03, 7 spms; - DIVA 2 PL 04, 13 spms; suction sample among mussels in shimmering water, 5 spms; - DIVA 2 PL 05, 2 young; - DIVA 2 PL 06, 3 spms; - DIVA 2 PL 07, 3 young; 2 suction samples among mussels and hydrothermal sediment, 4 and 2 spms; on mussels, 2 spms; - DIVA 2 PL 08, 11 spms; 2 suction samples among mussels and hydrothermal sediments, 1 spm and 1 young; - DIVA 2 PL 09, 2 spms; suction sample among mussels and hydrothermal sediments, 3 spms; - DIVA 2 PL 10, 10 spms; on a rock, 21 spms; 2 suction samples among mussels and hydrothermal sediments, 1 and 10 spms; in retrieval box, 286 spms; - DIVA 2 PL 17, 33 spms; - DIVA 2 PL 19, 5 spms; - DIVA 2 PL 20, 78 spms; - DIVA 2 PL 21, 8 spms; - DIVA 2 PL 25, 8 spms; - DIVA 2 PL 26, 272 spms; - ALVIN dive 2605, 8 spms; - ALVIN dive 2606, 7 spms; - LUSTRE Exp., Tour Eiffel, on mussels, 10 spms; Sintra site, on mussels, 24 spms; - MARVEL PL1191, Bairro Alto, retrieval box, 3 spms; - MARVEL PL1192, Bairro Alto, retrieval box, 1630 m, 4 spms; - MARVEL PL1193, Tour Eiffel, retrieval box, 19 spms; - MARVEL PL1194, Tour Eiffel, retrieval box, 14 shs; - MARVEL PL1195, Tour Eiffel, retrieval box, 29 spms; - MARVEL PL1200, Bairro Alto, 0.25 m^2 rock surface close to edifice, 14 spms; - MARVEL PL1205, Bairro Alto, retrieval box, 10 spms; - MARVEL PL1206, retrieval box, 1700 m, 1 spm. *Snake Pit:* - ALVIN dive 2615, 15 spms.

Distribution: MAR, between 38°N and 23°N, in 850–3500 m depth. Mainly found on mussels and rocks in the vicinity of vents, usually in large quantities.

Etymology: "*atlanticus*" alluding to it being the first species of its genus known from the Atlantic.

Description: *Shell (Figures 19a–f).* Small for the genus, brownish-greenish, rather fragile, ovate and elevated limpet-shaped with overhanging initial part. Protoconch (Figure 15i) irregularly shaped, spirally coiled, but without defined suture. The sculpture consists of irregular, spirally arranged ridges and pits, diameter about 1–4 μm. The maximum diameter of the protoconch is 200 μm. The teleoconch consists of about 1.25 whorls of rapidly increasing diameter, tightly joined to earlier ones, and forming a columellar shelf. The whole shell is covered by a tough, greenish-brownish periostracum, which extends about $1/12$ the width of the aperture across the calcareous peristome. The muscle scars are well demarcated in adult specimens, equally developed on both sides, reach the anterior ¼ of the shell and cross the columellar shelf as a narrow line.

Dimensions. Maximum shell length 7.2 mm.

Soft parts (Figures 20a–d). The foot is rounded, anteriorly somewhat truncated and with a distinctly set-off propodium. It is surrounded by an epipodial membrane with one pair of triangular processes on each side at the posterior ⅓ and a single such process below the anterior part of the shell muscle. The membrane continues anteriorly as a ridge, turns across the shell muscle, and ends in the pallial cavity, when reaching the lateroventral part of the neck. The pallial margin is bilobed, with an inner crenulated lobe, demarcated by a deep fissure where the periostracum is produced. The head is large, with a slightly tapering snout, apical demarcating ridge, and apical-ventral mouth. The cephalic tentacles are conical, slightly longer than the snout in preserved specimens; their base is encircled, ventrally and laterally by a skin flap (tentacle collar). Both males and females have a simple appendage, latero-ventrally at the right base of the snout. The size is variable, from a small plough-shaped skin fold in fe-

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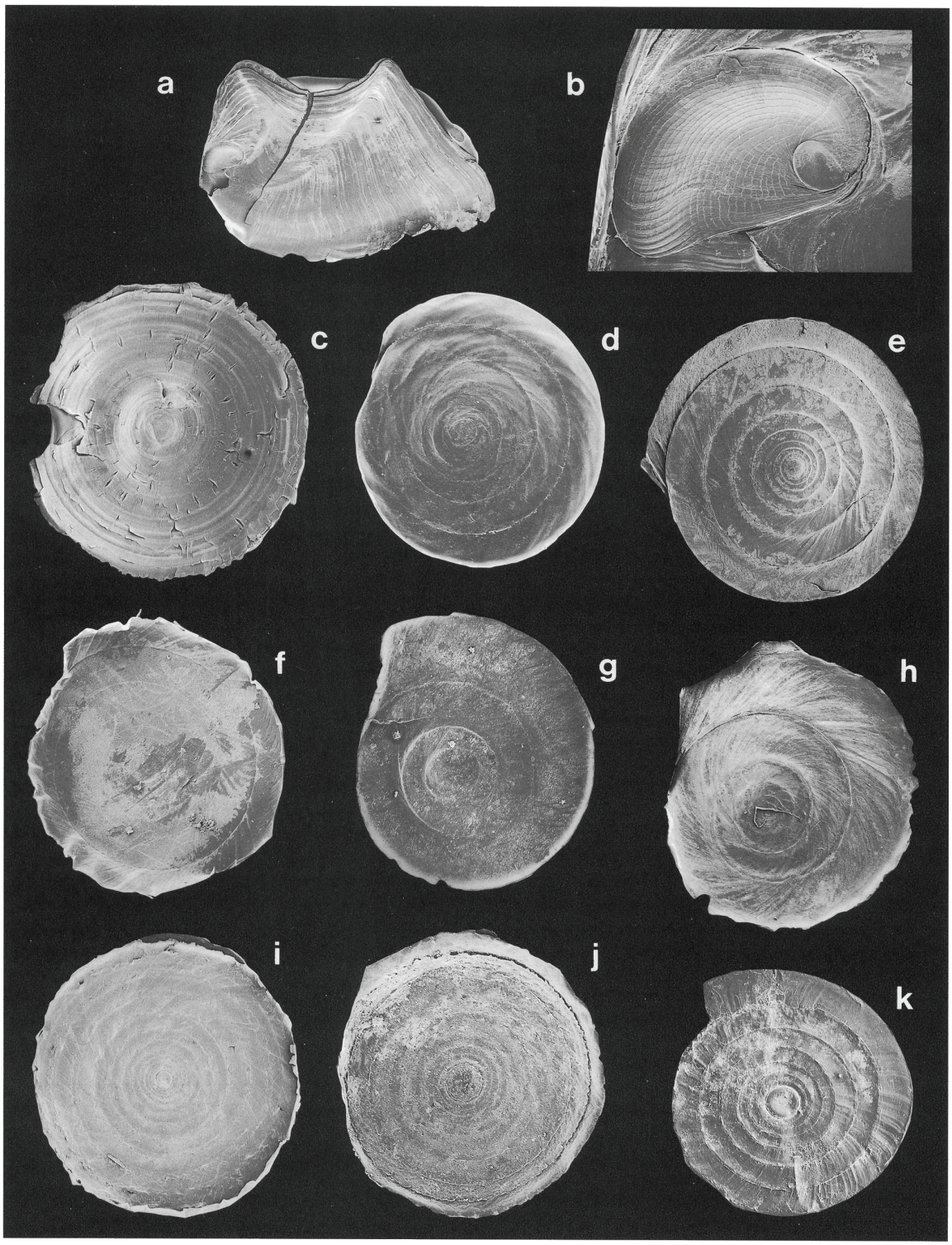
Figure 15. Protoconchs. *a–c. Neolepetopsis densata,* EPR, 13°N. *d.* ***Sahlingia xandaros*** Warén & Bouchet, gen. & sp. nov., Aleutian Seeps, Shumagin site. *e. Bruceiella* ***athlia*** Warén & Bouchet, sp. nov., Aleutian Seeps, Shumagin site. *f. Sutilizona* ***tunnicliffae*** Warén & Bouchet, sp. nov., holotype. *g. S.* ***pterodon*** Warén & Bouchet, sp. nov., holotype. *h. Pseudorimula midatlantica,* MAR, Lucky Strike. *i. Lepetodrilus* ***atlanticus*** Warén & Bouchet, sp. nov., MAR, Menez Gwen. *j.* ***Retiskenea diploura*** Warén & Bouchet, gen. & sp. nov., Aleutian Seeps, Shumagin site. *k. Melanodrymia* ***galeronae*** Warén & Bouchet, sp. nov., paratype. *l. Adeuomphalus* ***trochanter*** Warén & Bouchet, sp. nov., holotype. *m. Lirapex* ***costellata*** Warén & Bouchet, sp. nov., paratype. *n. Peltospira* ***smaragdina*** Warén & Bouchet, sp. nov., MAR, Menez Gwen. *o. Depressigyra globulus,* JdF, Fairy Castle Vent site. Scale bars 50 μm, except Figure b, which is 100 μm.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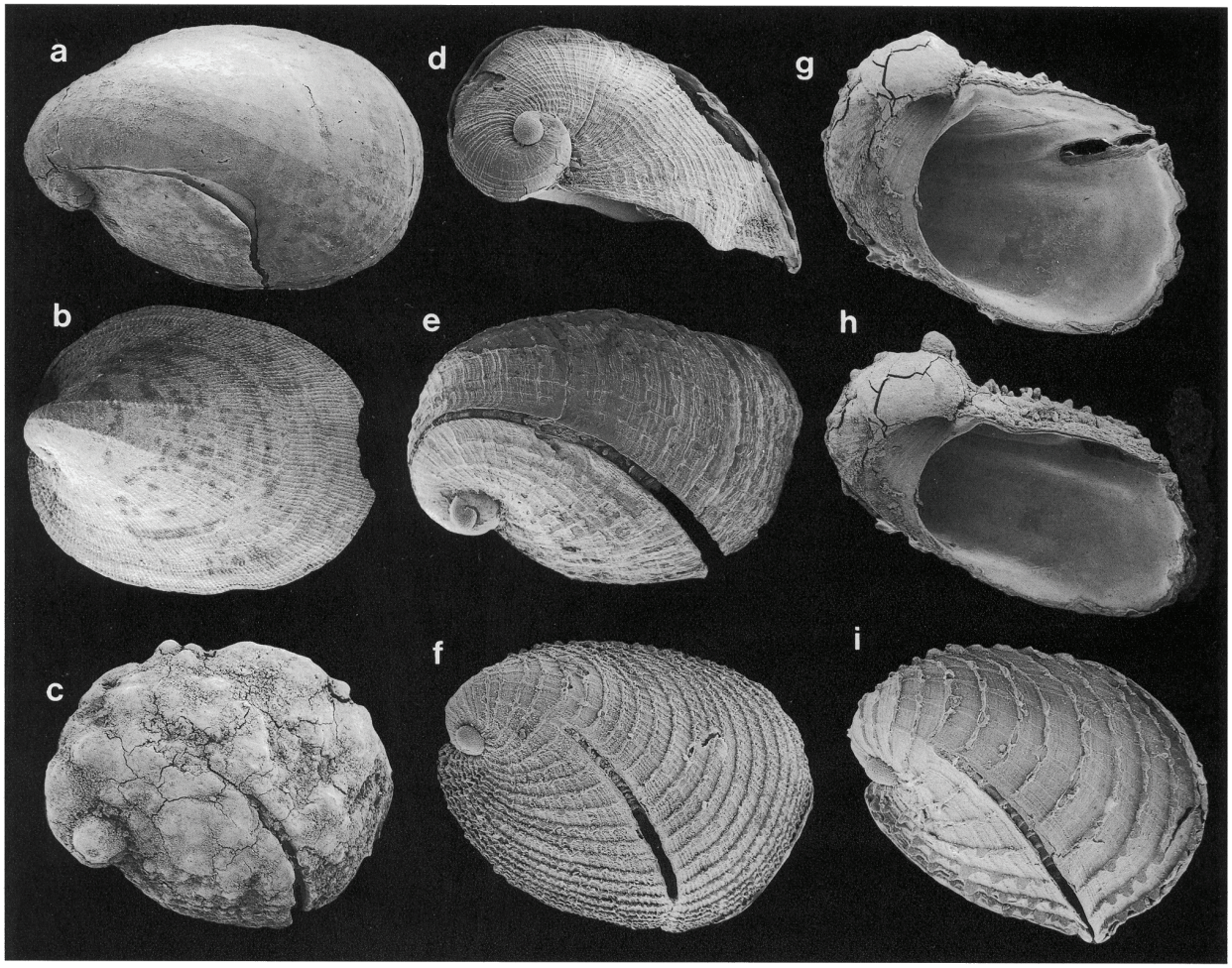

Figure 17. *Gorgoleptis* and *Sutilizona*, shells. *a. G. spiralis*, EPR, 13°N, diameter 3.5 mm. *b. G. emarginatus*, EPR, 13°N, diameter 5.4 mm. *c. S.* ***pterodon*** Warén & Bouchet, sp. nov., MAR, Lucky Strike, shell not cleaned, diameter 2.2 mm. *d. S.* ***tunnicliffae*** Warén & Bouchet, sp. nov., holotype, diameter 2.2 mm. *e. S.* ***pterodon*** Warén & Bouchet, sp. nov., MAR, Lucky Strike, diameter 2.2 mm. *f. S. theca*, EPR, 13°N, diameter 1.8 mm. *g, h. S.* ***pterodon*** Warén & Bouchet, sp. nov., MAR, Lucky Strike, diameter 1.7 mm. *i. S. theca*, EPR, 13°N, diameter 1.5 mm.

males, to comparable to that of the snout in males. A ciliated tract starts from an area one tentacle length posterior to this process, extends forward, covering much of the dorsal side of the organ, and ends between the appendix and the tentacle collar. In males the appendage has a dorsal grove, which continues across the right side of the neck backward to the male pore. At the left ventral side of the neck is a small short tentacle or papilla, as-

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Figure 16. Opercula. *a, b. Shinkailepas* ***briandi*** Warén & Bouchet, sp. nov., MAR, Lucky Strike, maximum diameter 3.8 mm *b.* Detail showing the operculum of the settling veliger, diameter 0.55 mm *c. Falsimargarita* ***nauduri*** Warén & Bouchet, sp. nov., holotype, diameter 4.9 mm. *d. Adeuomphalus* ***trochanter*** Warén & Bouchet, sp. nov., holotype, diameter 1.05 mm. *e. Fucaria* ***mystax*** Warén & Bouchet, sp. nov., holotype, diameter 3.3 mm. *f. Melanodrymia* ***galeronae*** Warén & Bouchet, sp. nov., paratype, diameter 1.07 mm. *g.* ***Retiskenea diploura*** Warén & Bouchet, gen. & sp. nov., holotype, diameter 0.76 mm. *h.* ***Sahlingia xandaros*** Warén & Bouchet, gen. & sp. nov., Aleutian Seeps, Edge site, diameter 3.5 mm. *i. Lirapex* ***costellata*** Warén & Bouchet, sp. nov., MAR, Lucky Strike, diameter 2.0 mm. *j. Bruceiella* ***athlia*** Warén & Bouchet, sp. nov., Aleutian Seeps, Shumagin site, diameter 1.5 mm. *k. Peltospira lamellifera*, EPR, 13°N, diameter 0.94 mm.

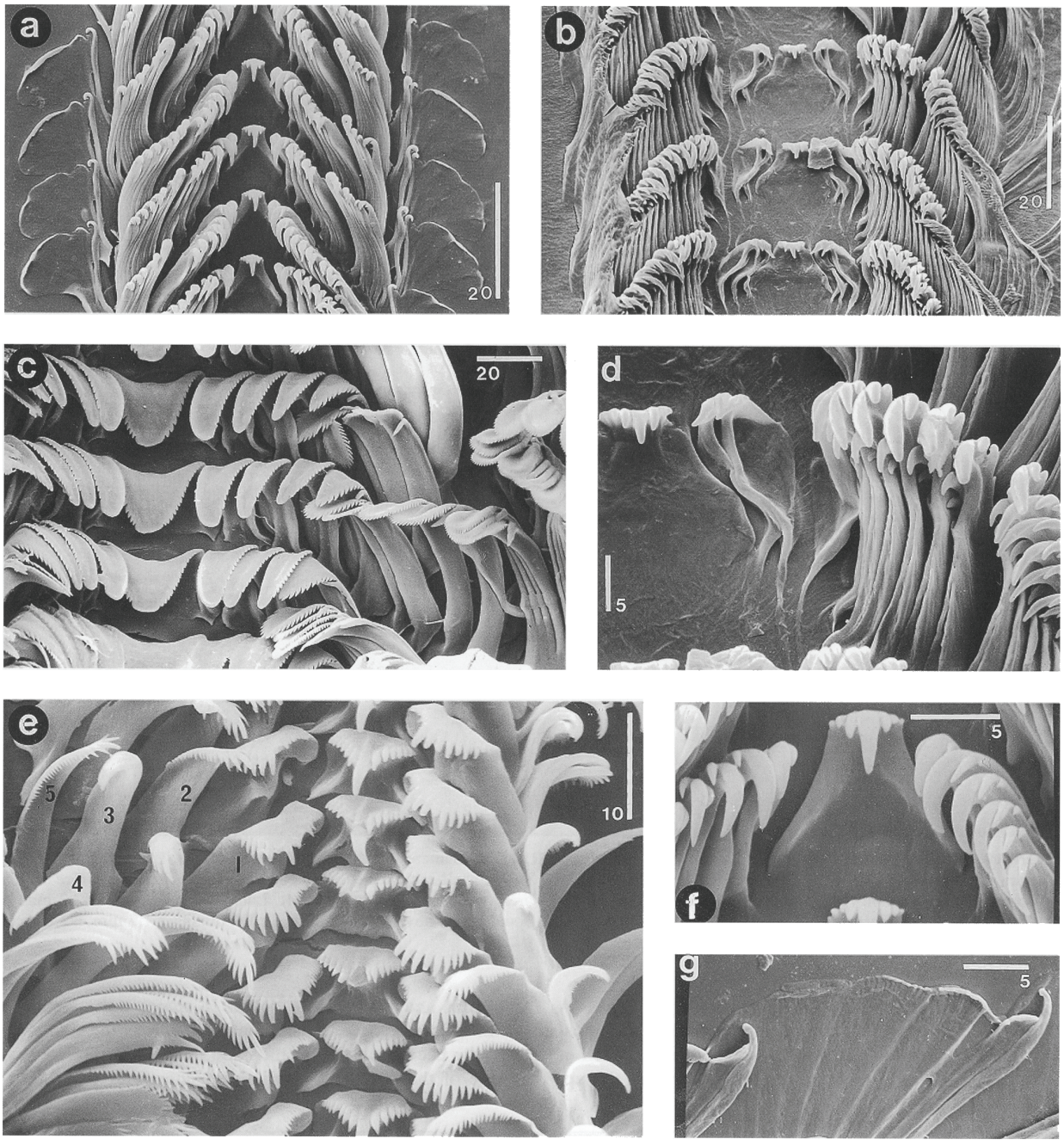


Figure 18. Radulae. Numbers indicate sequential order of teeth with central tooth as 0. *a, f. Sutilizona* ***pterodon*** Warén & Bouchet, sp. nov., MAR, Lucky Strike. *f.* Detail of central tooth. *b, d, g. S.* ***tunnicliffae*** Warén & Bouchet, sp. nov., holotype. *b.* Whole width. *d.* Detail of central field *g.* Detail of outer marginals. *c. Pseudorimula midatlantica,* MAR, Lucky Strike. *e.* ***Retiskenea diploura*** Warén & Bouchet, gen. & sp. nov., Aleutian Seeps, Shumagin site. Scale bars in μm.

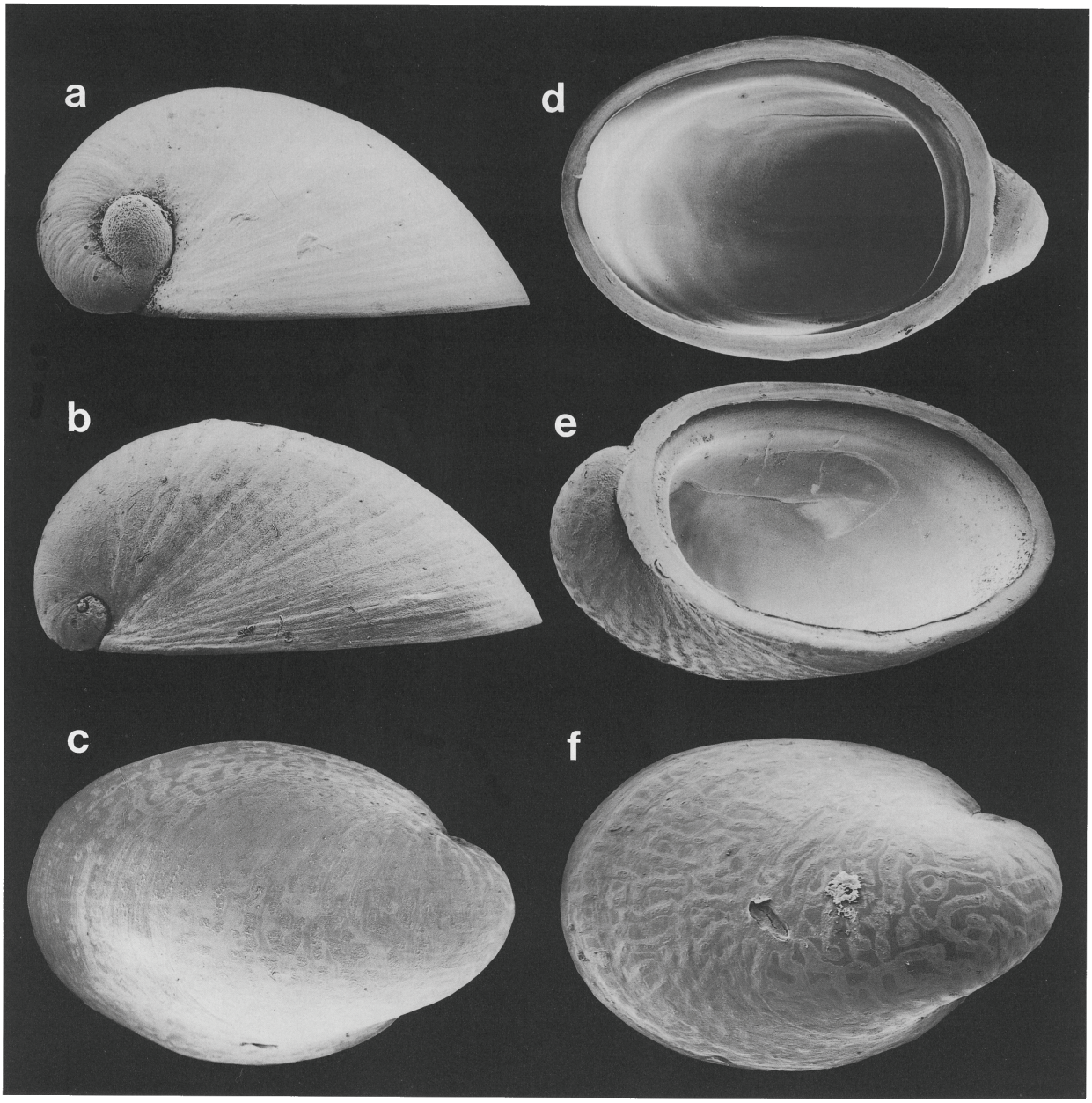


Figure 19. *Lepetodrilus* ***atlanticus*** Warén & Bouchet, sp. nov., MAR, Menez Gwen. *a.* Young specimen, 1.0 mm diameter. *b.* Adult, apical view, 5.9 mm diameter. *c.* Apical view, weakly patterned specimen, 5.7 mm diameter. *d.* Interior, diameter 6.0 mm. *e.* Oblique view of interior, diameter 6.7 mm. *f.* Strongly patterned specimen, diameter 3.4 mm.

sumed to be sensory. The gill is monopectinate and only the efferent axis developed. The leaflets are 0.7 mm wide and 1.3 mm high in a large specimen, slightly more than 50 in number. There is one major afferent vessel, transversing the most posterior part of the pallial skirt, from the rectum toward the gill, where it makes a 90° turn anteriorly, and numerous vessels in the hypobranchial gland, which seem to join the leaflets. The rectum is inconspicuous, very thin, usually empty and flat. To the right of the rectum and fused to it is the pallial part of the gonoduct. The male one is much larger than the female one and reaches up to ⅓ of its length in front of the rectum. The female one parallels ⅔ of the rectum and is inconspicuous. Farther to the right is a low ridge which

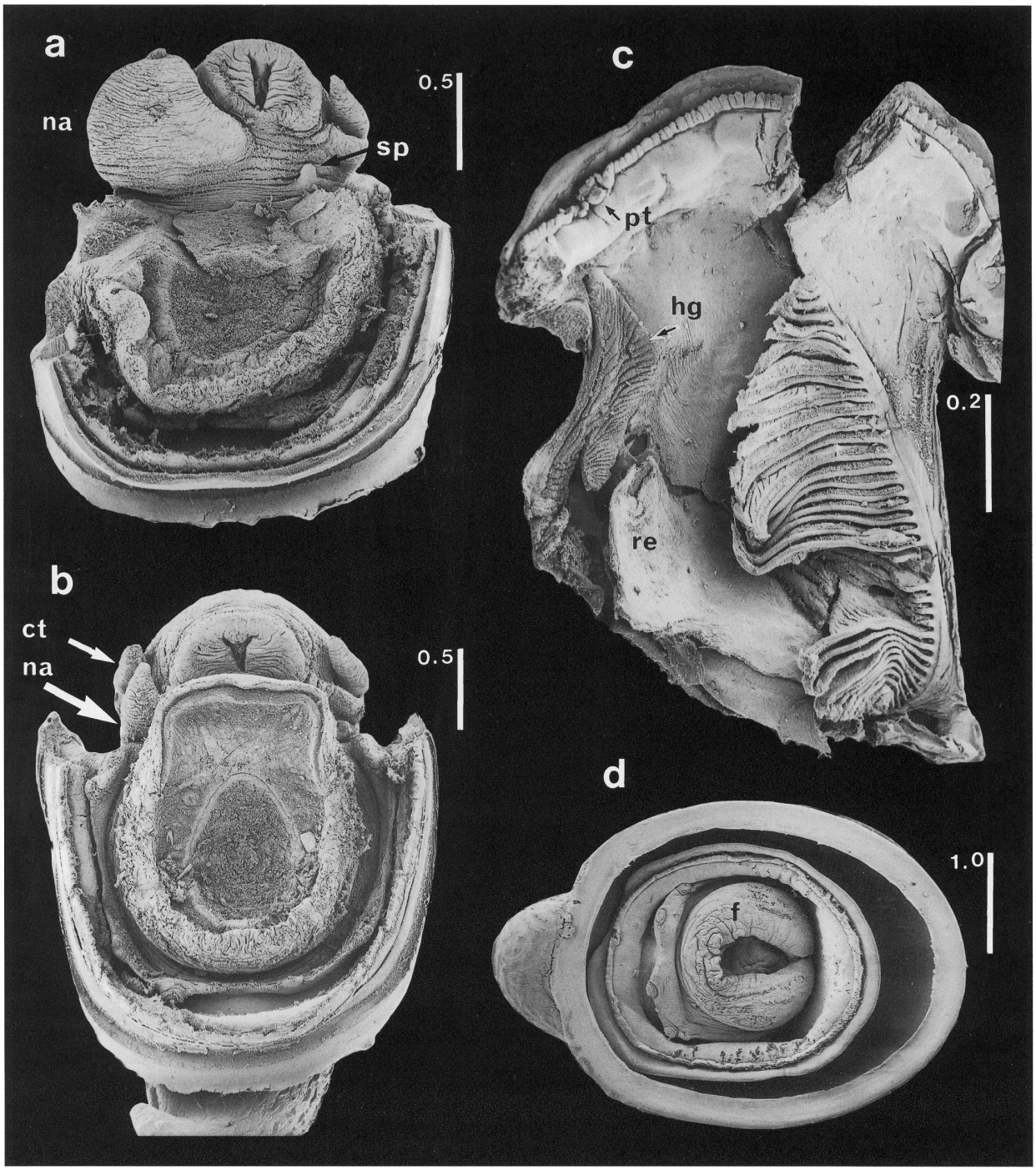


Figure 20. *Lepetodrilus* ***atlanticus*** Warén & Bouchet, sp. nov., critical-point dried, MAR, Menez Gwen. *a.* Male, anterior part of foot removed. *b.* Female. *c.* Pallial skirt; some central leaflets of gill removed. *d.* Animal in shell; normal contraction. ct - cephalic tentacle; f - foot; hg - hypobranchial gland; na - neck appendage; pt - pallial tentacle; re - rectum; sp - sensory papilla. Scale bars in mm.

seems to leave the most posterior part of the gonoduct and cross the pallial skirt to the thickened margin, dorsal to the sensory papilla. It contains a large blood vessel. The posterior part of this ridge has a comblike appearance from numerous small ridges formed by the hypobranchial gland and leaving it at approximately right angle, toward the gonoduct-rectal complex.

Radula (Figures 21a, b). n - 5 - 1 - 5 - n. As described for the genus but the central tooth is very low and sturdy. The first lateral tooth has an evenly serrated, narrow apical plate. The marginals start as rather sturdy, tall teeth with interlocking shafts and serrated, triangular, anteriorly directed apical plate. After about six to seven of these, they gradually transform into tall, narrow, tightly stacked laminar structures with the simple, serrated, ovate apical plate directed 45° from the longitudinal axis of the radula (and the shaft) by a subapical flexure of the shaft. The outer side of the shaft has a conspicuous spine at the base of the plate.

Remarks: About 40 specimens from Menez Gwen and Lucky Strike were sexed by light staining with karm alum, which accentuates the external appearance of the gonad; long acicular lobes in the male; granular in females. No questionable specimens were found, and although the males often are smaller, 0.5–0.7 of the size of the females, there is no indication of protandrous hermaphroditism, and the largest specimen of *L.* ***atlanticus*** (7.2 mm) was a male.

It is quite noticeable that *L.* ***atlanticus*** contracts more firmly when preserved than other species of the genus (Figure 20d). The contents of the gut consist of a mixture of sediment and organic material, possibly of planktonic origin.

Lepetodrilus cristatus McLean, 1988

(Figure 22a)

Lepetodrilus cristatus McLean, 1988: 15, figs. 13, 14, 57–65.
Lepetodrilus cristatus: Fretter, 1988: 53, figs. 11–12.

New records: *EPR at 13°N:* - HERO 91 PL 04, 34 spms; - HERO 91 PL 05, 2 spms; - HERO 91 PL 12, 3 spms; - HERO 91 PL 13, 35 spms; - HERO 91 PL 17, 3 spms; - HERO 91 PL 19, 1 spm; - HERO 91 PL 21, 1 spm; - HERO 91 PL 22, 1 spm; - HERO 91 PL 23, 1 spm; - HERO 91 PL 25, 4 spms; - HERO 92 dive 2514, 4 spms; - HERO 92 dive 2516, 3 spms; - HERO 92 dive 2517, 7 spms; - HERO 92 dive 2520, 1 spm; - HERO 92 dive 2521, 3 spms; - HERO 92 dive 2522, 22 spms; - HERO 92 dive 2523, 10 spms; - HERO 92 dive 2524, 1 spm; - HERO 92 dive 2528, 1 spm; - HERO 92 dive 2531, 2 spms.

Distribution: EPR at 21°N and 13°N, and the Galapagos Rift in 2500–2600 m depth.

Remarks: Almost all specimens were obtained from the retrieval box after recovery of tubes of Vestimentifera.

Lepetodrilus elevatus McLean, 1988

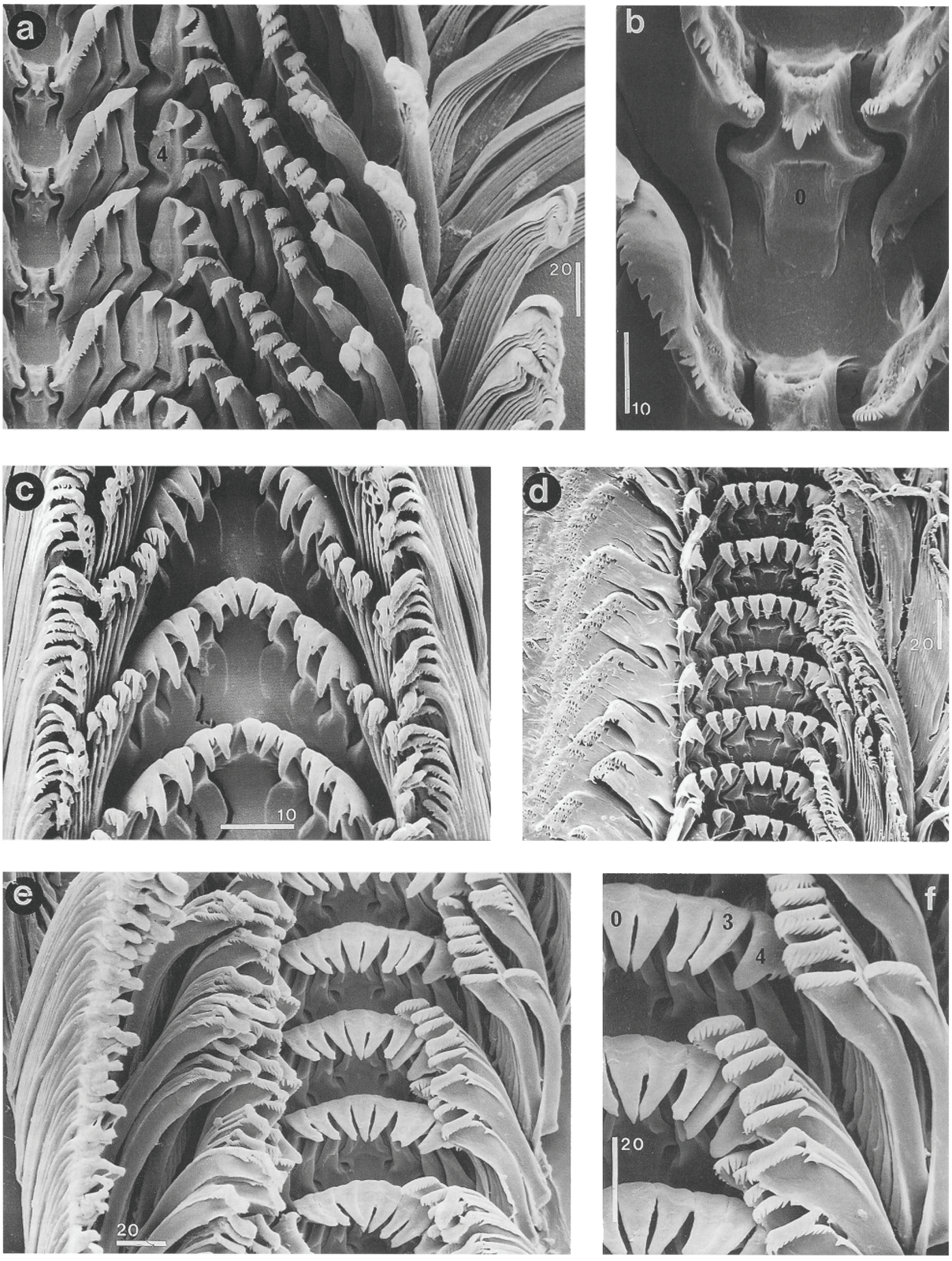
(Figure 22c)

Lepetodrilus elevatus McLean, 1988:11, figs. 5, 6, 36–44.
Lepetodrilus elevatus: Fretter, 1988:49, figs. 7–8; McLean 1993:32, figs. 17–25; Beck, 1993:175.

New records: *EPR at 13°N:* - HERO 91 PL 09, 7 spms; - HERO 91 PL 10, 5526 spms; Genesis, 201 spms; - HERO 91 PL 11 (Genesis), 175 spms; - HERO 91 PL 12, 8900 spms; - HERO 91 PL 13 (Elsa), 3462 spms; - HERO 91 PL 17, 12063 spms; - HERO 91 PL 19, 1250 spms; - HERO 91 PL 21, 11773 spms; - HERO 91 PL 23, 4025 spms; - HERO 91 PL 24 (Elsa), 79 spms; - HERO 91 PL 25, 23 spms; - HERO 91 PL 26, 17000 spms; - HERO 91 PL 27, 20 spms; - HERO 92 dive 2512, 12440 spms; - HERO 92 dive 2514, 7340 spms; - HERO 92 dive 2516, 4440 spms; - HERO 92 dive 2517, 9968 spms; - HERO 92 dive 2519, 1800 spms; - HERO 92 dive 2520, 7100 spms; - HERO 92 dive 2521, 6290 spms; - HERO 92 dive 2522, 4050 spms; - HERO 92 dive 2523, 6370 spms; - HERO 92 dive 2524, 3000 spms; - HERO 92 dive 2525, 9700 spms; - HERO 92 dive 2526, 6700 spms; - HERO 92 dive 2528, 6900 spms; - HERO 92 dive 2531, 12840 spms; - HERO 92 dive 2532, 6830 spms. *EPR at 09°50'N:* - HERO 91 PL 09, 1 spm. *EPR at 17°S:* - NAUDUR PL 06, site Rehu, 50 spms; - NAUDUR PL 12 (Animal Farm), 1 spm; - NAUDUR PL 18 (Le Chat), 3 spms; - NAUDUR PL 18, site Rehu, 11 spms.

Distribution: Uncertain, see below. It does, however, seem certain that *L. elevatus* follows the EPR from 21°N to 17°S and also is present at the Galapagos rift (subspecies *galriftensis* McLean, 1988), at a depth of 2400–2700 m. Almost all specimens above come from tubes of Vestimentifera.

Remarks: McLean (1993) recorded *L. elevatus* from the Mariana Trough and noticed that a penis was absent. Warén & Bouchet (1993) recorded it from the North Fiji and Lau Basins. Beck (1993) found that none of 38 specimens from the Mariana Trough had a penis and questioned these identifications. We examined some 25 males from the North Fiji Basin (YOKOSUKA material) and found that most lack a penis, although scattered specimens have it well developed and several have more than the trace that is present in females. Beck (1993, in press) discussed the possibility of periodic reproduction and corresponding development of the penis, but at present there is no information to support this because we found that the gonads of the YOKOSUKA males were full and contained mature sperm also in specimens lacking a penis. These details, however, make the records from the western Pacific unreliable, and although we tentatively reidentify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them as *L. schrolli,* they should not be used for zoogeographic and similar discussions. The specimens from the EPR at 17°S do have a penis. Based on genetical distances, Craddock et al. (1997) hypothesized a low dispersal between populations of *L. elevatus* from the EPR.

It is also worth noticing that the proportions between the sexes vary considerably from one site to another (44–65% females in three samples of about 150 specimens each from three adjacent localities at EPR, 13°N). The gonad and male reproductive organ seem to become functional at a size between 2.5 and 3 mm. Also the size is somewhat variable. HERO 91 PL 13 hit a spot with an average size of 9–10 mm and a maximum size of 12.5 mm, while an average size of 5.5 mm and a maximum size of 6–7 mm is normal. The soft parts of these larger specimens agreed perfectly with those from other localities (outer part of gill bipectinate; penis present; sensory neck tubercle present).

The huge quantities of *L. elevatus* were obtained from vestimentiferan tubes, which are the main habitat of *L. elevatus.*

Lepetodrilus guaymasensis McLean 1988

Lepetodrilus guaymasensis McLean, 1988:16, figs. 15, 16, 66–74.
Lepetodrilus guaymasensis: Fretter, 1988:54, figs. 13–14.

New records: *Guaymas Basin:* - GUAYANAUT PL 07, 5 spms; - GUAYANAUT PL 15, 1 spm; - GUAYANAUT PL 17, 1 spm.

Distribution: Only known from the Gulf of California, Guaymas Basin, at about 2000 m depth.

Remarks: Fretter (1988:fig. 13) mentioned a pair of small post-tentacular appendages at the left side of the neck of males in this species. We have not been able to find them.

Lepetodrilus ovalis McLean, 1988

(Figure 22b)

Lepetodrilus ovalis McLean, 1988:14, figs. 9–12, 51–56.
Lepetodrilus ovalis: Fretter, 1988:50, figs. 8–10.

New records: *EPR at 13°N:* - HERO 91 PL 11 (Genesis), 3 spms; - HERO 91 PL 12, 1 spm; - HERO 91 PL 17, 1 spm; - HERO 91 PL 26, 1 spm; - HERO 92 dive 2517, 22 spms; - HERO 92 dive 2519, 1 spm; - HERO 92 dive 2523, 1 spm; - HERO 92 dive 2528, 22 spms; - HERO 92 dive 2531, 1 spm; - HERO 92 dive 2532, 2 spms. *EPR at 09°50'N:* - HERO 91 PL 09, 21 spms. *EPR at 17°S:* - NAUDUR PL 06, Rehu, 111 spms; on mussels, 6 spms.

Distribution: EPR from 21°N to 17°S, at ca. 2500–2600 m depth. The specimens above were recovered from tubes of vestimentifera and from mussels.

Remarks: This species can be recognized by the presence of a small "sensory" tubercle at the ventral, right side of the neck; not the left as in other species with such a tubercle.

Lepetodrilus pustulosus McLean, 1988

(Figures 22d–e)

Lepetodrilus pustulosus McLean, 1988:8, figs 1–4, 25–35.
Lepetodrilus pustulosus: Fretter, 1988:35, figs 1–6.

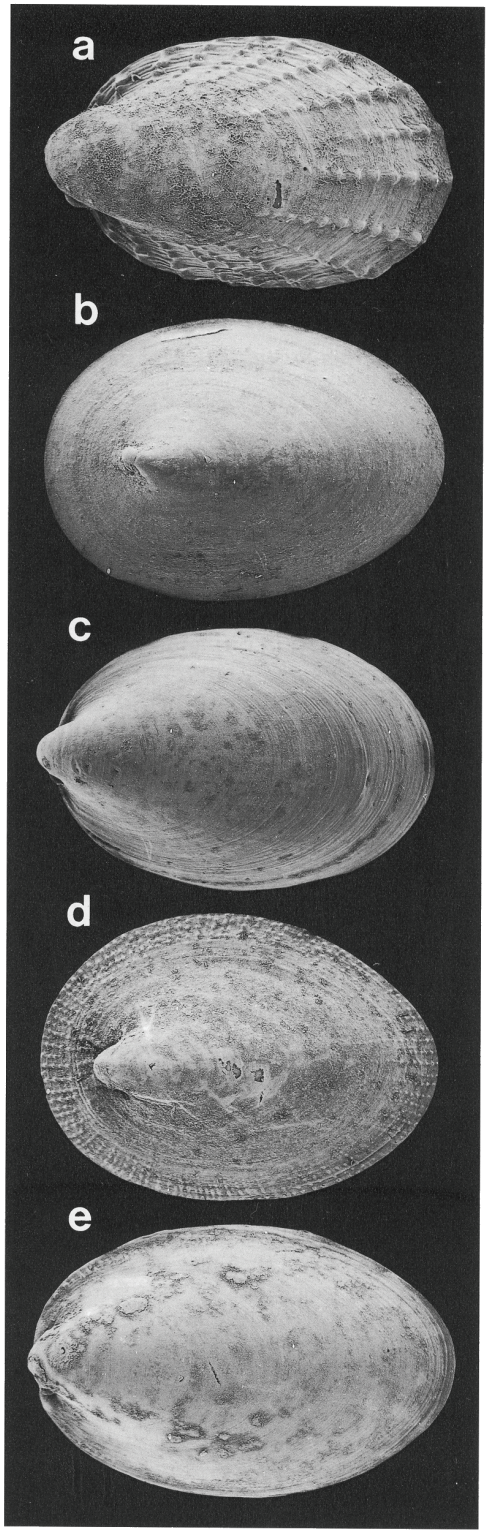
New records: *EPR at 13°N:* - HERO 91 PL 10 (Genesis), a few hundred spms; - HERO 91 PL 11 (Genesis), 10 spms; - HERO 91 PL 12, 12 spms; - HERO 91 PL 13, 37 spms; - HERO 91 PL 17, 103 spms; - HERO 91 PL 19, 41 spms; - HERO 91 PL 21, 276 spms; - HERO 91 PL 22, 137 spms; - HERO 91 PL 24 (Elsa), 3 spms; - HERO 91 PL 25, 2 spms; - HERO 91 PL 26, 81 spms; - HERO 91 PL 27, 3 spms; - HERO 92 dive 2512, 357 spms; - HERO 92 dive 2514, 233 spms; - HERO 92 dive 2516, 42 spms; - HERO 92 dive 2517, 188 spms; - HERO 92 dive 2519, 41 spms; - HERO 92 dive 2520, 104 spms; - HERO 92 dive 2521, 125 spms; - HERO 92 dive 2522, 14 spms; - HERO 92 dive 2523, 245 spms; - HERO 92 dive 2525, 232 spms; - HERO 92 dive 2526, 169 spms; - HERO 92 dive 2528, 93 spms; - HERO 92 dive 2531, 197 spms; - HERO 92 dive 2532, 168 spms. *EPR at 17°S:* - NAUDUR PL 06, site Rehu, 2 spms; - NAUDUR PL 18 (Gwen Meur), 2 spms; Le Chat, 8 spms; Rehu, 3 spms; - NAUDUR PL 04.8b, site Rehu, 10 spms.

Distribution: EPR from 21°N to 17°S, at about 2600 m depth. Most specimens were recovered from tubes of vestimentifera.

Remarks: Young specimens of *Lepetodrilus pustulosus* may be difficult to identify, because there is a considerable variation in shell shape. Up to a size of about 1 mm they are short and broad with a distinct spire and resemble *Gorgoleptis spiralis.* Then they become more slender, up to 2–2.5 mm in length, but still the "spire" is touching the posterior shell margin. At this size the species resembles *L. elevatus.* At 2.5–3 mm in length the "spire" starts

←

Figure 21. Radulae. *a, b.* Numbers indicate sequential order of teeth with central tooth as 0. *Lepetodrilus* ***atlanticus*** Warén & Bouchet, sp. nov., MAR, Menez Gwen. *a.* Half width. *b.* Detail of central and first lateral teeth. *c. Melanodrymia* ***galeronae*** Warén & Bouchet, sp. nov., paratype. *d. Melanodrymia* sp., "rust covered," EPR, 13°N, Caldera. *e, f. Peltospira* ***rigneae*** Warén & Bouchet, sp. nov., holotype. *e.* Whole width. *f.* Detail of marginals. Scale bars in μm.



its relative movement toward the center of the shell, and in adult specimens its posterior margin is situated 1/5 from the posterior shell margin. The pustulose sculpture starts its development at the same time as the change in shape starts. This ontogenetic change in shell shape varies between different localities, at some it starts earlier, at others later. The consequence of this is that in some cases different populations have the "spire" situated more or less close to the posterior margin when specimens of the same size are compared (Figures 22d–e.) The shape of the shell closely resembles young specimens of *L. ovalis* (Figure 22b), but that species has a perfectly smooth shell at a size of 2–4 mm, when there is risk for confusion. *Lepetodrilus cristatus* is easy to separate because of its much stronger sculpture (Figure 22a). Based on genetical distances, Craddock et al. (1997) hypothesized a high dispersal between populations of *L. pustulosus* from the EPR.

Lepetodrilus fucensis McLean, 1988

Lepetodrilus fucensis McLean, 1988:18, figs. 17–20, 75–83.

New records: *JdF, Axial Seamount:* - ROPOS 406, 10 spms (FMNH 280890).

Distribution: Most localities investigated at the JdF, ca. 1500–2200 m.

Remarks: The basal plane of the shell of *L. fucensis* is more irregular than in any other species of the genus, probably indicating a more sedentary life.

Gorgoleptis McLean, 1988

Gorgoleptis McLean, 1988:19.

Type species: *G. emarginatus* McLean, 1988; by original designation; hydrothermal vents at the EPR.

Remarks: All species of *Gorgoleptis* keep the operculum until just below the maximum size. The species are usually rare, much more so than the species of *Lepetodrilus*. We figure shells of *G. emarginatus* and *G. spiralis* to supplement McLean's figures; our single specimen of *G. patulus* is too poor for figuring.

Gorgoleptis emarginatus McLean, 1988

(Figure 17b)

Gorgoleptis emarginatus McLean, 1988:22, figs. 21–24, 84–92.

←

Figure 22. *Lepetodrilus* spp. young specimens *a. L. cristatus,* EPR, 13°N, 1.9 mm. *b. L. ovalis,* EPR, 13°N, 2.4 mm. *c. L. elevatus,* EPR, 13°N, 2.6 mm. *d. L. pustulosus,* EPR, 13°N, 3.2 mm. *e. L. pustulosus,* EPR, 13°N, 2.9 mm. Notice the start of radial sculpture at the posterior end. The initiation of this sculpture coincides with the beginning displacement of the apex toward the center.

Gorgoleptis emarginatus: Fretter, 1988:58, figs. 16–17.

New records: *EPR at 13°N:* - HERO 91 PL 10, 2 spms; - HERO 91 PL 11 (Genesis), 2 spms; - HERO 92 dive 2517, 2 spms; - HERO 92 dive 2528, 1 spm.

Distribution: EPR at 21°N to 09°50'N, about 2600 m depth, mostly from vestimentiferan tubes.

Remarks: *Gorgoleptis emarginatus* was earlier known only from 21°N. Typical features are the slender and evenly tapering labial penis, flat and broad shell, and narrow periostracal strip at the columella.

The larva of *Gorgoleptis* sp. was identified in plankton samples taken a few meters above the sea floor at the EPR at 09°50'N (Mullineaux et al., 1996).

Gorgoleptis spiralis McLean, 1988

(Figure 17a)

Gorgoleptis spiralis McLean, 1988:23, figs. 93–97.
Gorgoleptis spiralis: Fretter, 1988:64, fig. 18b–c.

New records: *EPR at 13°N:* - HERO 91 PL 19, 1 spm; - HERO 92 dive 2517, 44 spms; - HERO 92 dive 2523, 1 spm; - HERO 92 dive 2526, 1 spm; - HERO 92 dive 2528, 14 spms.

Distribution: EPR at 13°N, ca. 2630 m, from vestimentiferan tubes.

Remarks: This species was described from three specimens in not very good condition. The maximum size in our material is 4.4 mm. A good character to recognize males of this species is the penis which is not evenly tapering as in *G. emarginatus* but ends in an uneven bifurcation with a larger, urn-shaped limb (Warén, in press: fig. 7b, d). The shell is almost smooth, with some indistinct indications of spiral lines.

Gorgoleptis patulus McLean, 1988

Gorgoleptis patulus McLean, 1988:24, figs. 98–102.
Gorgoleptis patulus: Fretter, 1988:65, figs. 18b, c; Warén in press.

New records: *EPR at 13°N:* - HERO 91 PL 19, 1 spm, from tubes of vestimentifera.

Distribution: EPR at 13°N, ca. 2600 m depth.

Remarks: The specimen is not in good condition and the identification is tentative. It does however have the narrow strip of periostracum at the rear end of the body, not a semicircular zone as in *G. spiralis,* although the shell is more similar to this species than to *G. emarginatus.* The length of the shell is 4.6 mm, considerably larger than the two specimens on which the name was founded (2.8 mm).

Clypeosectus McLean, 1989

Clypeosectus McLean, 1989:17.

Type species: *C. delectus* McLean, 1989; by original designation; hydrothermal vents at the Galapagos Rift.

Clypeosectus delectus McLean, 1989

Clypeosectus delectus McLean, 1989a:18, figs. 7A–H, 8A–H, 9A–F, 11A–E.
Clypeosectus delectus: Haszprunar, 1989b:5, fig. 4; Warén, in press.

New records: *EPR at 13°N:* - HERO 92 dive 2516, 2 spms; - HERO 92 dive 2521, 1 spm; - HERO 92 dive 2523, 1 spm; - HERO 92 dive 2528. 1 spm; - HERO 92 dive 2532, 1 spm. *EPR at 17°S:* - NAUDUR PL 06, site Rehu, 6 spms.

Distribution: EPR from 21°N to 17°S and the Galapagos Rift, ca. 2400–2600 m from vestimentiferan tubes.

Remarks: The larva of *Clypeosectus delectus* was identified in plankton samples taken a few meters above the sea floor at the EPR at 09°50'N (Mullineaux et al., 1996).

Clypeosectus curvus McLean, 1989

Clypeosectus curvus McLean, 1989a:21, figs. 10A–H, 11F.

New records: *JdF, Axial Seamount,* Ashes vent field: - ROPOS R406, 2 spms (FMNH 280887).

Distribution: JdF, 1500–2200 m depth.

Pseudorimula McLean, 1989

Pseudorimula McLean, 1989a:22.

Type species: *P. marianae* McLean, 1989; by original designation; vents at the Mariana Back Arc Basin.

Remarks: There are two known (and one undescribed, Beck, personal communication) species of the genus, both of a fairly uniform shell morphology. The main difference between *P. marianae* and *P. midatlantica* is that the right part of the shell muscle forms a single entity of even thickness in the latter, while it is divided in two main parts in *P. marianae.*

Pseudorimula midatlantica McLean, 1992

(Figures 15h, 18c, 23a–h)

Pseudorimula midatlantica McLean, 1992a:116, figs. 1–7.
Pseudorimula midatlantica: Warén, in press.

New records: *MAR, Lucky Strike:* - DIVA 1 PL 09, 1 spm; - DIVA 1 PL 19, among mussels, 2 spms; - DIVA 2 PL 01, 9 spms; - DIVA 2 PL 02, 2 spms; - DIVA 2 PL 04, 3 spms; - DIVA 2 PL 05, 5 spms; - DIVA 2 PL 07,

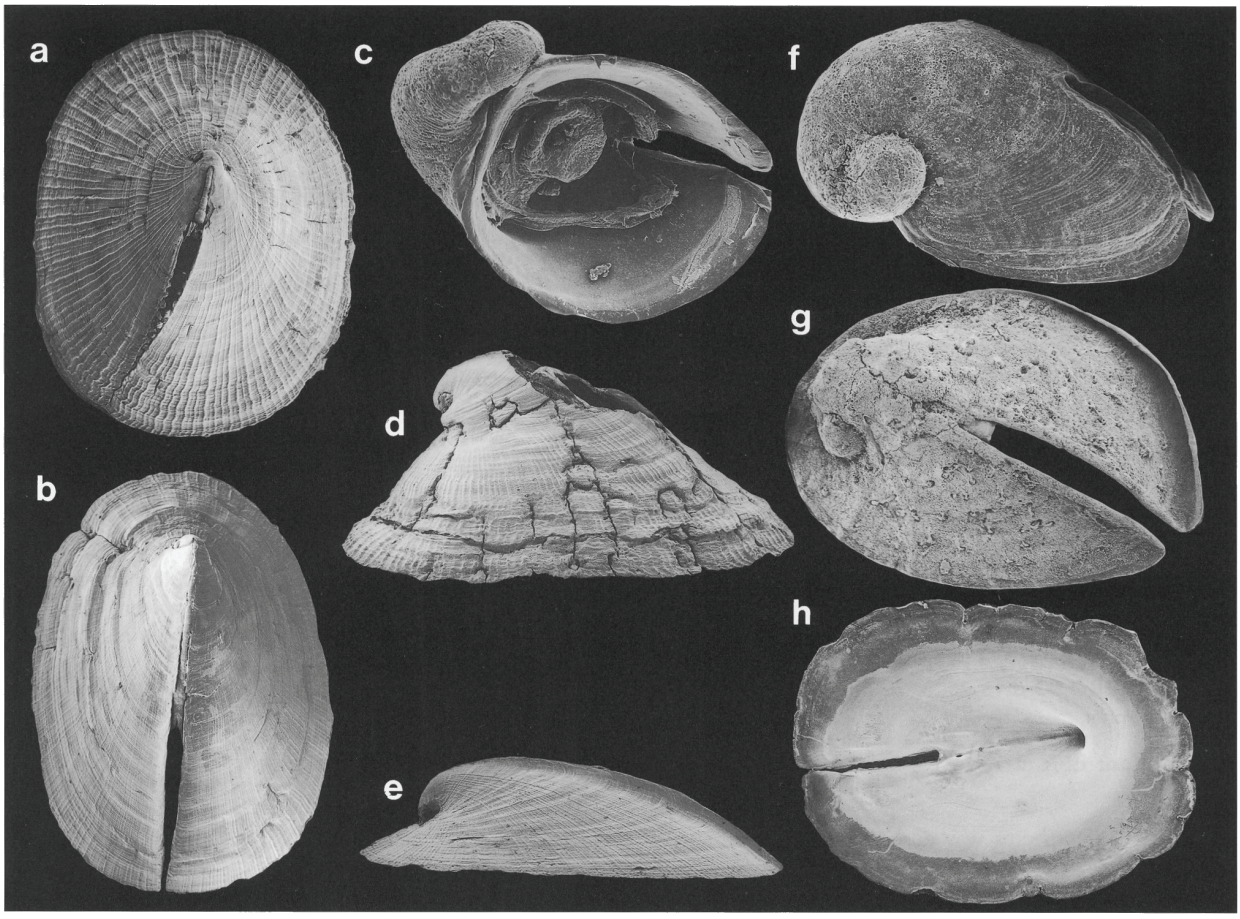


Figure 23. *Pseudorimula midatlantica,* MAR, shell morphology. *a.* Menez Gwen, diameter 6.6 mm. *b.* Lucky Strike, diameter 6.3 mm. *c.* Young specimen, Lucky Strike, diameter 0.75 mm. *d.* Cleaned shell, damaged by corrosion and repaired, apical part of slit enlarged, Lucky Strike, diameter 4.9 mm. *e.* Unusually flat specimen. Lucky Strike, diameter 8.4 mm. *f.* Young specimen, Lucky Strike, diameter 0.7 mm. *g.* Half grown specimen, not cleaned, Lucky Strike, diameter 2.4 mm. *h.* Inside, Lucky Strike, diameter 7.7 mm.

1 young; - DIVA 2 PL 10, on a rock, 1 spm; in retrieval box, 1 spm; - DIVA 2 PL 20, 9 spms; - DIVA 2 PL 21, 1 spm; - DIVA 2 PL 24, 5 spms; - LUSTRE Exp. Tour Eiffel, on mussels, 5 spms; - Sintra site, on mussels, 2 spms; - MARVEL PL1191, Bairro Alto, retrieval box, 1 spm; - MARVEL PL1192, Bairro Alto, retrieval box, 1630 m, 2 spms; - MARVEL PL1193, Tour Eiffel, retrieval box, 1 spm; on *Bathymodiolus,* 3 shs; - MARVEL PL1200, Bairro Alto, 0.25 m^2 rock surface close to edifice, 5 spms; - MARVEL PL1205, Bairro Alto, retrieval box, 2 spms. *Snake Pit:* - ALVIN dive 2613, 11 spms; - ALVIN dive 2614, 38 spms; - ALVIN dive 2615, 1 spm; - ALVIN dive 2617, 64 spms; - ALVIN dive 2619, 55 spms; - ALVIN dive 2621, 19 spms; - ALVIN dive 2622, 2 spms; - MICROSMOKE PL 07, 1 spm. *Logatchev site:* - MICROSMOKE PL 20, 1 spm.

Distribution: The MAR from 38°N to 14°45′N, in 1500–3500 m depth. *Pseudorimula midatlantica* lives on rocks and mussels.

Remarks: *Pseudorimula midatlantica* is highly variable in shape and sculpture, from large, flat, almost smooth specimens (Figures 23b, e) to smaller and taller specimens with more pronounced sculpture (Figure 23d). We have, however, not been able to distinguish more than one species. When McLean (1992a) described the species, only a single well preserved shell was available, and we have illustrated additional specimens to show the variation. The protoconch (Figure 15h) is of normal appearance for Lepetodriloidea and of a diameter of about 215 μm.

The shell is frequently covered by thick crusts of bacterially precipitated iron and manganese oxides which obviously form an obstacle for the water circulation since frequently only a narrow hole remains open (Warén, in

press, fig. 1E). This causes a reaction from the snail which tries to widen the outlet, from the long, narrow slit typical for specimens with no rust cover, to a wide irregular opening (Figure 23d).

Warén (in press) described many details in the ontogeny and morphology of this species.

The food consists of a mixture of mineral particles and organic material scraped off from the surface of the rocks and shells it lives on.

Subclass Uncertain

Superfamily NEOMPHALOIDEA McLean, 1981

Remarks: The systematic position of Neomphaloidea ("Hot Vent Taxa" sensu Ponder & Lindberg, 1997) was considered somewhat uncertain by these authors, and their analysis indicated paraphyly. On the other hand, monophyly of Peltospiroidea and Neomphaloidea was supported by molecular information (McArthur, 1996; McArthur & Tunnicliffe, 1998). Ongoing anatomical work (Israelsson, 1998, in press) on several species of Neomphalidae, Cyathermiidae and Melanodrymiidae is producing evidence that the species of these families are quite closely related, and we place them together under Neomphalidae. They share, in addition to similarities in internal anatomy, the type of protoconch sculpture and a tendency to specialization of the left cephalic tentacle as a copulatory organ.

We have also moved *Planorbidella* and *Pachydermia* from Peltospiridae to Neomphalidae, since they have the same type of protoconch as *Neomphalus*. A result of our view is that the concept Neomphaloidea becomes synonymous with Neomphalina.

Family NEOMPHALIDAE McLean, 1981

Retiskenea Warén & Bouchet, gen. nov.

Type species: ***Retiskenea diploura,*** sp. nov.

Diagnosis: Shell small, globular, transparent, narrowly umbilicate with exquisite net sculpture on protoconch. Cephalic tentacles joined by a skin fold across the snout, laterally ciliated, possibly also with some additional skin folds between tentacles, left one probably with a basal penial process in adult males. No sensory papillae. Snout slightly flattened, distally broader. Foot broad, flat, and rounded, anteriorly drawn out to small corner tentacles, posteriorly broadly rounded and notched. Single epipodial tentacle at each side of anterior part of operculum. Gill small, centrally situated in pallial cavity, bipectinate. Stomach very large, intestine with single, simple anterior loop in head-foot, then a posterior loop to the right of stomach before entering pallial cavity. Conspicuous seminal vesicle at right side behind pallial cavity. Two large salivary glands open into the buccal cavity via short ducts. Jaw yellowish, present, not examined in detail. Radula n - 1 - 1 - 1 - n, about four times as long as broad. Radular sac bilobed. Central tooth rather low, with antero-lateral supports and posterior, winglike projections, together forming a support for the first lateral tooth. Lateral tooth rather short and broad; marginals gradually more oarlike toward edge of radula. Operculum multispiral, with central nucleus, width of last whorl corresponds to 20% of diameter.

Etymology: From "rete" (Latin), net and "*Skenea,*" a genus of gastropods of similar shell shape.

Remarks: We have made a new genus for this little species because of the strange combination of posteriorly bifurcated foot, ciliated snout and tentacles (heterobranch characters), and a protoconch, epipodial tentacle, and radula with bilobed sac, which are more traditional vetigastropod features. The radula is also quite similar to some species of Seguenziidae. The sculpture of the protoconch closely resembles the type found in Neomphalidae; a slight difference is that the ridges that form the net are of a fairly uniform size, while in the neomphalids their strength is more variable. The shape of the central tooth comes close to several species of *Ancistrobasis* (Marshall, 1991:fig. 271) or *Vetulonia* (Warén & Bouchet, 1993:figs 8B–C), species classified in Seguenziidae and Calliotropinae respectively. The lateral tooth, at the same time as it is similar to that of these genera, also resembles that of *Hyalogyrina,* but is more sturdy.

Four specimens of a size between 1.3 and 1.5 mm were critical-point dried but with meager results. The specimens were poorly preserved, except one which was badly covered by mucus. That specimen showed some signs of developing additional cephalic appendages not present in the others. That one was also the largest specimen with soft parts, diameter 1.5 mm, while a couple of almost fossilized shells had a diameter of 2.2 mm. This indicates that our specimens were immature, and perhaps, had not yet developed the tentacular appendages. We have therefore figured a critical-point dried specimen of ***Retiskenea*** sp. from off Oregon, which we could not safely identify, since it was decalcified. The radula is, however, identical, the soft parts agree with what can be seen in our specimens of ***R. diploura,*** and the periostracum gave an idea of a very similar shape of the shell. It may, however, represent a second species.

It is not easy to classify this genus because of the strange combination of characters. We have placed ***Retiskenea*** in Neomphalidae because of presence of epipodial tentacles, similarity in protoconch sculpture, supposed dimorphism of cephalic tentacles, and strange plate between the cephalic tentacles, which closely resembles that in the male of *Melanodrymia.*

Depressigyra? *statura* Goedert & Benham, 1999, from Middle Eocene seep deposits in the state of Washington closely resembles ***R. diploura*** in the shape of the protoconch and teleoconch. The protoconch sculpture was well

enough preserved to allow examination, and is very similar (specimens through the courtesy of the authors). Another difference from *Depressigyra* is that the aperture is almost tangential, while it is clearly radial in *Depressigyra.* We therefore transfer *D. statura* to ***Retiskenea.***

Retiskenea diploura Warén & Bouchet, sp. nov.

(Figures 15j, 16g, 18e, 24c)

Type material: Holotype SMF 311984 and 17 paratypes SMF 311985, 9 paratypes MNHN.

Type locality: Aleutian Trench, Shumagin site, TVGKG 40, 54°18.17'N, 157°11.82'W, 4808 m.

Material examined: The type material and: *Aleutian Trench:* - TVGKG 49, 2 specimens.

Distribution: Only known from the Aleutian Trench, Shumagin site at 4800 m.

Etymology: From "diplo," double and "oura," tail (Greek), referring to the posteriorly bifurcated foot.

Description: *Shell (Figure 24c).* Small, greyish semitransparent with a very thin periostracum, of a tall skeneidlike shape. The protoconch (Figure 15j) consists of ⅔ of a whorl, has a large initial part and is completely covered by fine ridges, forming a network with slightly variable mesh size, distinctly smaller toward the peristome. Its diameter is 300 μm. The teleoconch consists of up to three distinctly convex whorls, united by a deep suture and sculptured by irregularly spaced growth lines of variable strength. There is also a microsculpture of small pits, diameter 1–2 μm, evenly distributed over all the surface. The umbilicus is narrow and deep. The outer lip is thin and sharp, the peristome almost round, slightly indented by the preceding whorl.

Dimensions. Diameter of holotype 1.20 mm, height 1.34 mm, maximum diameter 2.2 mm (old shells only).

Operculum (Figure 16g) and radula (Figure 18e). See generic diagnosis.

Remarks: As mentioned above, it seems likely that our specimens are immature. This is also supported by the fact that the protoconchs were perfectly preserved in all live taken specimens, while in other species from the same locality and of similar size, it was completely lost.

Retiskenea sp.

(Figures 25a–e)

Material examined: *Oregon Margin:* - ROPOS 341, suction sample 1, 1 decalcified specimen.

Remarks: A single completely decalcified specimen had the thin colorless periostracum remaining and showing the shape of the shell. It was very similar to ***R. diploura,*** diameter ca. 2.4 mm, with 3.2 whorls left and no trace of the apex remaining. It was used for critical-point drying and radula preparation. We figure it since it gives a better idea about the soft parts of ***Retiskenea*** than our SEM photos of the type species.

Cyathermia Warén & Bouchet, 1989

Cyathermia Warén & Bouchet, 1989:69.

Type species: *C. naticoides* Warén & Bouchet, 1989; by original designation; hydrothermal vents at EPR.

Cyathermia naticoides Warén & Bouchet, 1989

Cyathermia naticoides Warén & Bouchet, 1989:70, figs. 6–10, 15, 16, 18, 21–23, 71, 80.
Cyathermia naticoides: Warén & Bouchet, 1993:33.

New records: *EPR at 13°N:* - HERO 91 PL 10, 900 spms; Genesis, 10 spms; - HERO 91 PL 11 (Genesis), 59 spms; - HERO 91 PL 12, 2 spms; - HERO 91 PL 13, 883 spms; - HERO 91 PL 17, 992 spms; - HERO 91 PL 19, 9 spms; - HERO 91 PL 21, 1565 spms; - HERO 91 PL 23 (Elsa), 131 spms; - HERO 91 PL 24 (Elsa), 5 spms; - HERO 91 PL 26, 140 spms; - HERO 92 dive 2512, 315 spms; - HERO 92 dive 2514, 970 spms; - HERO 92 dive 2516, 32 spms; - HERO 92 dive 2517, 6 spms; - HERO 92 dive 2519, 96 spms; - HERO 92 dive 2520, 713 spms; - HERO 92 dive 2521, 713 spms; - HERO 92 dive 2522, 147 spms; - HERO 92 dive 2523, 1400 spms; - HERO 92 dive 2524, 103 spms; - HERO 92 dive 2525, 1125 spms; - HERO 92 dive 2526, 129 spms; - HERO 92 dive 2528, 822 spms; - HERO 92 dive 2531, 822 spms; - HERO 92 dive 2532, 852 spms. *EPR at 09°50'N:* - HERO 91 PL 07, 7 spms; - HERO 91 PL 09, 2 spms.

Distribution: EPR between 09°50'N and 21°N, in about 2600 m depth. Almost all specimens come from tubes of vestimentifera.

Remarks: The anatomy is described by Israelsson (in press). It is there shown that the species is closely related to *Neomphalus.*

The larva of *C. naticoides* was identified in plankton samples taken a few meters above the sea floor at the EPR at 09°50'N (Mullineaux et al., 1996).

Melanodrymia Hickman, 1984

Melanodrymia Hickman, 1984:19.

Type species: *M. aurantiaca* Hickman, 1984; by original designation; hydrothermal vents at the Galapagos Rift Zone and the EPR.

Remarks: *Melanodrymia* ***galeronae*** may perhaps look very different from *M. aurantiaca,* but this is only the result of a slightly taller spire. Other details are quite

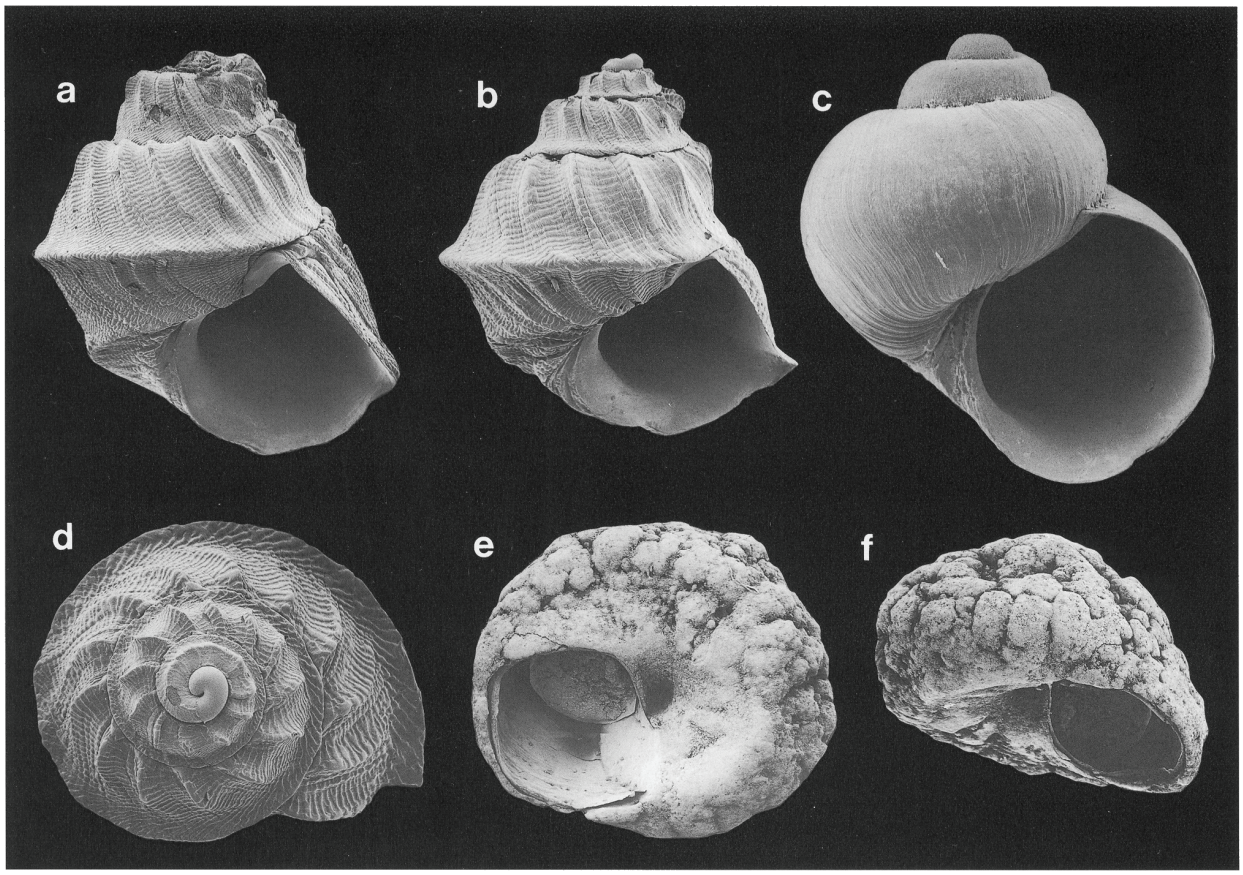


Figure 24. Neomphalidae, shells. *a, b, d. Melanodrymia* ***galeronae*** Warén & Bouchet, sp. nov., paratypes. *a.* Adult shell, 3.0 mm height. *b.* Subadult shell, 2.6 mm height. *d.* Apical view, diameter 1.74 mm. *c.* ***Retiskenea diploura*** Warén & Bouchet, gen. & sp. nov., paratype, diameter 1.34 mm. *e, f. Melanodrymia sp.*, "rust covered", EPR, 13°N, Caldera. *e.* Basal view, diameter 3.6 mm. *f.* Apertural view, diameter 3.2 mm.

similar to the type species, and the genus forms a morphologically rather narrow group.

Melanodrymia aurantiaca Hickman, 1984

Melanodrymia aurantiaca Hickman, 1984:20, figs. 1–2.
Melanodrymia aurantiaca: Haszprunar, 1989a:175; Warén & Bouchet, 1993:41; Israelsson, 1998:105.

New records: *EPR at 13°N:* - HERO 91 PL 10, 3 spms; - HERO 91 PL 11 (Genesis), 12 spms; - HERO 91 PL 19, 2 spms; - HERO 91 PL 25 (Caldera), 5 spms; - HERO 92 dive 2512, 1 spm; - HERO 92 dive 2522, 54 spms; - HERO 92 dive 2523, 8 spms. *EPR at 17°S:* - NAUDUR PL 03 (Nadir), 1 spm; - NAUDUR PL 04, site Rehu, 1 spm; - NAUDUR PL 06, site Rehu, 17 spms.

Distribution: EPR from 21°N to 17°S, in 2500–2600 m depth.

Remarks: The largest specimen has a shell diameter of 3.6 mm.

Melanodrymia brightae Warén & Bouchet, 1993

Melanodrymia brightae Warén & Bouchet, 1993:43, figs. 34A–C, 35A–B.

New records: *JdF, Endeavour Segment:* - ROPOS 278, from rocks, 37 spms (MNHN, Tunnicliffe ref. coll.).

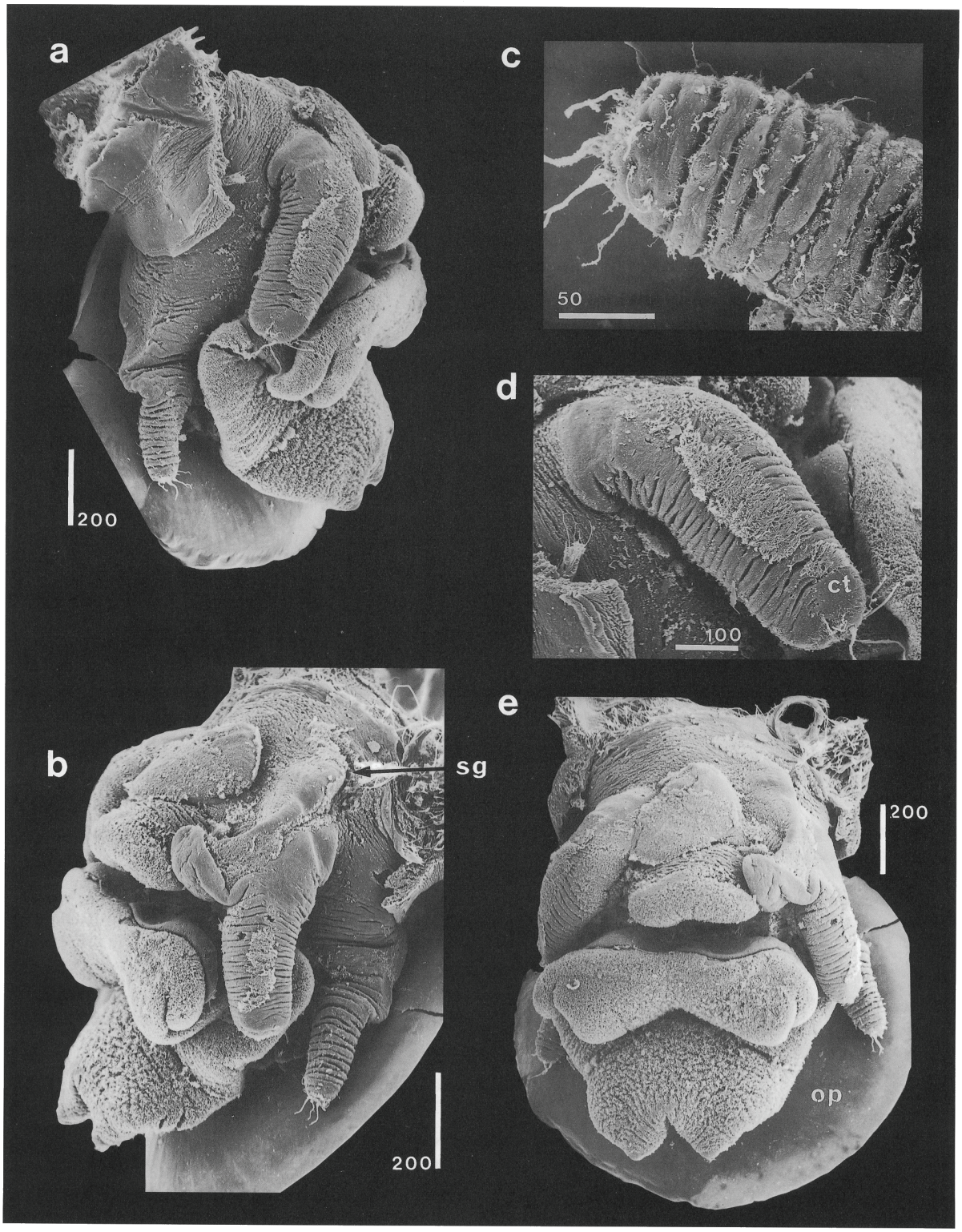
Distribution: JdF, Endeavour Segment, 2200 m depth.

Melanodrymia sp. "rust covered"

(Figures 21d, 24e, f)

Material examined: *EPR at 13°N:* - HERO 91 PL25 (Caldera), 10 spms; - HERO 91 PL27, 1 spm.

Description: The shape is roughly as in *M. aurantiaca,* but the shell lacks any trace of calcareous matter. Instead of a shell there is a solid cover of bacterially precipitated rust enveloping the periostracum, with a rich fauna of *Folliculina*-like ciliates (caeciform, 200–300 μm long and 70–80 μm in diameter, buried in the rust, only ap-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erture protruding). Radial ribs are visible on the periostracum around the umbilicus. The periostracum is thin and fragile and it is impossible to crack the rust without breaking the periostracum also. The maximum diameter is 3.2 mm.

Remarks: We do not know if the specimens described above represent a new species or specimens of *M. aurantiaca* which for some reason have not been able to form a shell. Such a phenomenon is known for *Depressigyra globulus* which at one locality of the JdF was found and observed alive without a shell, the body surrounded only by the periostracum (Tunnicliffe & Fontaine, 1987).

The shape of the interior is closest to *M. aurantiaca,* but the specimens occurred sympatrically with this species so it is difficult to explain why some specimens form a shell and some do not. Furthermore, the shape and the structure of the rust cover is very uniform in all specimens, not variable in thickness and shape as in species of *Lirapex* and *Pachydermia* which often have deposits of comparable thickness. The external morphology of the soft parts and radula could, however, not be distinguished from *M. aurantiaca.*

One female, egg diameter in gonad ca. 130 μm, had two lanceolate objects, supposed to be spermatophores, attached in the rear part of the pallial cavity, with a kind of outer, transparent cover and inner fibrous structure, size 350 × 80 μm. Two more females lacked these. This is the first evidence of spermatophores in the Neomphalina.

Melanodrymia ***galeronae*** Warén & Bouchet, sp. nov.

(Figures 15k, 16f, 21c, 24a, b, d)

Type material: Holotype, 5 dry and 11 alcohol paratypes in MNHN.

Type locality: EPR at 13°N, HERO 91 PL25, 10 km south of main locality, 12°42.65'N, 103°54.65'W, 2563 m, at the "Caldera."

Material examined: The types and: *EPR at 13°N:* - HERO 92 dive 2528, 1 specimen.

Distribution: EPR at 13°N, at about 2600 m depth.

Etymology: Named after Joëlle Galeron at IFREMER, who has sorted much of the material from the French deep-sea program.

Description: *Shell (Figures 24a, b, d).* Tall and sturdy, with thin, transparent periostracum, a strong peripheral keel, oblique axial ribs, obliquely radiating axial striae, and shallow umbilical crevice in young specimens. The protoconch (Figure 15k) is completely covered by a fine net sculpture, consists of ¾ of a whorl, and has a distinctly expanded peristome. Its diameter is 250 μm. The teleoconch has up to 3.5 distinctly shouldered whorls. They have a very strong peripheral keel and a weaker basal one which connects to the basal corner of the peristome; up to 16 strong, oblique axial ribs which fade away at the keel and a second set of similar, obliquely aligned, basal ribs which reach this keel. In addition there is a much finer and uniform striation of irregular, sometimes double, obliquely radiating raised lines which are generated close to the suture by dichotomy of earlier lines. The columella is sturdy with the lower part of the inner lip reflected over it.

Dimensions. Maximum shell height 3 mm.

Operculum (Figure 16f) and *soft parts* as in *Melanodrymia aurantiaca* (see Warén & Bouchet, 1989, Haszprunar, 1989a, Israelsson, 1998).

Radula (Figure 21c). Ca. 20 - 4 - 1 - 4 - 20. The marginal teeth are fewer in number than normal in Neomphalina. The central tooth is dominated by the anterior supporting ridges, and the apical plate is weakly serrated. The inner three laterals are much more slender than the fourth and they have a single denticle on the inner side of the main cusp; number four has a denticle on its outer side also. The marginals are flat; the inner ones with a handlike apical part with one major cusp, flanked by two to three smaller ones on each side; more laterally the cusps become smaller and the outermost teeth are finely serrated apically.

Remarks: This new species can easily be recognized by, contrary to previously described species of *Melanodrymia,* being much taller than broad. We have examined the soft parts only very superficially, in order to save material if needed for future work, and also since from the shell morphology there seems little reason to question the systematic position.

Pachydermia Warén & Bouchet, 1989

Pachydermia Warén & Bouchet, 1989: 75.

Type species: *P. laevis* Warén & Bouchet, 1989; by original designation; hydrothermal vents at EPR.

Pachydermia laevis Warén & Bouchet, 1989

Pachydermia laevis Warén & Bouchet, 1989:76, figs. 28–29, 34, 37–40, 41, 42, 76, 85–86.

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Figure 25. ***Retiskenea*** cf. ***diploura*** Warén & Bouchet, gen. & sp. nov., Oregon Margin. *a.* Head-foot, right side. *b.* Head-foot, left side. *c.* Tip of epipodial tentacle. *d.* Right cephalic tentacle. *e.* Head-foot, front view. ct - cephalic tentacle; op - operculum; sg - sperm groove. Scale bars in μm.

Pachydermia laevis: Warén & Bouchet, 1993:40; Israelsson, 1998:95.

New records: *EPR at 13°N:* - HERO 91 PL05, 14 spms; - HERO 91 PL12, 25 spms; - HERO 91 PL17, 2 spms; - HERO 91 PL19, 42 spms; - HERO 91 PL21, 31 spms; - HERO 91 PL25 (Caldera), 5 spms; - HERO 91 PL26, 161 spms; - HERO 92 dive 2516, 2 spms; - HERO 92 dive 2517, 1 spm; - HERO 92 dive 2524, 2 spms; - HERO 92 dive 2526, 1 spm; - HERO 92 dive 2528, 1 spm; - HERO 92 dive 2531, 3 spms. *EPR at 09°50'N:* - HERO 91 PL09, 2 spms. *EPR at 17°S:* - NAUDUR PL06, site Rehu, 5 spms; on mussels, 1 spm.

Distribution: EPR from 21°N to 17°S, in 2500–2600 m depth.

Remarks: Almost all new specimens come from vestimentiferan tubes, but from earlier samplings, the species seems to be more common on other substrates.

Planorbidella Warén & Bouchet, 1993

Planorbidella Warén & Bouchet, 1993:35.

Type species: *Depressigyra planispira* Warén & Bouchet 1989; by original designation; hydrothermal vents at EPR.

Planorbidella planispira (Warén & Bouchet, 1989)

Depressigyra planispira Warén & Bouchet, 1989:81, figs. 48–50, 53, 54, 74, 84.
Planorbidella planispira: Warén & Bouchet, 1993:37, fig. 29D.

New records: *EPR at 13°N:* - HERO 91 PL10, 1 spm; - HERO 91 PL11 (Genesis), 8 spms; - HERO 91 PL17, 2 spms; - HERO 91 PL19, 3 spms; - HERO 91 PL21, 7 spms; - HERO 91 PL26, 3 spms; - HERO 92 dive 2523, 1 spm. *EPR at 17°S:* - NAUDUR PL06, site Rehu, 2 spms.

Distribution: EPR from 21°N to 17°S, in 2500–2600 m depth.

Neomphalus McLean, 1981

Neomphalus McLean, 1981:294.

Type species: *N. fretterae* McLean, 1981; by original designation; hydrothermal vents at the Galapagos Rift.

Neomphalus fretterae McLean, 1981

Neomphalus fretterae McLean, 1981:294, figs. 1–10.
Neomphalus fretterae: Warén & Bouchet, 1993:33.

New records: *EPR at 13°N:* - HERO 92 dive 2522, 2 spms (diameter 1.1 mm).

Distribution: EPR, 21°N to 09°50'N and the Galapagos Rift at about 2400–2600 m depth.

Remarks: The larva of *Neomphalus fretterae* was identified from plankton samples taken a few meters above the sea floor at the EPR at 09°50'N (Mullinéaux et al., 1996).

Lacunoides Warén & Bouchet, 1989

Lacunoides Warén & Bouchet, 1989:72.

Type species: *L. exquisitus* Warén & Bouchet, 1989; by original designation; Galapagos Rift vents.

Remarks: The new species described below is quite similar to the type species, although we have not been able to examine a male to verify that the left cephalic tentacle is modified to a copulatory organ. The operculum has the same kind of overlapping edges of the preceding whorls; the shell has very similar shape and sculpture (although the spiral sculpture is less conspicuous in *L. **vitreus***), and the central tooth of the radula shares the same type of unusually large, flat, and elongate apical plate.

*Lacunoides **vitreus*** Warén & Bouchet, sp. nov.

(Figures 29a–e)

Type material: Holotype (FMNH 280088) and paratypes 2 spms dried, 1 empty sh (FMNH 280924), 6 spms wet (FMNH 280901) in FMNH; 2 paratypes in MNHN.

Type locality: JdF, Axial Seamount, Ashes vent field, 45°56.00'N, 130°00.86'W, 1543 m depth, ROPOS R406, in a "worm grab."

Material examined: Only known from the type material.

Distribution: Only known from the type locality.

Etymology: "*vitreus,*" Latin, like glass, referring to the transparent, colorless shell.

Description: *Shell (Figures 29c, d).* Small, globular, transparent, with depressed spire, large aperture, and rapidly increasing diameter of whorls. The protoconch (Figure 29e), diameter 180 μm, consists of about half a whorl, is loosely coiled and initially covered by an irregular net-sculpture which becomes less obvious toward the distinctly expanded peristome. The teleoconch consists of about two whorls of rapidly enlarging diameter and round cross section. The first whorl is sculptured by weak incremental lines, which gradually become larger and after 1.1–1.2 teleoconch whorls form sharp axial low lamellae. One-tenth of a whorl later, also a much finer, dense spiral striation commences, which covers all the surface of the final half whorl. The peristome is round, not indented by the preceding whorl, thin and sharp, tangential and strongly prosocline.

Dimensions. Diameter of holotype, 2.4 mm; maximum diameter 2.5 mm.

Soft parts. The foot can be folded 180° to close the

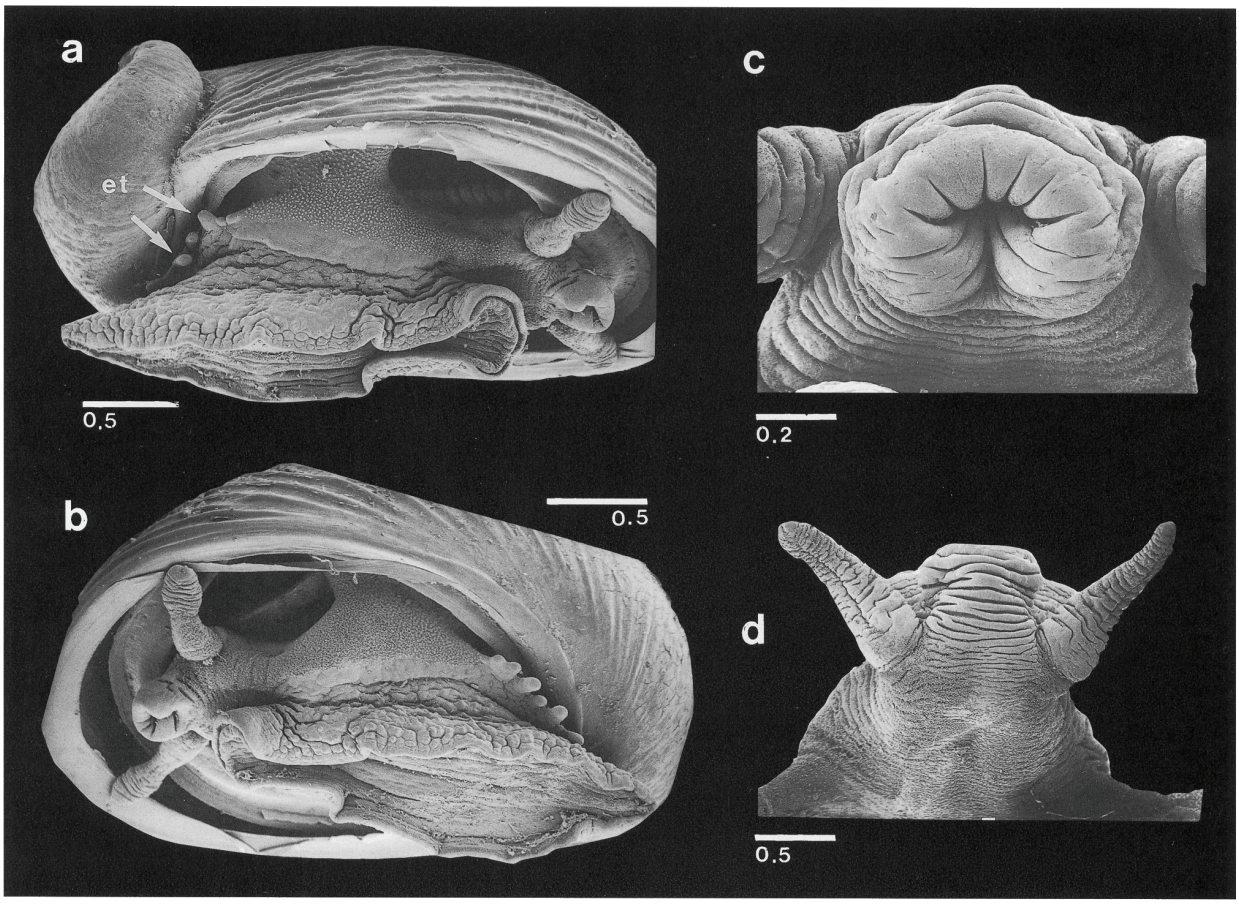


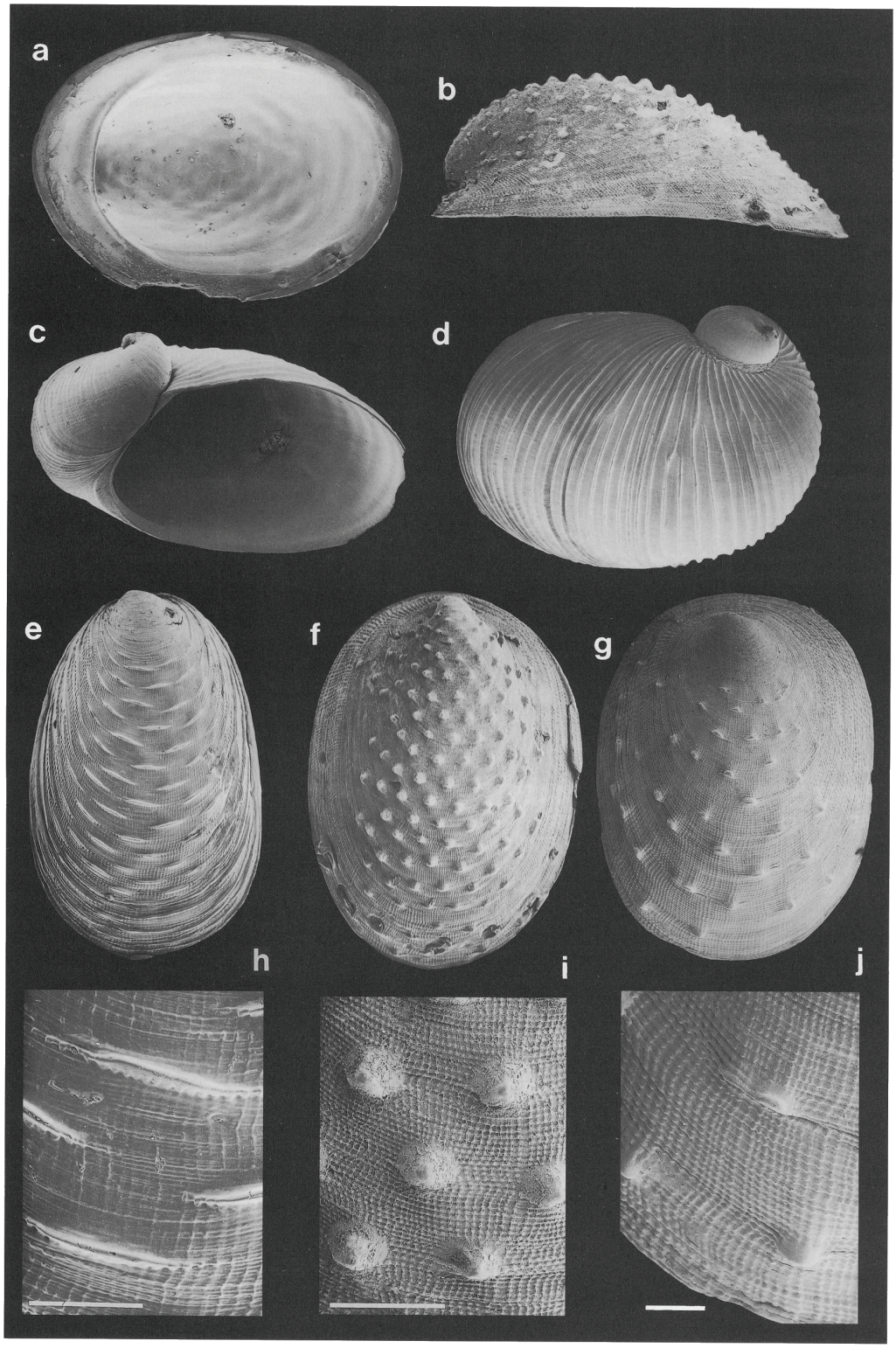
Figure 26. *Peltospira* ***smaragdina*** Warén & Bouchet, sp. nov., critical-point dried. *a.* Right side of animal. *b.* Left side of animal. *c.* Snout, ventral view. *d.* Dorsal view of head. et - epipodial tentacle. Scale bars in mm.

aperture (Figure 29c). The head is small, the cephalic tentacles slightly longer than the snout. The snout is apically strongly bilobed and drawn out to fine points. The presence of a ventral-lateral furrow could not be verified. Dorsally, across the neck, shortly behind the cephalic tentacles runs a well demarcated furrow. It starts behind the left cephalic tentacle, continues past the right one, turns to the right and backward at the right columellar muscle and fades out in the external pallial furrow. The end of its right side is flanked by a low skin-fold. The foot is large, low, and flat, anteriorly truncate and drawn out to small corner tentacles; posteriorly it is broadly rounded. A propodium is present. Posteriorly, along the sides, is a membrane with a series of five to six small epipodial tentacles under the operculum. No other appendices. The columellar muscle is very short, a narrow strip across the inner side of the aperture, distinctly enlarged at the right side. Its left side is mainly ventral and ends as a narrow wedge. The pallial margin is smooth. The gill is bipectinate with about 25 pairs of leaflets; it is restricted to the left posterior quadrant of the pallial cavity, with a roughly diagonal direction. It is attached mainly by the efferent membrane which is unusually large. A transverse pallial vein runs from the posterior, right part of the gill to the anterior part of the rectum (joining the rectal sinus?).

Operculum (Figure 29c). Multispiral center bulging out in retracted specimens, thin and colorless, slightly larger than the aperture. The edge of previous whorl forms a distinct overlap over next whorl.

Radula (Figures 29a–b). Ca. 10-4-1-4-ca. 10. The central tooth has a long and slender, finely serrated, apical cutting plate, almost twice as long as that of the first lateral tooth. The lateral teeth have longer and more slender apical plate toward the side, with a serration similar to the central. The marginal teeth are oar-shaped with the apical third of the outer margin finely serrated. The serration is basally demarcated by a small spur. Toward the edge the marginals are more slender and lack the spur.

Remarks: This new species is an interesting addition to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the fauna of the JdF system, because it contributes to a reduction of the differences in generic composition between the vent systems. There should be no difficulties in recognizing this species. *Lacunoides exquisitus* from the Galapagos Rift, differs by having a much stronger spiral sculpture and a more widely spaced net sculpture on the protoconch.

Family PELTOSPIRIDAE McLean, 1989

Remarks: We have kept *Depressigyra* and *Lirapex* with the peltospirid limpets, since both have a protoconch similar to *Peltospira.*

Peltospira McLean, 1989

Peltospira McLean, 1989b:51.

Type species: *P. operculata* McLean, 1989; by original designation; EPR at 21°N.

Remarks: The species of *Peltospira* form a series in the degree of limpetization, from *P. lamellifera,* where the operculum is retained and of a size corresponding to the aperture. This species can also fold the foot 180° to close the aperture with the operculum. In *P. operculata* the foot can be folded only 90° and the species cannot close the aperture, although the operculum is large enough. In *P. delicata* and *P. **smaragdina*** the foot does not have a long, posterior "tail" for carrying the operculum, and the operculum is lost. They have thus achieved the limpet organization, although the foot is not as muscular and large as in patellogastropod or fissurellid limpets. It seems likely that the other limpetlike peltospirid genera simply are more advanced on this evolutionary pathway and that these genera may be paraphyletic. This, however, remains to be shown.

*Peltospira **smaragdina,*** Warén & Bouchet, sp. nov.

(Figures 15n, 26a–d, 27c, d, 31e, f)

Type material: Holotype and 43 paratypes in MNHN.

Type locality: MAR, Lucky Strike, ALVIN dive 2606, 37°17.55'N, 32°16.47'W, 1628 m, Statue de la Liberté.

Material examined: The types and: *MAR, Menez Gwen:* - DIVA 1 PL 14, on sulfide rock with Hydrozoa, 1 spm; - DIVA 2 PL 11, suction sample among mussels, 1 spm; - DIVA 2 PL 12, 1 spm. *Lucky Strike:* - DIVA 1 PL 04, on inactive chimney among Hydrozoa and sponge *Cladorhiza,* 5 spms; - DIVA 1 PL 17, 42 spms; on a black smoker, 5 spms; - DIVA 2 PL 02, 231 spms, on sulfide flanges, 17 spms; - DIVA 2 PL 04, 1 spm; - DIVA 2 PL 05, 20 spms; - DIVA 2 PL 06, 1 spm; - DIVA 2 PL 07, 10 spms; - DIVA 2 PL 08, 1 spm; - DIVA 2 PL 09, suction sample among mussels and hydrothermal sediments, 1 sh; - DIVA 2 PL 10, 2 suction samples among mussels and hydrothermal sediments, 1 and 9 spms; - DIVA 2 PL 23, 2 spms; - DIVA 2 PL 25, 152 spms; - DIVA 2 PL 26, 1 spm; Sintra, 20 spms; - ALVIN dive 2606, 55 spms; - ALVIN dive 2607, 12 spms; - MARVEL PL1200, Bairro Alto, 0.25 m^2 rock surface close to edifice, 16 spms; - MARVEL PL1205, Bairro Alto, retrieval box, 2 spms. *Snake Pit:* - ALVIN dive 2613, from gut of a shrimp, 1 spm; - ALVIN dive 2618, 30 spms; - ALVIN dive 2620 on a smoker, 11 spms; - ALVIN dive 2622, 22 spms; - GRAVINAUT PL16, 53 spms. *Logatchev site:* - MICROSMOKE PL12 (Ruches), 3 spms; - MICROSMOKE PL20 (Irina), 15 spms.

Distribution: MAR, from Menez Gwen to Logatchev site, in 850–3500 m, mainly on rocks in the vicinity of vents.

Etymology: *"smaragdina"* from the bright green color of the periostracum of perfect specimens.

Description: *Shell (Figures 27c, d).* Of medium size for its group, haliotiform, with very rapidly increasing diameter, fragile, with thick greenish periostracum, usually axially ridged. The protoconch (Figure 15n) has no obvious coiling and is sculptured by about 12 "spiral" ridges which do not reach the slightly expanded peristome. The diameter is 250 μm. The teleoconch consists of about 1.7 whorls of rapidly increasing diameter, and is sculptured by regularly spaced, strong axial ribs, which give the shell an appearance of corrugated sheet metal. The spiral striation varies in distinctness and strength. The outer lip is not thickened, the inner lip forms a thickened callus on the columella. The periostracum is tough, thick, dark greenish, reflected across the shell margin.

Dimensions. Maximum diameter of shell 12 mm.

Soft parts (Figures 26a–d). The foot is muscular and fleshy, anteriorly broadly rounded, posteriorly tapering; the propodium demarcated by a narrow fissure. The sides of the foot are covered by irregularly shaped tubercles. The epipodium consists of about 10 irregularly shaped

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Figure 27. Peltospiridae, shells. *a, b, f, i. Nodopelta **rigneae*** Warén & Bouchet, sp. nov., holotype, diameter 7.1 mm. *a.* Ventral view. *b.* Lateral view, right side. *f.* Apical view. *i.* Detail of sculpture. *c, d. Peltospira **smaragdina*** Warén & Bouchet, sp. nov., Menez Gwen. *c.* Apertural view, diameter 3.6 mm. *d.* Dorsal view, diameter 9.4 mm. *e, h. Nodopelta subnoda,* EPR, 13°N. *e.* Dorsal view, 8.4 mm. *h.* Detail of sculpture. *g, j. Nodopelta heminoda,* EPR, 13°N. *g.* Dorsal view, 11.0 mm. *j.* Detail of sculpture, notice that the magnification is only half of Figures h and i. Scale bars 0.5 mm.

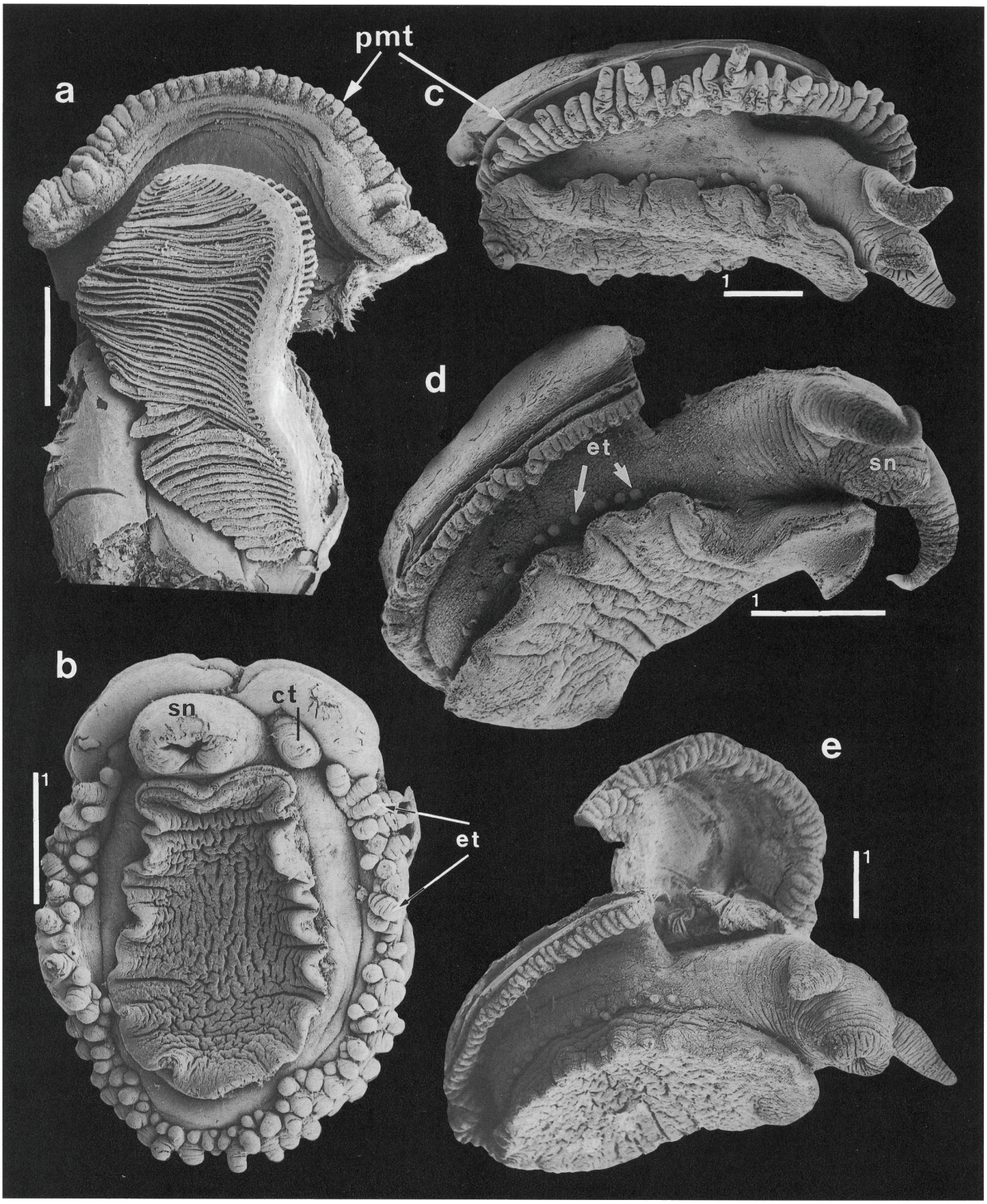


Figure 28. Peltospirid limpets, critical-point dried. *a, d. Nodopelta* ***rigneae*** Warén & Bouchet, sp. nov., holotype. *a.* Pallial skirt. *d.* Head-foot, right side, left side of foot removed. *b. Echinopelta fistulosa.* EPR at 13°N. *c. N. subnoda,* EPR at 13°N. *e. N. heminoda,* EPR at 13°N. ct - cephalic tentacle; et - epipodial tentacle; pmt - pallial margin tentacle; sn - snout. Scale bars in mm.

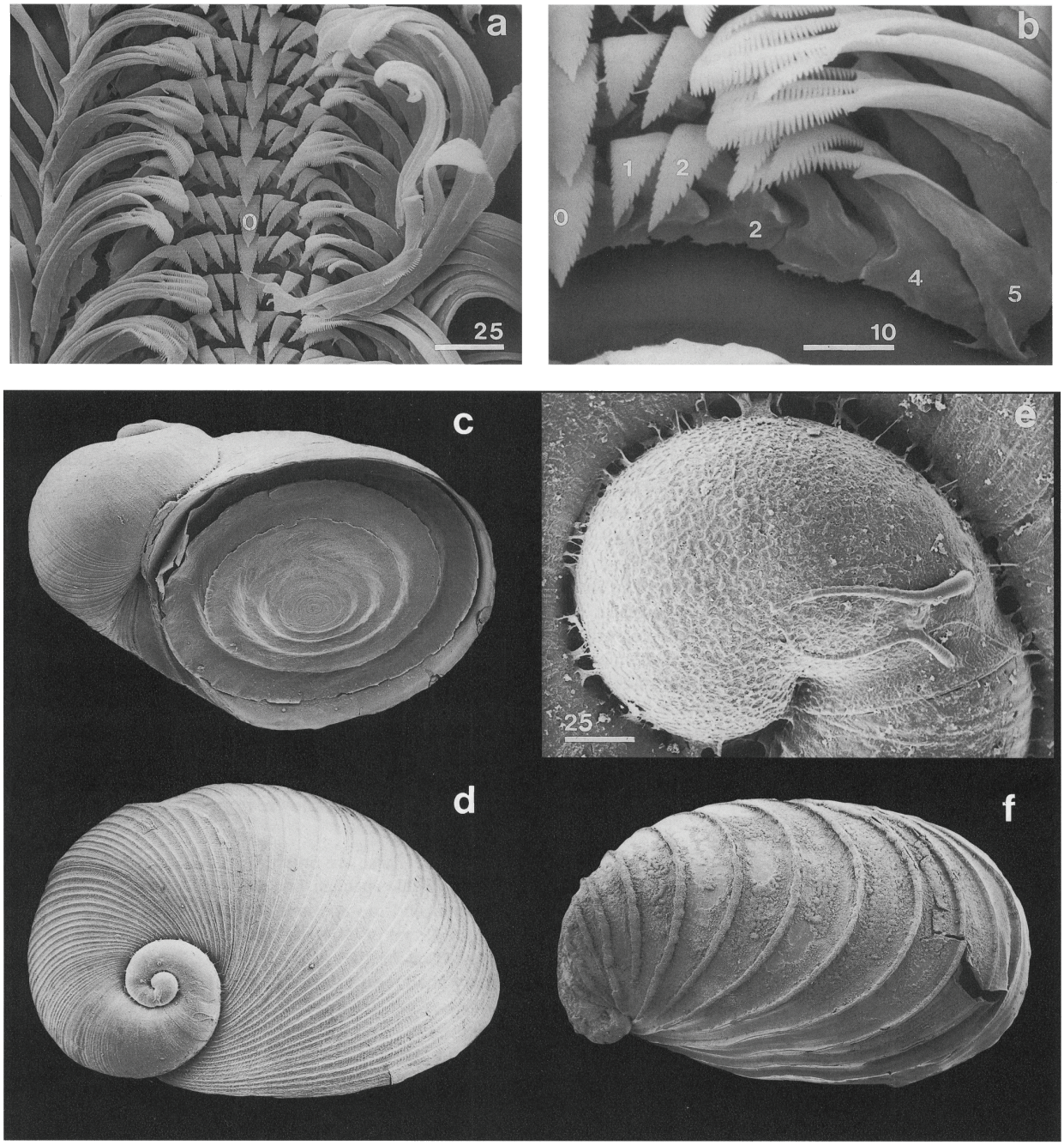


Figure 29. *a–e. Lacunoides* ***vitreus*** Warén & Bouchet, sp. nov. Teeth numbered sequentially with central tooth as 0. *a, b.* Radula, outermost lateral tooth is number 4. *c–e.* Shells. c. Holotype, diameter 2.4 mm. *d, e.* Paratype, diameter 2.2 mm. *f. Peltospira delicata,* unusually strongly sculptured specimen, maximum diameter 4.5 mm. EPR at 13°N. Scale bars in μm.

tentacles and papillae on a low ridge along the posterior 4/5 of the foot; more anteriorly the ridge levels out and disappears on the neck. Just above the two most posterior epipodial tentacles is a small pore, perhaps some rudiment of the operculum. The head is well demarcated, rather slender with tapering snout and a pair of long, tapering cephalic tentacles, more than twice the length of the snout and without a trace of eyes. The snout has an apical demarcating ridge and an almost ventral mouth. There are no cephalic lappets or other cephalic appendages. The pallial margin is tripartite with periostracum adhering in the inner furrow. The gill is very large, bipectinate, both axes attached for half their length. There are no sensory bursicles visible in the adult, and cephalic and epipodial tentacles lack sensory papillae. The shell muscle is almost aequilateral; the left part slightly more slender and narrow. There are no external differences between the sexes and no ciliated sperm tract was found in the males.

Operculum. Lost at a size below 1 mm.

Radula (Figures 31e–f). n - 4 - 1 - 4 - n. The whole central field is quite narrow and its teeth considerably lower than the marginals. Its teeth are sturdy and interlocking, but only the outermost one has denticles, and only along the outer side of the apical plate. The inner marginals are the shortest; they are flat, aligned in the direction of the row, and have an apical, truncate, reflected serration. Farther laterally the teeth are densely packed with the flat side at right angle to the earlier ones and a deeply serrated scythelike apical part above a basal spur.

Jaw. Thin and membranous, no prisms visible.

Remarks: The sculpture of *P. **smaragdina*** is variable, and the spiral striation is often absent; the axial ribbing may also be absent especially on the early spire. The gut contains sediment and mineral particles.

Peltospira delicata McLean, 1989

(Figure 29f)

Peltospira delicata McLean, 1989b:53, figs. 9–16.

New records: *EPR at 13°N:* - HERO 91 PL21, 1 spm; - HERO 92 dive 2519, 1 spm; - HERO 92 dive 2520, 1 spm; - HERO 92 dive 2521, 2 spms; - HERO 92 dive 2522, 1 spm; - HERO 92 dive 2531, 1 spm. *EPR at 09°50'N:* - HERO 91 PL09, 2 spms. *EPR at 17°S:* - NAUDUR PL08, 1 spm; - NAUDUR PL09 (Fromveur), 1 spm; - NAUDUR PL18.4.8b, site Rehu, 12 spms.

Distribution: EPR from 13°N to 17°S, at 2500–2600 m depth.

Remarks: Almost all specimens come from vestimentiferan tubes. The sculpture of the shell is quite variable; some specimens have strong axial ribs (Figure 29f), others are smooth; most are intermediate.

Peltospira operculata McLean, 1989

Peltospira operculata McLean, 1989b:51, figs. 1–8.

New records: *EPR at 13°N:* - HERO 91 PL04, 20 spms, 12 young; - HERO 91 PL11, 11 spms; Genesis, 8 spms; - HERO 91 PL13, 15 spms; - HERO 91 PL14 (Elsa), 4 spms; - HERO 91 PL18, 83 spms; - HERO 91 PL20, 8 spms; - HERO 91 PL21, 1 spm; - HERO 91 PL24 (Elsa), 1 spm; - HERO 91 PL26, 1 spm; - HERO 91 PL27 (Totem), 2 spms; - HERO 92 dive 2516, 13 spms; - HERO 92 dive 2519, 8 spms; - HERO 92 dive 2520, 20 spms; - HERO 92 dive 2521, 1 spm; - HERO 92 dive 2523, 3 spms; - HERO 92 dive 2524, 2 spms; - HERO 92 dive 2525, 2 spms; - HERO 92 dive 2532, 4 spms. *EPR at 09°50'N:* - HERO 91 PL06, 2 spms. *EPR at 17°S:* - NAUDUR PL18.4.8b, site Rehu, 1 spm.

Distribution: EPR from 21°N to 17°S, at a depth of 2500–2600 m.

Remarks: Most specimens above were obtained from tubes of vestimentifera, but the species probably has its main distribution on rocks, since it is proportionally more common in such samples.

The larva of *P. operculata* was identified in plankton samples taken a few meters above the sea floor at the EPR at 09°50'N (Mullineaux et al., 1996).

Peltospira lamellifera Warén & Bouchet, 1989

(Figures 16k, 46b, 48c, d)

Peltospira lamellifera Warén & Bouchet, 1989:74, fig. 24.

New records: *EPR at 13°N:* - HERO 91 PL05, 1 spm; - HERO 92 dive 2516, 1 spm.

Distribution: Only known from the EPR at 13°N, ca. 2600 m depth.

Remarks: These are only the second and third specimens known of this species. The soft parts can be retracted into the shell and the aperture entirely closed by the operculum at a size of 1.2 mm shell diameter. The holotype is larger than the two new specimens, 2.1 mm, but was an empty shell, and the ability to completely retract the soft parts was not known.

We figure a critical-point dried specimen (Figure 46b); although poorly preserved and contracted, it shows clearly the basic difference from the species of the limpet stage, i.e., the foot folded 180° and the aperture completely closed by the operculum. The protoconch is not known, but the simple snout and radular morphology (Figures 48c, d) indicate that this species really is a peltospirid.

Nodopelta McLean, 1989

Nodopelta McLean, 1989b:53.

Type species: *N. heminoda* McLean, 1989; by original designation; hydrothermal vents at EPR.

Nodopelta heminoda McLean, 1989

(Figures 27g, j, 28e)

Nodopelta heminoda McLean, 1989b:53, figs. 17–23.

New records: *EPR at 13°N:* - HERO 91 PL12, 1 spm; - HERO 91 PL18, 2 spms; - HERO 91 PL26, 1 spm; - HERO 92 dive 2517, 1 spm.

Distribution: EPR at 21°N and 13°N, at about 2600 m depth.

Remarks: We figure *N. heminoda* for comparison with *N. subnoda* and *N. **rigneae,*** from which it differs by its larger size, and more widely scattered tubercles.

Nodopelta subnoda McLean, 1989

(Figures 27e, h; 28c)

Nodopelta subnoda McLean, 1989b: 56, figs. 24–31.

New records: *EPR at 13°N:* - HERO 91 PL04, 30 spms; - HERO 91 PL05, 5 spms. *EPR at 17°S:* - NAUDUR PL06, site Rehu, 3 spms; - NAUDUR PL18 (Le Chat), I spm; - NAUDUR PL18.4.8b, site Rehu, 9 spms.

Distribution: EPR from 21°N to 17°S, at a depth of 2500–2600 m.

Remarks: Six specimens from HERO 91 PL04, smaller than 4-5 mm, have shorter tubercles on the inner part of the pallial fold, and the pallial margin tubercles are thus arranged in a more or less double row. Regrettably all these specimens had lost their shell before we received them and we can not say if this is a juvenile character or if one more species is involved. We figure *N. subnoda* for comparison with *N. heminoda* and *N. **rigneae.***

*Nodopelta **rigneae*** Warén & Bouchet, sp. nov.

(Figures 21e, f, 27a, b, f, i, 28a, d)

Type material: Holotype and two paratypes in MNHN.

Type locality: EPR at 13°N, site Elsa, 12°48.09′N, 103°46.34′W, 2630 m depth, from vestimentiferan washings.

Material examined: *EPR at 13°N:* - HERO 92 dive 2517, 2 spms, paratypes.

Distribution: Only known from the type locality.

Etymology: Named after Mrs. Kerstin Rigneus (SMNH) who sorted and identified much of the material used for this paper.

Description: *Shell (Figures 27a, b, f, i).* Haliotiform, of medium size for the group, ovate, convex, pustulose with thick, brown periostracum. The protoconch is not known. The shell is 2.9 times as long as high and the apex is situated 2–4% of the length in front of the posterior margin. The whole shell is covered by a fine sculpture (Figure 27i) of concentric ridges and tubercles, the latter giving an impression of a radial striation. There are also strong tubercles, diameter 0.15–0.20 mm, more concentrated over the central part of the shell. The periostracum is reflected across the margin of the shell. The posterior inside is strengthened by a strong, convex shelf of a maximum width corresponding to about $1/10$ of the diameter of the shell. The muscle scar is indistinct, horseshoe-shaped with the anteriorly wider and rounded limbs reaching the anterior ⅓ of the shell. The peristome is almost perfectly flat.

Dimensions. Diameter of the holotype 7.1 mm, maximum diameter 8.7 mm.

Soft parts (Figures 28a, d). Normal for the genus; pallial margin with a single series of small, short tentacles of even size all along its circumference. The epipodial tentacles are small and inconspicuous, about 15 in number along each side and cover almost the whole length of the foot.

Radula (Figures 21e–f). As for genus, slender, n - 4 - 1 - 4 - n, end of radular sac bilobed. The outermost lateral tooth is weakly serrated along the outer side of the apical plate. The change to the marginals is abrupt. The marginal teeth are flat, apically truncated at right angle, have a series of recurved comblike denticles and, below these, a small spur at each side.

Remarks: *Nodopelta **rigneae*** differs from *N. heminoda* by being smaller, having a finer sculpture, and the tubercles are more concentrated to the central part of the shell. During dive 2517 it was collected with *N. heminoda. Nodopelta subnoda* is much flatter, has elongate sculptural elements, and the apex is situated outside (behind) the peristome.

Hirtopelta McLean, 1989

Hirtopelta McLean, 1989b:60.

Type species: *H. hirta* McLean, 1989; by original designation; hydrothermal vents at EPR.

Hirtopelta hirta McLean, 1989

Hirtopelta hirta McLean, 1989b:62, figs. 49–55.
Hirtopelta hirta: Warén & Bouchet, 1993:35, fig. 26a–c.

New records: *EPR at 13°N:* - HERO 92 dive 2523, 1 spm.

Distribution: EPR from 21°N to 13°N, at a depth of 2500–2600 m.

Remarks: This and the following species are known from very few specimens, and only from 13°N at the EPR.

Ctenopelta Warén & Bouchet, 1993

Ctenopelta Warén & Bouchet, 1993:33

Type species: *C. porifera* Warén & Bouchet, 1993; by original designation; hydrothermal vents at EPR.

Ctenopelta porifera Warén & Bouchet, 1993

Ctenopelta porifera Warén & Bouchet, 1993:34, figs. 26D–G, 27A–F, 28A–D.

New records: *EPR at 13°N:* - HERO 92 dive 2512, 1 spm; - HERO 92 dive 2528, 1 spm.

Distribution: EPR at 13°N, ca. 2600 m depth.

Remarks: *Ctenopelta porifera* is usually badly discolored by sulfides, and the pores penetrating the shell may perhaps be involved in chemosynthetic activity.

Echinopelta McLean, 1989

Echinopelta McLean, 1989b:58.

Type species: *E. fistulosa* McLean, 1989; by original designation; hydrothermal vents at EPR.

Echinopelta fistulosa McLean, 1989

(Figure 28b)

Echinopelta fistulosa McLean, 1989b:60, figs. 41–48.

New records: *EPR at 13°N:* - HERO 91 PL04, 9 spms; - HERO 91 PL05, 1 spm.

Distribution: EPR at 21°N and 13°N, at a depth of about 2600 m.

Remarks: This is the first record outside the type locality. The specimens were found in residues from tubes of vestimentifera. We figure a critical-point dried specimen for comparison with the species of *Nodopelta,* to show the abundance of epipodial tentacles.

Rhynchopelta McLean, 1989

Rhynchopelta McLean, 1989b:57.

Type species: *R. concentrica* McLean, 1989; by original designation; hydrothermal vents at EPR.

Rhynchopelta concentrica McLean, 1989

Rhynchopelta concentrica McLean, 1989b:58, figs. 32–40.

New records: *EPR at 13°N:* - HERO 91 PL 13, 14 spms; - HERO 91 PL 11 (Genesis), 8 spms; - HERO 91 PL 17, 13 spms; - HERO 91 PL 19, 34 spms; - HERO 91 PL 21, 74 spms; - HERO 91 PL 26, 57 spms; - HERO 92 dive 2512, 8 spms; - HERO 92 dive 2514, 1 spm; - HERO 92 dive 2516, 3 spms; - HERO 92 dive 2517, 77 spms; - HERO 92 dive 2519, 1 spm; - HERO 92 dive 2521, 1 spm; - HERO 92 dive 2523, 1 spm; - HERO 92 dive 2524, 8 spms; - HERO 92 dive 2528, 1 spm; - HERO 92 dive 2531, 3 spms. *EPR at 09°50'N:* - HERO 91 PL 09, 1 sh. *EPR at 17°S:* - GEOCYARISE 84, 17°26'S, 113°12'W, 2600 m, 1 spm.

Distribution: EPR from 21°N to 17°S, ca. 2500–2600 m, usually living on tubes of Vestimentifera.

Remarks: The larva of *R. concentrica* was identified in plankton samples taken a few meters above the sea floor at the EPR at 09°50'N (Mullineaux et al., 1996).

Lirapex Warén & Bouchet, 1989

Lirapex Warén & Bouchet, 1989:84.

Type species: *L. humata* Warén & Bouchet, 1989; by original designation; vents at the EPR at 21°N.

Remarks: The three species now classified in *Lirapex* share the presence of axial sculpture, usually most developed at the shoulder of the whorls and hooklike marginal teeth (flat, truncated with recurved comblike apical serration in *Depressigyra*).

Lirapex ***costellata*** Warén & Bouchet, sp. nov.

(Figures 15m, 16i, 30a–c, 31a–c)

Type material: Holotype and 7 paratypes in MNHN.

Type locality: MAR, Lucky Strike, DIVA 1 PL 04, Tour Eiffel, 37°17.32'N, 32°16.51'W, 1685 m, on inactive chimney among Hydrozoa and the sponge *Cladorhiza.*

Material examined: *Lucky Strike:* - DIVA 1 PL 04, in baited trap, 3 spms; - DIVA 2 PL 04, 12 spms; suction sample among mussels in shimmering water, 1 spm; - DIVA 2 PL 07, 2 suction samples among mussels and hydrothermal sediments, 6 and 2 spms; - DIVA 2 PL 10, suction sample among mussels and hydrothermal sediments, 1 spm, retrieval box, 1 spm; - DIVA 2 PL 24, 3 spms; - DIVA 2 PL 25, 2 spms; - MARVEL PL1191, Bairro Alto, suction sample, 1 spm; - MARVEL PL1195, Tour Eiffel, 1685 m, retrieval box, 5 spms.

Distribution: Only known from the MAR at the Lucky Strike site, 1600–1700 m, among mussels and in sediment.

Etymology: "*costellata,*" Latin, with small ribs.

Description: *Shell (Figures 30a–c).* Of medium size for the group, skeneimorph, rather sturdy, brownish, with axial ribs, usually covered by thick crusts of rust, with umbilicus and partly detached last whorl. Protoconch (Figure 15m) with indistinct coiling, with about half a dozen, strong, spirally directed ridges on its initial part, later smooth, and with slightly expanded peristome. Diameter 250 μm. The teleoconch has 2.5–3 whorls of almost

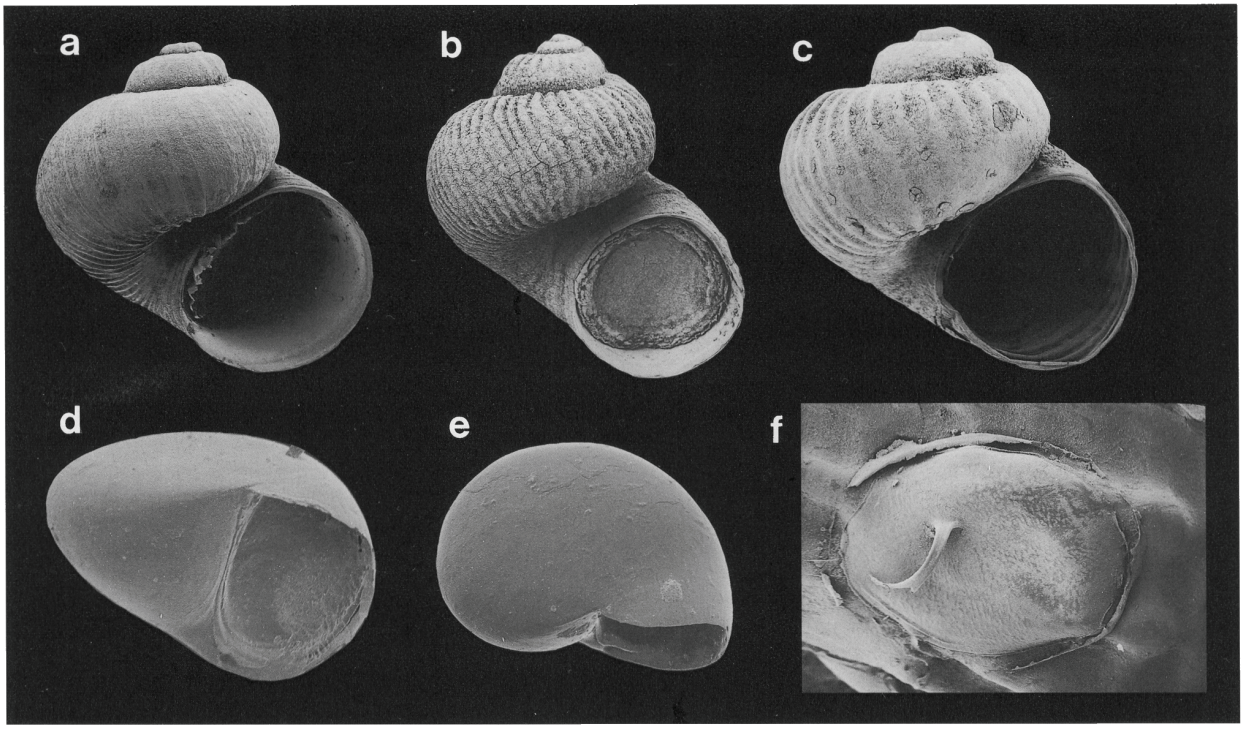


Figure 30. *a–c. Lirapex* ***costellata*** Warén & Bouchet, sp. nov., paratypes, Lucky Strike. *a.* Diameter 2.7 mm. *b.* Diameter 3.2 mm. *c.* Young, diameter 2.1 mm. *d–f. Bathynerita naticoidea,* Bush Hill Seep. *d, e.* Larval shells from egg capsules (protoconch 1), diameter 135 μm and 150 μm. *f.* Egg capsule, diameter 1.3 mm.

round cross section and axial, prosocline, thick and rounded ribs. The ribs are highly variable in their development, sometimes crowded and strong, sometimes more distant, sometimes only traces remain at the shoulder and base of the body whorl. The outer lip is simple and slightly thickened. The umbilicus is not very broad and in adult specimens obscured by the detachment of the last ¼ whorl.

Dimensions. Maximum shell height 3.2 mm at a diameter of 3.6 mm.

Soft parts. The foot is flat and muscular, anteriorly bluntly rounded with well developed propodium and the corners drawn out to small tentacles. The epipodial arrangement could not be worked out in detail, but there are at least five tentacles at each side, placed rather far back. The head is large with a short snout and subventral mouth. The cephalic tentacles are short, conical, and stout (contracted). No sensory papillae, neck-lobes or cephalic lappets. The pallial margin lacks appendages. The gill is bipectinate and seems to lack bursicles.

Operculum (Figure 16i). Brown, multispiral with about 12 whorls, concentric nucleus, and short growth zone.

Radula (Figures 31a–c). n-4-1-4-n. The central tooth has a triangular, smooth apical plate. The three inner lateral teeth are uniform, with smooth apical plates, the fourth one is more obliquely directed, broader, and has a small serration at each side of the large main cusp. The marginal teeth are densely packed, the innermost two to three equipped with a triangular cusp and a few denticles, the outer ones have a series of five to seven apical, longitudinally arranged hooks.

Remarks: The four specimens (from different samples) used for examination of the soft parts were all rather poorly preserved and little information could be extracted. The position in *Lirapex* seems, however, quite certain, judging from good similarity in shell and radula and no remarkable deviations in the soft parts.

Lirapex sp. nov.

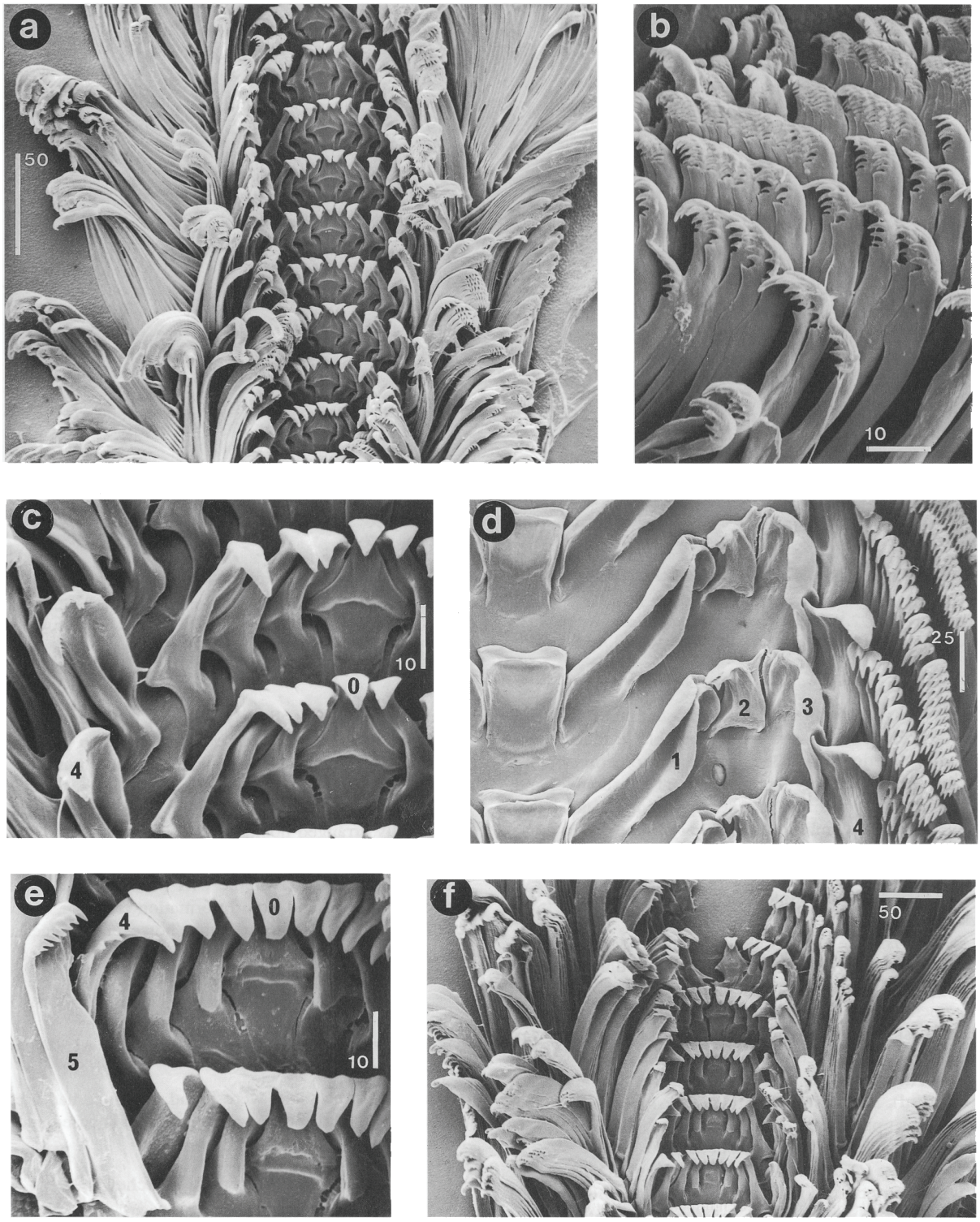
Material examined: MAR at Snake Pit: - ALVIN dive 2615, 3 shs.

Remarks: Three shells were found, but none had a protoconch left and the systematic placement is based mainly on intuition.

Depressigyra Warén & Bouchet, 1989

Depressigyra Warén & Bouchet, 1989:80.

Type species: *D. globulus* Warén & Bouchet, 1989; by original designation; hydrothermal vents at EPR.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Depressigyra globulus Warén & Bouchet, 1989

(Figure 15o)

Depressigyra globulus Warén & Bouchet, 1989:80, figs. 30–31, 45–47, 51–52, 73, 83.
Depressigyra globulus: Warén & Bouchet, 1993:35.

New records: *JdF,* Fairy Castle Vent site: 1 spm (Figure 15o). *Axial Seamount,* Ashes vent field: - ROPOS R406, 10 spms (FMNH 280889).

Distribution: JdF in 1500–2400 m depth.

Remarks: We have finally been able to examine specimens young enough to show the protoconch (Figure 15o), which is strongly ridged, like all the peltospirid limpet groups and *Lirapex.* This indicates that the genus belongs to that group of genera and not to the neomphalid radiation.

Subclass NERITIMORPHA

Superfamily NERITOIDEA Rafinesque, 1815

Remarks: Three endemic genera of Neritoidea have been reported from vents and seeps, *Bathynerita, Shinkailepas,* and *Olgasolaris* but their relations remain uncertain. *Bathynerita naticoidea* closely resembles Neritidae, and the only noteworthy anatomical difference from shallow water species of that family is the presence of cephalic lappets in *Bathynerita.* Their presence is, however, probably plesiomorphic since such lappets occur in most vetigastropod taxa and since the penis of male *Bathynerita* is a modified such lappet. A very similar penis is present in all Neritoidea and we believe they have lost the lappets.

The two limpet-shaped genera *Shinkailepas* and *Olgasolaris* appear quite different, and Beck (1992b) assumed *Olgasolaris* to have "been adapted to hydrothermal vents for a very long time" (contrasting *Shinkailepas*). McArthur & Tunnicliffe (1998) considered *Olgasolaris* to be phylogenetically close to *Nerita,* while *Shinkailepas* and *Bathynerita* were believed to form a more distant group.

A problem in the assessment of relations is that little is known about Neritopsidae, the second main group of Neritopsina. Their radula has lost most of the central field (Warén & Bouchet, 1993), as in Titiscaniidae, and is of little use for comparative purposes. We have seen no protoconchs of *Neritopsis* good enough to allow comparison with *Shinkailepas,* and the soft parts have not been described in enough detail to allow comparison (only a female described, Fischer 1875). Species of Neritopsidae live deep down in the interstices in coarse coral gravel and in submarine caves (Kase & Hayami, 1992).

The third group of Neritimorpha is better known (Fretter, 1984). Species of the family Phenacolepadidae usually live under buried, decaying wood, under rocks, or in subterranean tidal water passages in coral platforms where high bacterial activity can be expected from the presence of organic material and dissolved, reducing compounds (Fretter, 1984; Bouchet & Warén, 1993, unpublished observations). Due to this way of living, they are rarely found alive, and fresh shells of most species frequently are covered by or have remains of crusts of rust. An ability of the larvae to recognize these kinds of biotopes, as well as their use of hemoglobin as respiratory pigment, may have been a starting point for the evolution of taxa restricted to vents and seeps.

The radula of *Bathynerita* resembles that of shallow water neritids in the massive development of tooth number 5, while in *Olgasolaris* and *Shinkailepas* it is smaller with a few well developed cusps. This may, however, be caused by heterochrony since very young *Smaragdia* and *Nerita* have a small tooth number 5 with strong cusps (unpublished). When discussing the relations of *Olgasolaris* and *Shinkailepas,* Beck (1992b) commented that their outermost marginal tooth was "flabelliform as in Pleurotomariacea." The latter statement needs some comments. Similar marginal teeth were considered typical for Eucyclinae (Trochidae, Trochoidea) by Hickman & McLean (1990:74, fig. 43F), but this kind of outer marginals, sometimes very broad (as in *Sutilizona* ***pterodon,*** Figure 18a), sometimes more slender (Figure 18g), seems to occur in most groups of vetigastropods, although they may be difficult to distinguish because they have a strong tendency to stick together (Warén, in press).

Olgasolaris has well developed cephalic lappets like *Bathynerita* and is in this aspect probably plesiomorphic, while *Shinkailepas* lacks them.

The shell characters of *Shinkailepas, Olgasolaris,* and Phenacolepadidae are difficult to use for classification since much homoplasy probably is involved in the process of limpetization. Nevertheless it should be noticed that the veliger larvae of *Shinkailepas* do resorb the internal coiling of the protoconch. So do also the species of Neritidae with both protoconch and teleoconch, while species of Neritopsidae do not resorb the early whorls.

This discussion can hardly be carried further until more anatomical information is available, which is beyond the

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Figure 31. Radulae. Teeth numbered sequentially with central tooth as 0. *a–c. Lirapex* ***costellata*** Warén & Bouchet, sp. nov., paratypes. *a.* Full width of radula. *b.* Detail of marginal teeth. *c.* Detail of central field. *d. Shinkailepas* ***briandi*** Warén & Bouchet, sp. nov., MAR, Menez Gwen. *e, f. Peltospira* ***smaragdina*** Warén & Bouchet, sp. nov., MAR, Menez Gwen. *e.* Central field and first marginal tooth. *f.* Whole width of radula. Scale bars in μm.

intentions of this paper, and we keep *Bathynerita* in Neritidae and *Olgasolaris* and *Shinkailepas* in Phenacolepadidae.

Family PHENACOLEPADIDAE Pilsbry, 1895

Shinkailepas Okutani, Saito & Hashimoto, 1989

Shinkailepas Okutani, Saito & Hashimoto, 1989:224.

Type species: *Shinkailepas kaikatensis* Okutani, Saito & Hashimoto, 1989; by original designation; hydrothermal vents at Kaikata Seamount, Japan.

Remarks: Beck (1992b) described a second species, *Shinkailepas tufari,* from hydrothermal vents at the Manus Back Arc Basin, and is in the process of describing a third species from the Fiji and Lau Basins. These species are all quite uniform in shell and soft part morphology and differ mainly in the position and development of the apex, size, and details in the shell sculpture.

Shinkailepas ***briandi*** Warén & Bouchet, sp. nov.

(Figures 16a, b, 31d, 32a–h, 33a–e)

Type material: Holotype and 8 paratypes in MNHN.

Type locality: MAR, Menez Gwen, DIVA 2 PL 26, 37°50.54'N, 31°31.30'W, 860–870 m.

Material examined: *MAR, Menez Gwen:* - DIVA 1 PL 13, 1 spm; on an active chimney, 24 spms + egg capsules; - DIVA 2 PL 12, 3 spms; - DIVA 2 PL 14, suction sample among mussels, 4 spms; - MARVEL PL1201, 850 m, 4 spms; - MARVEL PL1208, retrieval box, 5 spms. *Lucky Strike:* - DIVA 1 PL 01, among mussels, 23 spms + egg capsules; - DIVA 1 PL 03, 51 spms; - DIVA 1 PL 04, 2 spms; - DIVA 1 PL 08, on a rock, 55 spms; - DIVA 1 PL 17, 60 spms, among mussels, 3 spms; - DIVA 1 PL 18, among mussels, 5 spms; - DIVA 2 PL 1, 1 spm; - DIVA 2 PL 2, 429 spms; on chimney, 3 spms; on sulfide flange, 120 spms; - DIVA 2 PL 03, 1 spm; - DIVA 2 PL 04, 7 spms; - DIVA 2 PL 05, 7 spms; - DIVA 2 PL 07, 140 spms; on mussels, 26 spms; 3 suction samples among mussels and hydrothermal sediments, 1, 2 & 3 spms; - DIVA 2 PL 08, 32 spms; 2 suction samples among mussels and hydrothermal sediments, 1 spm each; - DIVA 2 PL 09, 12 spms; suction sample among mussels and hydrothermal sediments, 2 shs; - DIVA 2 PL 10, suction sample among mussels and hydrothermal sediments, 1 spm; retrieval box, 1 spm; - DIVA 2 PL 19, 1 spm; - DIVA 2 PL 20, 1 spm; - DIVA 2 PL 23, 19 spms; - DIVA 2 PL 25, 381 spms; - DIVA 2, in particle trap, 1 spm; - ALVIN dive 2604, 4 spms + egg capsules; 1636 m, 1 spm; - ALVIN dive 2605, 39 spms + egg capsules; - ALVIN dive 2606, 48 spms + 1 veliger; - LUSTRE Exp. Sintra site, on mussels, 27 spms; - MARVEL PL1193, Tour Eiffel, retrieval box, 1 spm; - MARVEL PL1200, Bairro Alto, 0.25 m^2 rock surface close to edifice, 39 spms; - MARVEL PL1205, Bairro Alto, retrieval box, 8 spms; - MARVEL PL1206, retrieval box, 1700 m, 4 spms. *Snake Pit:* - ALVIN dive 2622 (Elan), 16 spms. *Rainbow:* - MARVEL, 3 particle traps, 2 veligers, 3 young. *MAR Logatchev site:* - MICROSMOKE PL 14, 8 spms; - MICROSMOKE PL 20 (Irina), 1 spm.

Distribution: The MAR, from Menez Gwen to Logatchev site, at a depth of 850–3500 m, on mussels and rocks.

Etymology: Named after Patrick Briand at IFREMER, who has sorted much of the material from the French deep-sea program.

Description: *Shell (Figures 32a–d, g, h).* Limpet-shaped, ovate, low, rather sturdy, covered by a thin colorless periostracum, with distinct columellar shelf and apex situated straight above this. The protoconch (Figure 32f) is small and smooth with slightly expanded peristome; earlier whorls concealed by later ones, except a part of protoconch 1. Diameter 750–800 μm. The teleoconch consists of slightly more than one whorl, with the small spire situated at the posterior right 1/6, The sculpture consists of collabral, low lamellae and numerous spiral ridges which are crossed by the lamellae. The columellar shelf is wide, corresponding to ca. 1/5 of the length of the shell. The muscle scars are situated, one at each side, under the most anterior part of this shelf; they are as long as high and their length corresponds to ¼ of the shell. The shell margin is not thickened.

Dimensions. Holotype, maximum diameter 8.9 mm, average adult size 5 mm, maximum size 10 mm.

Soft parts (Figures 33a–e). The foot is low and flat, anteriorly truncated with rounded corners and a propodium demarcated by a fissure. The epipodium consists of a simple flat ridge or skin fold which encircles the foot, from the left to the right cephalic tentacle base. Its posterior part is thick and folded and can probably be expanded to cover the whole columella and shell margin,

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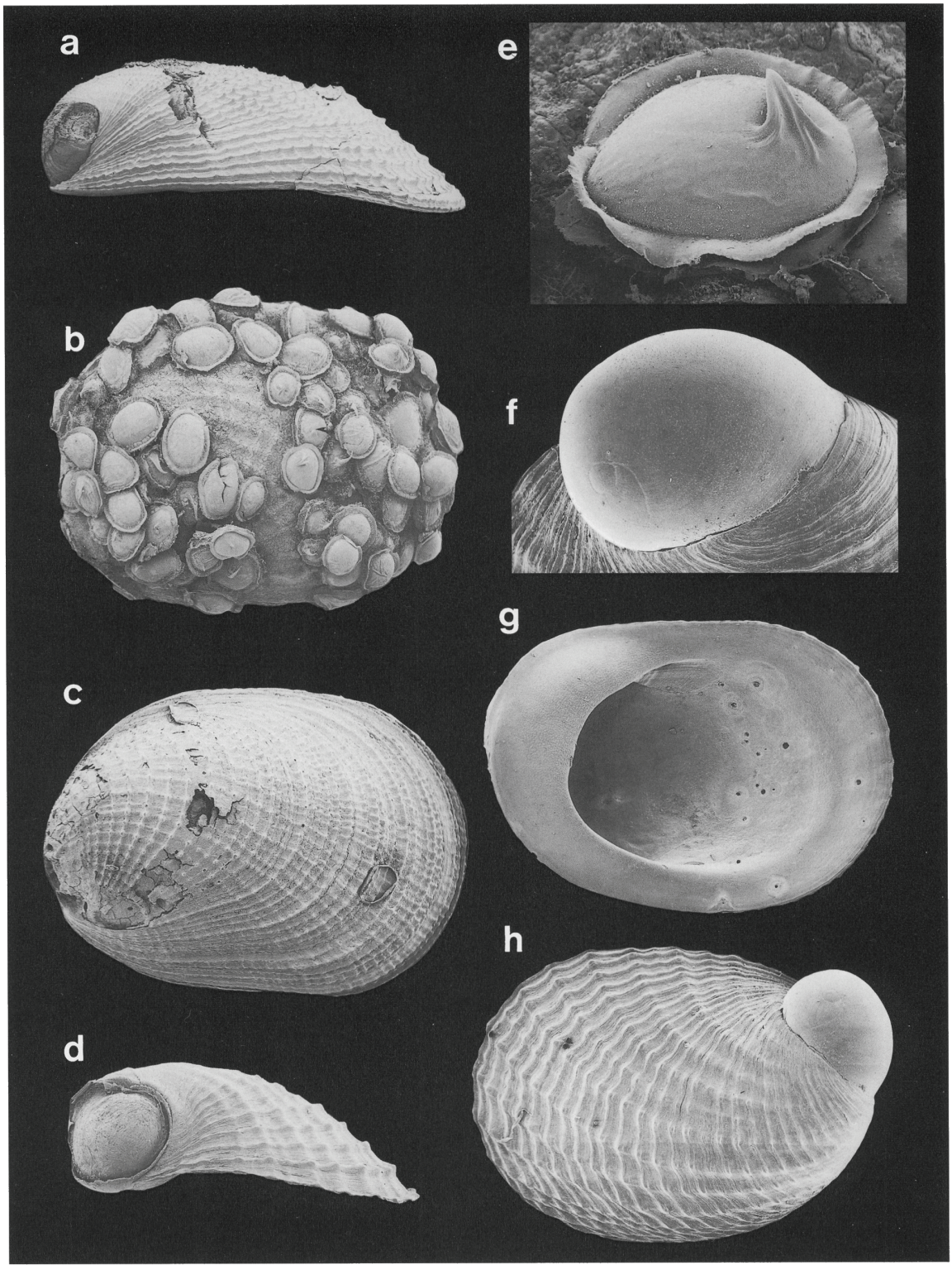
Figure 32. *Shinkailepas* ***briandi*** Warén & Bouchet, sp. nov., MAR. *a.* Adult specimen, Lucky Strike, lateral view, 5.6 mm. *b.* Adult specimen covered by egg capsules, Menez Gwen, diameter of shell 6.0 mm. *c.* Large shell, Menez Gwen, diameter 8.4 mm. *d.* Young specimen, protoconch corroded, Lucky Strike, diameter 1.9 mm. *e.* Egg capsule, Menez Gwen, diameter, 0.77 mm. *f.* Protoconch, Lucky Strike, diameter of shell 0.78 mm. *g.* Adult shell, apertural view, Lucky Strike, diameter 4.9 mm. *h.* Young specimen with preserved protoconch, Lucky Strike, diameter of shell 2.2 mm.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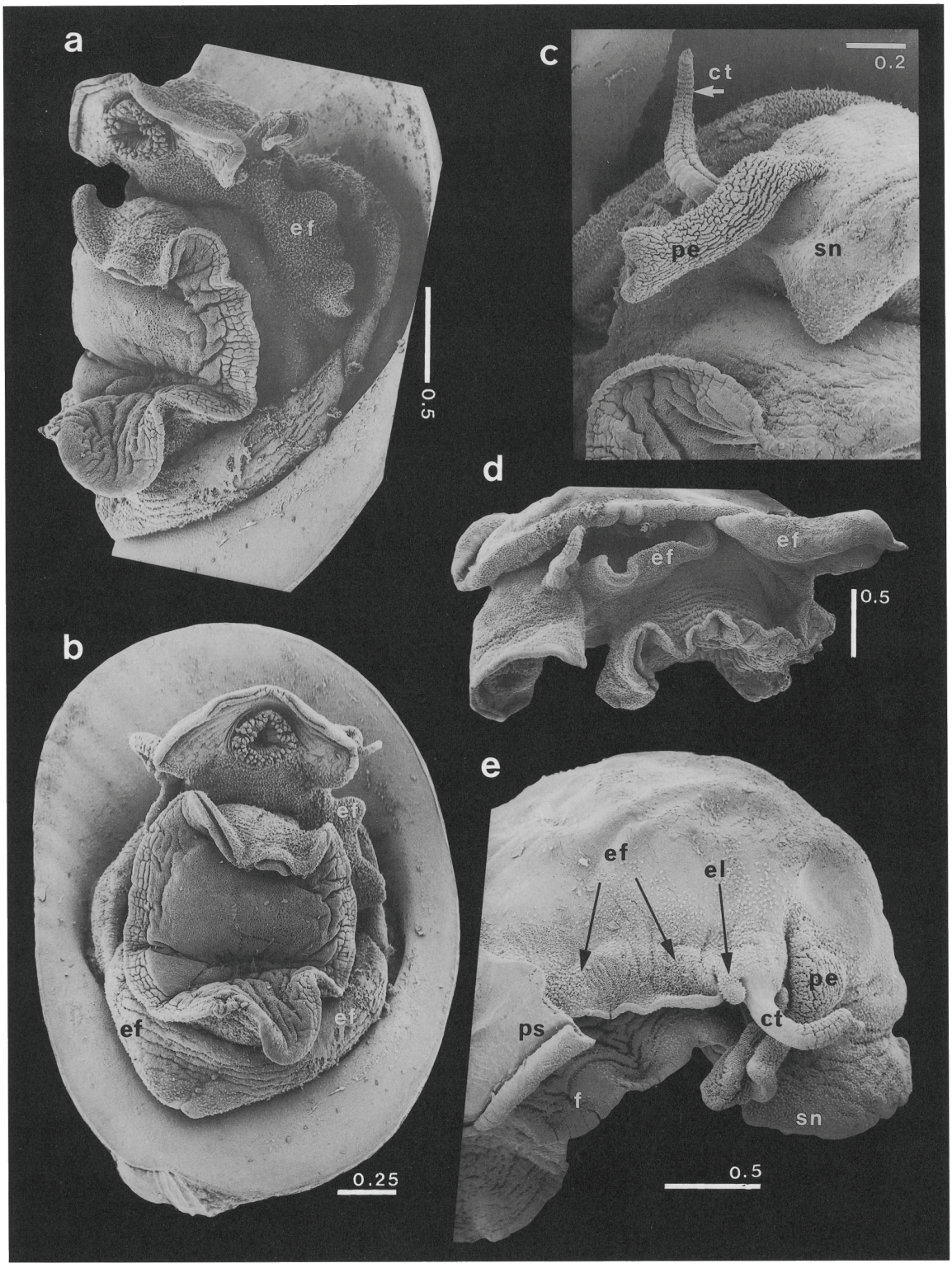
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as indicated by their smooth surface. The neck-lobe is not demarcated from the epipodium. The operculum is not visible from the outside but lies in a deep pocket between the epipodium and the visceral mass. The head is very large and broad, the snout even wider and drawn out to lateral flaps. The mouth is ventral and surrounded by a fringe of large papillae. The cephalic tentacles are long and slender, tapering, and have a small, basal eye-lobe, but no externally visible eye (except in the veligers). The male has a large, gutterlike penis attached anteriorly to the tentacle. The gill is large, bipectinate, lacks sensory bursicles, and is attached only very basally.

Egg capsules (Figure 32e). The capsules are tough and sturdy, maximum diameter 0.7–0.9 mm, and contain 5–13 eggs of a diameter of 90–100 μm. Veligers ready to hatch have a diameter of 125–135 μm. Recently laid capsules are transparent, older ones brownish opaque.

Operculum (Figures 16a, b). The operculum is irregularly shaped, rather thin, patchily calcified. The larval operculum is readily distinguished at the apex, partly surrounded by later growth. It consists of a small, smooth initial part, probably corresponding to the operculum of the hatching larva, diameter ca. 110 μm; then follows ¾ spirally striated whorl, corresponding to the planktotrophic life, diameter 0.55–0.60 mm. At this stage the operculum has a ridgelike muscle attachment with a small lateral peg on the inside (Warén & Bouchet, 1993:fig. 1d). The part formed during the benthic life is thin and fragile, sculptured with distinct growth lines. The length corresponds to about ⅓ of the length of the shell.

Radula (Figure 31d). n - 4 - 1 - 4 - n. The central tooth is a low, rectangular plate, slightly expanded apically and with one or two transverse ridges. The first lateral looks like a pair of parallel lamellae, which are joined at the outer extreme part. Lateral tooth number two is slightly smaller than the rhachidian, very irregular and shapeless with a "double" apical triangular plate, and a strong posterior supporting ridge. The third lateral tooth is simple, rounded, and scalelike, about twice the size of number 2. Lateral tooth four is large and robust, with a large, sturdy triangular apical plate which is weakly serrated at the inner edge. The outer supporting ridges, posterior and anterior ones, are fused to a large shield which forms a demarcation to the marginals. The inner marginal teeth are shorter than the outer lateral one, slightly longer toward the edge, flat, densely packed. The inner marginal teeth have a tricuspidate apical plate; farther toward the edge the cusps are more numerous and much smaller.

Remarks: The size of the veligers ready to hatch (125–135 μm) and the size of the recently settled larvae, maximum diameter 0.8 mm, clearly shows that the larvae pass through a planktotrophic phase. The soft parts of the newly settled larva are brightly pigmented with black, and the larva has eyes. The visceral mass is not coiled, but forms a round sac, because the interior of the whorls are resorbed also in the protoconch.

Shinkailepas ***briandi*** is one of the most common gastropods from the better investigated localities at the MAR. The veliger larva resembles that of *Smaragdia viridis* (Linnaeus, 1758) (Neritidae) in size and shape. Larvae of *Smaragdia* have, however, an opercular sculpture by growth lines only, no spiral lines.

Family NERITIDAE Rafinesque, 1815

Bathynerita Clarke, 1989

Bathynerita Clarke, 1989:125.

Type species: *B. naticoidea* Clarke, 1989; by original designation; Caribbean hydrocarbon seeps.

Taviani (1994) mentioned that, based on unpublished data, he considered *Thalassonerita* Moroni, 1966 a senior synonym of *Bathynerita.*

Bathynerita naticoidea Clarke, 1989

(Figures 30d–f)

Bathynerita naticoidea Clarke, 1989:125, figs. 3, 4; text figs.
Bathynerita naticoidea: Warén & Bouchet, 1993:3, figs. 1, 2, 3A–C.

New records: *Off Louisiana:* - Johnson Sealink dive 3129, 200 spms. *Off Barbados (El Pilar Sector):* - DIAPISUB 15-2, 35 spms.

Distribution: Recorded from five localities at 27°41–47′N, 91°13–30′W, 550–800 m depth (Zande, 1994); herein also from off Barbados, 11°14′N, 59°30′W, 1135 m.

Remarks: The ecology of *Bathynerita naticoidea* was studied by Zande (1994), who found no bacterial symbionts, only scattered fungi on the gill, and concluded that the main diet is chemosynthetically nourished macrofauna and flora obtained by scraping hard surfaces. She concluded that the development is lecithotrophic, but this was not clearly shown and we favor the opinion that the development is planktotrophic. The egg capsule is figured in Figure 30f and is of normal neritoid morphology (Neritidae: Andrews, 1935; Phenacolepadidae: Risbec, 1935, figs 6–8, as *Cocculina* sp.). Our egg capsules have a diameter of ca. 1.2 × 0.9 ± 0.2 mm and contain about 25–

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Figure 33. *Shinkailepas* ***briandi*** Warén & Bouchet, sp. nov., MAR, critical-point dried. *a.* Left side of body. *b.* Ventral view. *c.* Right side of head. *d.* Left side of body. *e.* Left side of head. ct - cephalic tentacle; ef - epipodial fold; el - eye-lobe; f - foot; pe - penis; ps - pallial skirt; sn - snout. Scale bars in mm.

35 eggs of a diameter of 90–100 µm which develop to veligers of a shell diameter of 130–140 µm (Figures 30d, e). Eckelbarger & Young (1997) investigated the oogenesis, and reported a maximum egg diameter of 135–145 µm, but this may refer to eggs flattened by deformation and compression in the gonad. Zande (1994) reported egg capsules of twice this size with 130–180 embryos of similar diameter. The measurements correspond well with the size of protoconch 1 of *Nerita atramentosa* Reeve, 1855, from Australia (own observation), *Neritina virginea* (L., 1758), *N. clenchi* (Russell, 1940), and *Nerita tesselata* Gmelin, 1791 (all Caribbean; Bandel, 1982). All these species are known to have planktotrophic development. Regrettably no benthic stages of *B. naticoidea* young enough to retain any trace of the protoconch have been seen by us (smallest specimen seen, 3.5 mm shell diameter), but this agreement in size gives an indication of planktotrophy, while there is no data to support lecithotrophy. The size of egg capsules (up to 2.9 × 2.15 mm) and numbers of embryos (130–180) given by Zande (1994) indicate a large variation (cf. 25–35, above), but the numbers correspond to the calculated increase in volume from a capsule diameter of 1.2 mm to 2.1 mm and are probably correct, since also the maximum size of the specimens varied considerably (11–19 mm) between the localities investigated by Zande.

Specimens from the Bush Hill Seep often have the egg capsules attached to their shell, but capsules were also found on *Provanna sculpta, Cataegis meroglypta,* and other shells. About half of the egg capsules from dive 3129 were hatched.

Subclass CAENOGASTROPODA

Family PROVANNIDAE Warén & Ponder, 1991

Remarks: Species of Provannidae have been found in fossil cold seeps back to Late Jurassic - Early Cretaceous deposits of the Great Valley Group in California (Campbell, personal communication). It is interesting that also species of *Abyssochrysos* (Abyssochrysidae) occurred there, since they have been assumed to be related to Provannidae (Warén & Ponder, 1991). Abyssochrysids have so far not been reported from recent vents or seeps, although they have recently been reported from younger fossil cold seeps (Middle Eocene, State of Washington: Goedert & Kaler, 1996). Some caution is suggested about these records since the specimens are either poorly preserved, and no protoconchs have been examined, or the reports are preliminary.

Provanna Dall, 1918

Provanna Dall, 1918:7.

Type species: *Trichotropis* (?) *(Provanna) lomana* Dall, 1918a; by monotypy; deep water off southern California.

Remarks: The new material of species of *Provanna* is of great interest since it adds considerably to the distribution of six species and reduces the initial impression that every new locality had its own set of species. This is also the first time that species of *Provanna* have been recorded from a biogenic substrate (*P. macleani* and *P. pacifica* on sunken driftwood).

It is very rare to find anything left of the protoconch in species of *Provanna,* and we want to draw the attention to Gustafson & Lutz's (1994, fig. 4:14) figure of a well preserved protoconch of *Provanna variabilis.*

Provanna lomana (Dall, 1918)

Trichotropis (Provanna) lomana Dall, 1918a:7.

Provanna lomana: Warén & Bouchet, 1986:161, figs. 1, 2, 18, 23.

New records: *Oregon Margin:* - TVG 115, from calcareous blocks, 2 spms, 5 shs; - ROPOS #339, Pete Vent Field, 17 spms; - ROPOS #339, 9 shs (SMF 311993); - TVG 11, 2 shs, 4 spms (SMF 311994, 311995).

Distribution: From southern California to the Oregon Margin, ca. 450–1200 m.

Remarks: Examination of the soft parts and the radula did not reveal any difference between specimens from southern California and the Oregon Margin.

Provanna goniata Warén & Bouchet, 1986

Provanna goniata Warén & Bouchet, 1986:163, figs. 5, 6, 19, 25.

New records: *Guaymas Basin:* - GUAYANAUT PL 07, 1 spm; - GUAYANAUT PL 08, 1 spm; - GUAYANAUT PL 15, 8 spms; - GUAYANAUT PL 16, 13 spms; - GUAYANAUT PL 18, 28 spms.

Distribution: Only known from the Gulf of California, Guaymas Basin, 2020 m.

Remarks: This is the largest known species of *Provanna* with a shell height of up to 16 mm.

Provanna ios Warén & Bouchet, 1986

Provanna ios Warén & Bouchet, 1986:162, figs. 8, 9, 20, 22.

New records: *EPR at 13°N:* - HERO 91 PL 21, 1 spm; - HERO 92 dive 2517, 2 spms. *EPR at 17°S:* - NAUDUR PL 06, site Rehu, 3 spms.

Distribution: EPR from 21°N to 17°S, in 2450–2600 m depth.

Provanna laevis Warén & Ponder, 1991 (Figure 6c)

Provanna laevis Warén & Ponder, 1991:53, figs. 3C–D, 4A, 20H–I, 21C–D, 23D.

New records: *JdF, Axial Seamount,* Ashes vent field: - ROPOS R406, 25 spms (FMNH 280891). *Oregon Margin:* - ROPOS #339, Pete Vent Field, 7 spms (3 with *Pyropelta corymba* attached), 3 shs; with no detail, 1 spm, 5 shs; - TVG 11, 2 spms (1 with *P. corymba*) (1 in SMF 311996). *Guaymas Basin:* - GUYANAUT PL 13, 28 spms; - GUYANAUT PL 15, 3 spms; - GUYANAUT PL 16, 4 spms; - GUYANAUT PL 18, 44 spms, 14 shs.

Distribution: Gulf of California, Guaymas Basin, ca. 2000 m depth, to the Oregon Margin, 500–600 m depth and JdF, Ashes vent field, ca. 1500 m.

Remarks: Examination of the soft parts and the radula did not reveal any difference between specimens from the three widely separated localities mentioned above. Several specimens from the Oregon Margin had the cocculiniform *Pyropelta corymba* (see above) attached to the shell, and it is worth noticing that *Provanna laevis* was described from the same seep field in the Guaymas Basin as *P. corymba,* and later was recorded (McLean, 1992b: 409) from the type locality of *P. laevis.*

Provanna sculpta Warén & Ponder, 1991

Provanna sculpta Warén & Ponder, 1991:53, figs. 3A–B, 8, 14, 18, 20C, E, 21A–B, 23B.

New records: *Off Louisiana:* Johnson Sealink dive 3129, 45 spms, 21 shs.

Distribution: Only known from off Louisiana, at the Bush Hill Seep, at a depth around 550 m.

Remarks: Two shells had damaged outer lip, typical for crab predation. About half of the specimens had up to eight neritid egg capsules attached to the shell, and three specimens had very young *Bathymodiolus* sp. attached to shell.

Provanna variabilis Warén & Bouchet, 1986

Provanna variabilis Warén & Bouchet, 1986:163, figs. 13–15, 26–28.
Provanna variabilis: Gustafson & Lutz, 1994:figs. 4:13–15.

New records: *Endeavour Segment:* - ATV 50-1, Fairy Castle edifice, 1 spm. *Oregon Margin:* - ALVIN dive 2796-2927, 9 spms (Tunnicliffe).

Distribution: JdF, Oregon Margin at 45°N, and the Gorda Ridge (Gustafson & Lutz, 1994), at 675–2200 m depth.

Remarks: Gustafson & Lutz (1994) figured the protoconch, which seems to be the only known, well preserved protoconch of a species of *Provanna.*

Provanna macleani Warén & Bouchet, 1989

Provanna macleani Warén & Bouchet, 1989:94, figs. 111–114.

New records: *Oregon Margin:* - 44°40′N, 125°33′W, 2750 m depth, 2 spms from a piece of sunken driftwood (FMNH 278325).

Distribution: Previously only known form the type locality, 44°52.4′N, 126°40.8′W, 2713 m depth, near the new record.

Remarks: This is not a record that belongs to the vent fauna, but it is of interest because the habitat was not known for this and the following species, and they are the first documented records of the genus outside vent and seep environments.

Provanna pacifica (Dall, 1908)

Cerithioderma pacifica Dall, 1908a:324.
Provanna pacifica: Warén & Bouchet, 1986:161, figs. 4, 17.

New records: *Oregon Margin:* - 44°40′N, 125°33′W, 2750 m depth, 4 spms from a piece of sunken driftwood (FMNH 278325).

Distribution: Previously only known form the type locality, Gulf of Panama, 07°05.5′N, 79°40′W, 2311 m.

Remarks: See *P. macleani.*

Provanna sp. 1

Material examined: *Edison Seamount:* - 66-GTVA, 6 shs.

Distribution: Only known from this locality.

Remarks: Six shells of variable quality were found, but they are not good enough to be sure that they represent only one species and we refrain from describing it (them?).

Provanna sp. 2

Material examined: *Aleutian Trench,* Shumagin site: - TVGKG 40, 1 sh, 1 spm (SMF 311992).

Distribution: Only known from this locality.

Remarks: This is certainly an undescribed species, but the specimens are young, and premature description may cause future problems.

Provanna sp. 3

Material examined: *Mid America Trench, Jalisco Block Seeps at 20°N:* - NAUTIMATE PL 10, 2 shs.

Distribution: Only known from this locality.

Remarks: Two shells resemble *P. macleani* in lacking axial sculpture, but have weaker spiral ribs and a taller spire. This is certainly an undescribed species, but the specimens are young and a formal description would be premature.

Family CERITHIOPSIDAE H. & A. Adams, 1853

Remarks: The family Cerithiopsidae is not very well known and its systematics even less understood. It comprises numerous species, as far as known spongivorous. A review of the family is presently being prepared by Bouchet & Warén.

Speculator Warén & Bouchet, gen. nov.

Type species: ***Speculator cariosus,*** sp. nov.

Diagnosis: Shell tall, of a general "*Cerithiella* appearance" with rounded, convex whorls, obliquely drawn-out siphonal canal; no basal-central spiral thread. Radula with seven rows of low, sturdy teeth with three to several cusps.

Etymology: "*speculator*" (Latin) means "explorer," alluding to the type species originating from the Explorer Ridge.

Remarks: The shell has a very generalized appearance for the family, but differs from *Eumetula* by lacking the basal thread typical for this genus, and by having undifferentiated lateral and marginal teeth in the radula. In *Eumetula* Thiele, 1912, the two marginals are tall, have a shaft, and are folded over the lateral tooth. ***Speculator*** superficially resembles species of *Cerithiella* Verrill, 1882, which also lack a basal thread but differ in having a longer, more curved siphonal canal and a different radular morphology with clawlike marginals (Bouchet & Warén, 1993:figs. 1273–1276).

The radula of ***S. cariosus*** is unusual in having a strong variation in the thickness and length of the cusps of the lateral and marginal teeth; these are usually quite uniform. It can only be speculated that this difference is caused by a change in diet in *S. cariosus* compared to other cerithiopsids. It was not possible to check the contents of the intestine, because we had to dry the soft parts in order to detach them from the columella, and rehydration afterward did not soften the body enough for dissection.

Speculator cariosus Warén & Bouchet, sp. nov.

(Figures 34c, d, 36c, 49g)

Type material: Holotype in MNHN.

Type locality: JdF, Explorer Ridge: Magic Mountain, Steve 4 vent, ROPOS #284, 49°45.53'N, 130°15.50'W, 1762 m.

Material examined: Only known from the holotype.

Distribution: Only known from the type locality.

Etymology: "*cariosus*" (Latin) referring to the decaying appearance of some of the cusps of the radular teeth.

Description: *Shell (Figure 34c).* Tall, slender, rather fragile, brownish yellow, with reticulate sculpture. The apical whorls have been lost by corrosion; slightly more than seven distinctly convex whorls remain, sculptured by ca. 30 slightly curved axial ribs on the body whorl. The axial ribs are of varying strength and to some extent intergrading with the incremental lines, less so on the upper whorls. The spiral sculpture consists of four strong cords on the exposed part of the spire whorls and two more basal cords on the last whorl (Figure 34d), encircling the base. Scattered and indistinct, much finer striae are occasionally present above and below these cords. The outer lip is evenly curved, not thickened, and goes smoothly over into the short but very distinct canal.

Dimensions. Height of shell 8.1 mm (apex missing), total height, estimated 8.3 mm.

Operculum (Figure 49g). It is thin, yellowish, paucispiral with indistinct coiling and strongly eccentric nucleus.

Radula (Figure 36c). Long and slender, with seven longitudinal rows of uniformly shaped teeth. Several cusps are in a process of becoming filamentous. The central tooth is very sturdy, low, and broad with three strong cusps of equal size and a smaller denticle at each side. The lateral and first marginal tooth are of very similar shape and their inner end has two well developed cusps of which the inner one is half the size of the one next to it. Then follows a series of about nine cusps of which the innermost is long, thin, and filiform; the following ones gradually increase in size so that the outer three cusps may be of the same width as the second inner cusp. There is, however, variation in this, and some teeth have no sturdy outer cusps, others have three, also in the same longitudinal row. Also the outer marginal tooth is similar, but here the sequence of the sturdy and variable cusps is inverted, so that the outer two or three cusps (often with a small denticle between the two outer ones) are sturdy and the inner teeth variable.

Remarks: As far as known, all species of Cerithiopsidae feed on sponges (Bouchet & Warén, 1993). This speci-

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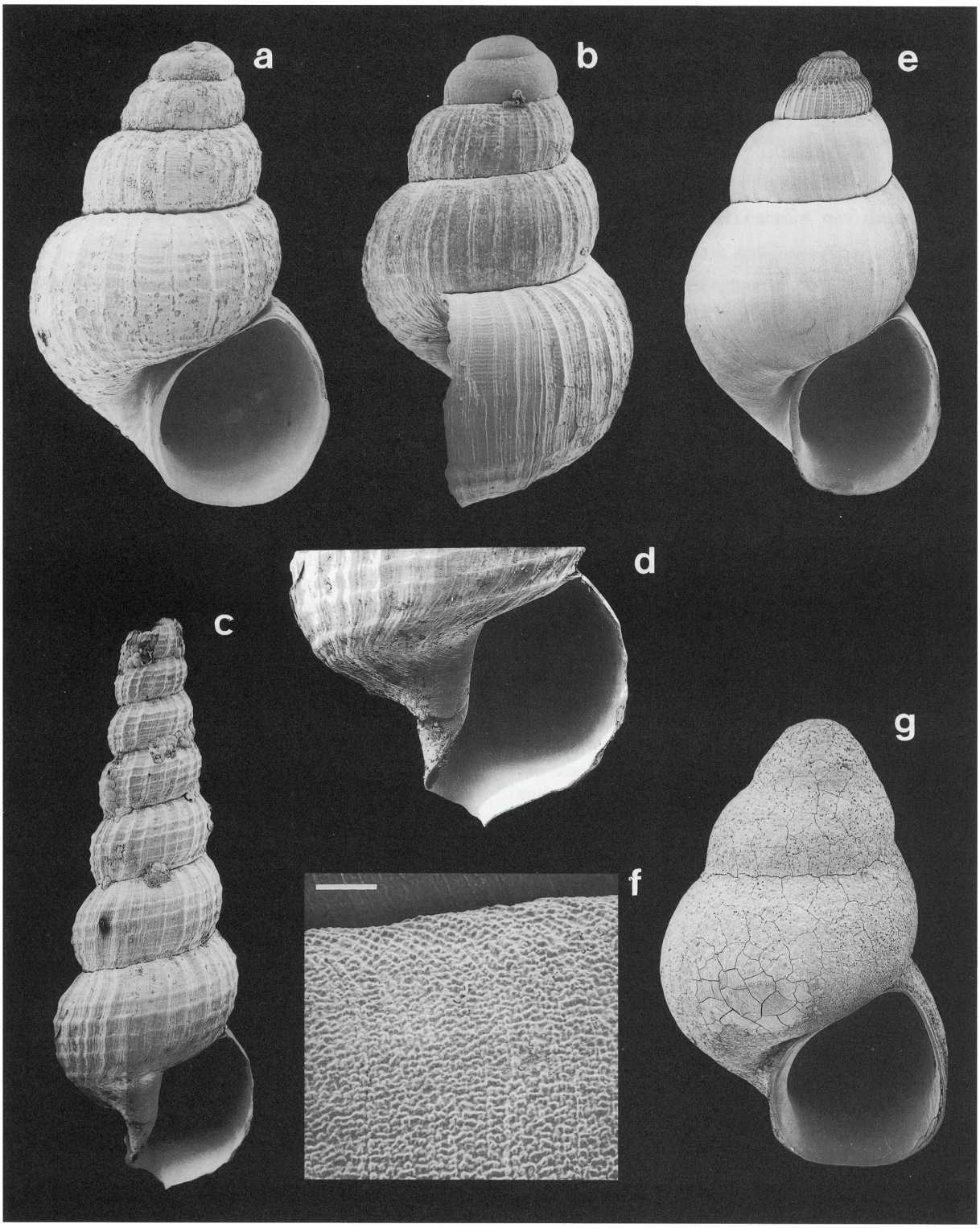
Figure 34. *a, b. Alvania* cf. *stenolopha,* Menez Gwen, 2.6 and 2.3 mm. *c, d.* ***Speculator cariosus*** Warén & Bouchet, gen. & sp. nov., holotype, height 8.5 mm. *e-g. Laeviphitus* ***desbruyeresi*** Warén & Bouchet, sp. nov., Lucky Strike. *e.* Cleaned shell, height 1.84 mm. *f.* Detail of sculpture. *g.* Shell with normal ferrugineous deposits, height 1.52 mm. Scale bar 20 μm.


a
b
e
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c
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f

men came from a grab with tube worms and no sponges in the vicinity. It seems thus possible that the species has another diet, which may be the reason for the strange appearance of the radula with some almost filiform denticles. Perhaps this is a case of recent immigration to the vent environment at the species level.

Family ELACHISINIDAE Ponder, 1985

Laeviphitus van Aartsen, Bogi & Giusti, 1989

Laeviphitus van Aartsen, Bogi & Giusti, 1989:20.

Type species: *L. verduini* van Aartsen, Bogi & Giusti, 1989; by original designation; upper bathyal, Mediterranean.

Remarks: The genus *Laeviphitus* was first known (but not described) from the characteristic veliger larvae (see Warén et al., 1990) which had been caught as plankton in the Mediterranean. A second species was reported as "unidentified veliger" by Turner et al. (1985: fig. 19) from bottom plankton at the Galapagos Rift Zone, and again by Mullineaux et al. (1996) from plankton samples taken a few meters above the sea floor at EPR, 09°50'N. Finally Okutani et al. (1993) described a species from a seep assemblage at the Kaikata Seamount (west of Ogasawara, Japan) at a depth of about 450 m. From the radular morphology they concluded that nothing contradicted a systematic position in the Elachisinidae (suggested by Warén et al., 1990), while a placement in the Epitoniidae, as suggested in the description of the genus, was untenable. Still, the anatomy of *Laeviphitus* has not been examined and the systematic position remains uncertain.

The genus is easy to recognize when the surface deposits of bacterially precipitated iron and manganese oxides has been removed (e.g., by treatment with alkaline hydrogen peroxide or commercial bleach; *caution!* this will also damage the soft parts). The strongly cancellate protoconch, combined with a smooth, rissoiform teleoconch are unique.

Laeviphitus ***desbruyeresi*** Warén & Bouchet, sp. nov.

(Figures 34e–g, 36a, 37b, 49e)

Type material: Holotype and 22 paratypes in MNHN.

Type locality: MAR, Lucky Strike, DIVA 2 PL 07, Tour Eiffel, 37°17.32'N, 32°16.51'W, 1685 m.

Material examined: *Menez Gwen:* - MARVEL PL1208, 850 m, retrieval box, 1 spm; - MARVEL PP50, particle trap, 1 protoconch. *Lucky Strike:* - DIVA 1 PL 01, 3 spms; - DIVA 2 PL 06, 1 spm; - DIVA 2 PL 07, 3 suction samples among mussels and hydrothermal sediments, 17, 5, and 2 spms; - DIVA 2 PL 08, retrieval box, 1 spm, suction sample among mussels and hydrothermal sediments, 2 spms; - ALVIN dive 2607, 1 spm; - LUSTRE Exp. Sintra site, on mussels, 2 spms (no teleoconch); - MARVEL PL1191, Bairro Alto, suction sample, 1 spm.

Distribution: From Menez Gwen, Lucky Strike, and Rainbow, 850–2300 m depth, among mussels and in sediment.

Etymology: Named after D. Desbruyères, co-ordinator of the European AMORES program of exploration of the Mid-Atlantic Ridge.

Description: *Shell (Figures 34e, g).* Small, not especially fragile, rissoiform, smooth, usually covered by thick crusts (Figure 34g), with a distinctly demarcated and cancellate protoconch (Figure 37b). The protoconch 1 consists of an initial whorl which was corroded in the specimens examined and measures about 110 μm in diameter. Protoconch 2 consists of about 2.2 whorls and is sculptured by ca. 40 strong, curved axial ribs and nine or 10 spiral cords which are fused to the ribs but do not cross them and frequently are not perfectly aligned on the two sides of the rib. The diameter of protoconch 2 is ca. 400 μm. The teleoconch consists of 2.25–2.5 smooth whorls, connected by a shallow suture which is more conspicuous in cleaned specimens since there is an open fissure where the rust deposits have peeled off. There is no sculpture visible except very faint incremental lines on the minutely granular surface (Figure 34f). The peristome is bluntly rounded anteriorly, slightly pointed posteriorly, and the basal corner typical for elachisinids is poorly developed. Behind the inner lip is a narrow umbilical crevice.

Dimensions. Height of holotype 1.80 mm, maximum height 1.85 mm.

Operculum (Figure 49e). Thin, yellowish brownish, paucispiral.

Radula (Figure 36a). Taenioglossate. The central tooth is not very sturdy, M-shaped in apical view, with central and three smaller lateral denticles; no additional lower denticles, only a strongly projecting, narrow support. The lateral tooth is triangular, long, and slender with the central $\frac{1}{5}$ of the apical margin equipped with denticles, two to three smaller ones facing the center, a large one and about eight more lateral denticles. The main cusp is supported by a ridge. The first marginal is broad and flat, apically obliquely truncated, and serrated apically and along $\frac{1}{10}$ of the outer margin. The outer marginal tooth is half the width of the first and apically more rounded.

Remarks: *Laeviphitus* ***desbruyeresi*** differs from *L. verduini* mainly by its smaller size, ca. 2 mm (4 mm in *verduini*), and by being considerably more slender with flatter whorls. It differs from *L. japonicus* Okutani, Fujikura & Sasaki, 1993, by having a more evenly rounded peristome, especially the basal part, which is more typically shaped for the family in *L. japonicus*.

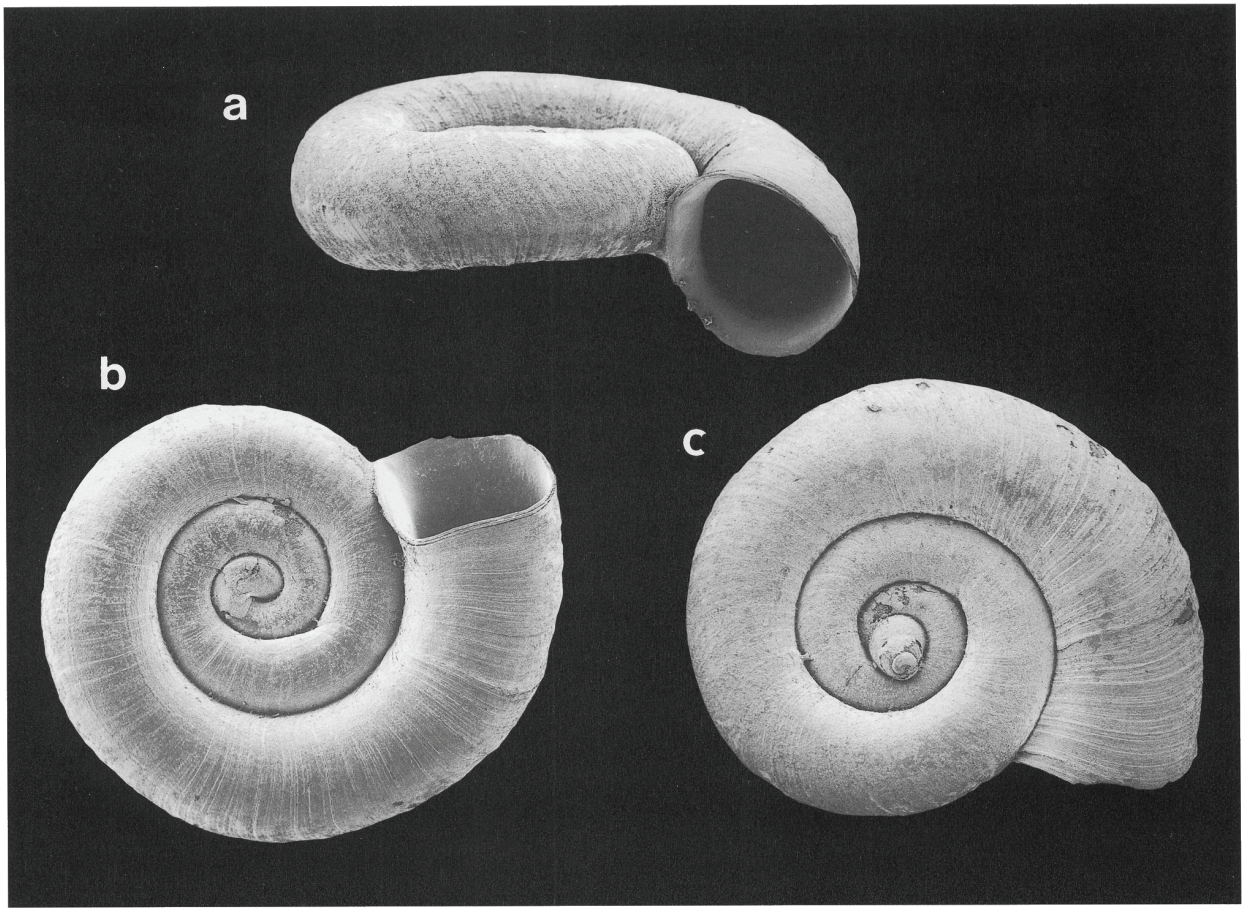


Figure 35. *a–c.* ***Neusas*** Warén & Bouchet, gen. nov., *marshalli,* MAR, Menez Gwen, diameter 2.06 mm.

Family VITRINELLIDAE Bush, 1897

Remarks: The family Vitrinellidae is presently not well understood, as is the case with the related Tornidae (for discussion see Ponder, 1994). Many species of the two families have a depressed to planispiral shell shape and a jaw similar to the new genus below (unpublished observations), and we have provisionally placed ***Neusas*** in the Vitrinellidae.

Neusas Warén & Bouchet, gen. nov.

Type species: *Homalogyra marshalli* Sykes, 1925.

Diagnosis: Small neotaenioglossate gastropods with more or less planispiral, slightly irregularly coiled teleoconch, strongly prosocline peristome, and a tall-spired, obliquely inserted protoconch. Operculum round, corneous, multispiral, with central nucleus. Radula 10 times as long as broad, taenioglossate, with very robust teeth. Central, lateral, and inner marginal tooth with strong irregularly shaped cusps often of alternating strength. Inner marginal tooth very broad, triangular, and low. Outer marginal tooth simple, claw-shaped with three major cusps. Jaw sturdy with hexagonal pattern. Soft parts with pigmented, brownish zone from rear, left corner of pallial cavity, diagonally to just above head. Snout large, distally bilobed; cephalic tentacles small and inconspicuous, situated far apart, with small basal eyes at outer sides.

Etymology: From "*neuo*" (Greek), to lean one's head, alluding to the inclined protoconch.

Remarks: We are not convinced that the type species belongs to the vent fauna, but take this occasion to make a new genus for a group of small, very rare gastropods. We have examined three similar species:

1. *Homalogyra marshalli,* treated here.
2. An undescribed, almost identical species from New Zealand, shells only (in National Museum of New Zealand).
3. An undescribed, less distinctly planispiral species from off New Caledonia, three specimens (in MNHN and

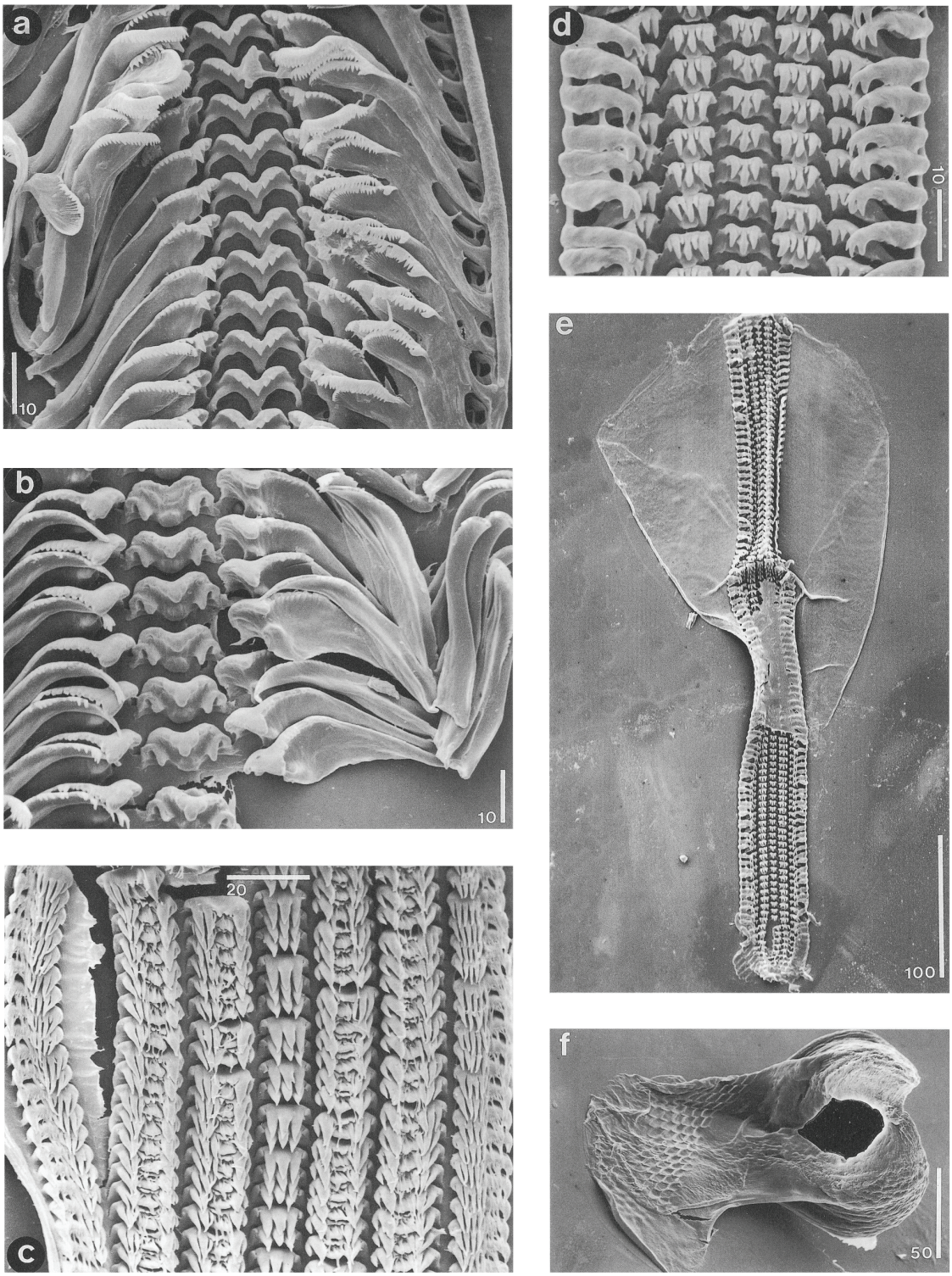


Figure 36. Radulae. *a. Laeviphitus* ***desbruyeresi*** Warén & Bouchet, sp. nov., MAR, Lucky Strike. *b. Alvania* cf. *stenolopha,* MAR, Lucky Strike. *c.* ***Speculator cariosus*** Warén & Bouchet, gen. & sp. nov., holotype. *d–f.* ***Neusas*** Warén & Bouchet, gen. nov., *marshalli,* MAR, Menez Gwen. *d.* Full width. *e.* Complete radula. *f.* Jaw. Scale bars in μm.

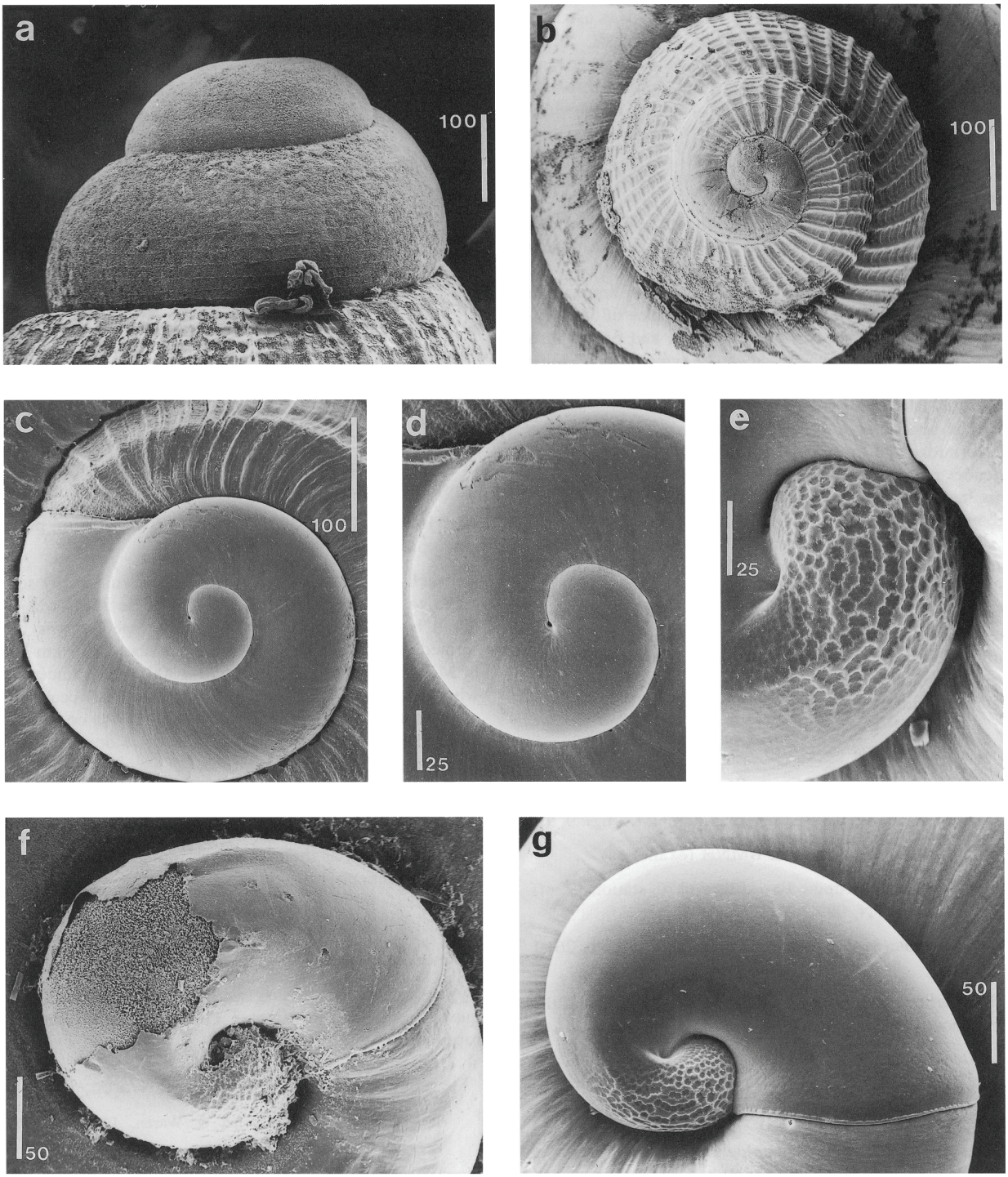


Figure 37. Protoconchs. *a. Alvania* cf. *stenolopha,* MAR, Lucky Strike. *b. Laeviphitus* ***desbruyeresi*** Warén & Bouchet, sp. nov., MAR, Lucky Strike. *c, d.* ***Lurifax vitreus*** Warén & Bouchet, gen. & sp. nov., MAR, Menez Gwen. *c.* Protoconch and first part of teleoconch. *d.* Detail of protoconch. *e, g. Hyalogyrina* ***umbellifera*** Warén & Bouchet, sp. nov., Aleutian Seeps, Shumagin site. *e.* Detail of initial whorl. *g.* Complete protoconch. *f. H.* ***globularis*** Warén & Bouchet, sp. nov., JdF, Endeavour Segment. Scale bars in μm.

Australian Museum, Sydney), of which one was used for examination of the radula after SEM of the shell.

Species 3 has an almost identical radula and jaw, in spite of being less distinctly planispiral, and the three are considered congeneric. The relation to other neotaenioglossate gastropods is uncertain but a few details give some clues.

-The teleoconch is evidently very modified and gives no hints.

-The protoconch has about 2.7 smooth and tall whorls and is well preserved in one of the specimens from New Caledonia.

-The structure of the jaw is not common among the Neotaenioglossa, but occurs in some species of Vitrinellidae (Ponder, 1994; own observations), and occurs also in a group of small species that can be typified by *Scrupus hyalinus* (Odhner, 1924) from New Zealand (also Vitrinellidae).

-The general style of the radula is most similar to the Littorinidae and Zerotulidae, which have a very long and slender radula, 20–50 times as long as broad. Also ***Neusas*** has a very high number of transverse rows of teeth, about 150.

The notes on the soft parts are based on the dried specimen and this information is obviously not enough to classify ***Neusas,*** but we have at present not wanted to use the remaining specimen of species 3 for anatomical work and leave the systematic position open. Vitrinellidae is in any case closer to the true systematic position than the original allocation of the species in the genus *Omalogyra* (Omalogyridae, "lower Heterobranchia").

Neusas marshalli (Sykes, 1925)

(Figures 35a–c, 36d–f, 49f)

Homalogyra marshalli Sykes, 1925:193, pl. IX, figs. 9, 9a.

Type material: Holotype in BMNH (examined).

Type locality: Porcupine Expedition 1870, station 17, off Portugal, 39°42'N, 09°43'W, 1092–1993 m.

New records: *MAR, Menez Gwen:* - DIVA 2 PL 26, 1 spm.

Distribution: Only known from the type locality and the new record, 850–2000 m.

Remarks: See "Diagnosis" of the genus for a redescription. The holotype is an empty shell, somewhat damaged, and our identification can be questioned. We have, however, not seen any additional species from the Atlantic and members the group are evidently very rare.

Family Rissoidae Gray, 1847

Remarks: The rissoids of the deep north-eastern Atlantic were recently revised (Bouchet & Warén, 1993) to which paper we refer for further discussions.

Alvania Risso, 1826

Alvania Risso, 1826:140.

Type species: *A. europaea* Risso, 1826; by subsequent designation by Nevill (1885:105); Mediterranean shallow water.

Alvania cf. *stenolopha* Bouchet & Warén, 1993

(Figures 34a, b, 36b, 37a)

Alvania stenolopha Bouchet & Warén, 1993b:653, figs. 1447, 1482–4.

New records: *MAR, Menez Gwen:* - DIVA 1 PL 16, on base of a black smoker, 1 spm; - DIVA 1 PL 14, on sulfide rock with Hydrozoa, 16 spms (decalcified). *Lucky Strike:* - DIVA 1 PL 04, on inactive chimney among Hydrozoa and sponge *Cladorhiza,* 1 spm; - DIVA 2 PL 02, 5 spms; - DIVA 2 PL 04, 1 spm; - DIVA 2 PL 09, 1 spm; - DIVA 2 PL 10, retrieval box, 3 spms; - ALVIN dive 2605, 1 spm; - ALVIN dive 2607, 17 spms, 1 egg capsule.

Distribution: MAR, 39.5–37.3°N, in 650–1850 m, probably epifaunal.

Remarks: The shell of this species seems unusually sensitive to formaldehyde and only a single shell was in good, but not perfect, condition. The species was described from two shells, from a place about 150 km NE of Menez Gwen at a depth of 650–1300 m. It is uncertain whether it is a member of the vent fauna or an occasional guest, but no other species which we know to occur outside vent areas was as frequent in samples dominated by "vent species," as *A. stenolopha.*

The egg capsule is spherical, with a transparent wall to which a few mineral grains are attached. It contains a single young ready to hatch and of the same size and structure (SEM) as the protoconch in our specimens, and the development is thus lecithotrophic.

Pseudosetia Monterosato, 1884

Pseudosetia Monterosato, 1884:281.

Type species: *Rissoa turgida* Jeffreys, 1870; by subsequent designation by Crosse (1885:140); northern Europe.

Pseudosetia azorica Bouchet & Warén, 1993

Pseudosetia azorica Bouchet & Warén, 1993:690, figs. 1603–4, 1615–7.

New records: *MAR, Menez Gwen:* - DIVA 2 PL 11, 3 spms.

Distribution: *Pseudosetia azorica* was described from three ocalities slightly farther to the east, on the southern slopes from the Azores, at a depth of about 350–850 m.

Remarks: We are not sure whether this is a species that belongs to the vent fauna, but since three specimens were found alive, and no details are known about the other localities from which it was described, we have included it here with a big question mark.

Family MURICIDAE Rafinesque, 1815

Trophon Montfort, 1810

Trophon Montfort, 1810:482.

Type species: *Murex magellanicus* Gmelin, 1791; by original designation; southern South America.

Remarks: The genus *Trophon* s.l. comprises numerous species with a northern or southern distribution, as well as in deep water (absent from shallow, warm water).

Trophon spp.

Material examined: *Off Barbados (Orenoque B and El Pilar Sector):* - DIAPISUB 10-4, 1 spm; - DIAPISUB 15-8, 1 spm; - DIAPISUB 16-3, 5 spms.

Remarks: Two species were present, one with a shell similar to *Trophon mucronae* Houart, 1991, from off Brazil, but with tall and slender protoconch. Species of *Trophon* usually are quite variable and we prefer to leave them undescribed, awaiting more material.

Family BUCCINIDAE Rafinesque, 1815

Remarks: Deep-sea buccinids in general were discussed by Bouchet & Warén (1986) and Lus (1989) and we refer there for some discussion of the group. Since then, several species have been recorded or described from hydrothermal vents, various kinds of seeps (Warén & Bouchet, 1993; Okutani et al., 1992, 1993; Okutani & Ohta, 1993) and whale skeletons (Naganuma et al., 1996, 1999), and it seems clear that members of the family are among the normal inhabitants in environments based on chemosynthetic activity. Buccinids belong to the gastropods known from the greatest depths, and *Calliloncha iturupi* Lus, 1989, is the deepest described gastropod, from a depth of 8240–8345 m in the Kuril-Kamchatka Trench.

Bayerius Olsson, 1971

Bayerius Olsson, 1971:57.

Type species: *Fusinus fragilissimus* Dall, 1908; by original designation; deep water off Ecuador.

Tacita Lus, 1971:62. **(New synonym)**

Type species: *T. holosericea,* Lus, 1971; by original designation; abyssal, 6090–6135 m, in the Kuril-Kamchatka Trench (Holotype in the Institute of Oceanology, Moscow; Figures 38f, g).

Remarks: The shell and radula of the type species of *Bayerius* and *Tacita* are so similar that there seems to be no reason for maintaining them as distinct genera. *Bayerius* was published March 1971; the volume of "Trudy Instituta Okeanologia" in which *Tacita* was described is dated 1971, and inquiries at the institute (through Dr. Y. Kantor) failed to produce a more precise date than this. We have therefore used the name *Bayerius. Calliloncha* Lus, 1978 (type species *C. solida* Lus, 1978 from almost 7000 m in the Izu-Bonin Trench [= Japan Trench]) may be a third name for this genus, but we have not examined actual specimens.

Olsson (1971) recorded *Bayerius fragilissimus* from the Gulf of Panama, but the precise type of habitat is not known. Such is the case also with *B. holosericeus* and the original material of *B. arnoldi.* All records of the two latter species do, however, come from the East and North Pacific trenches (not more shallow than 2877 m). Probably the species are not obligate members of this fauna since it seems unlikely that dredging and trawling should have produced as much material as was known before the exploration of the seep systems. *Bayerius holosericeus* differs distinctly from *B. arnoldi* and *B.* ***peruvianus*** by having an evenly and deeply sinuated outer lip, while that of the two others is considerably straighter. We figure the holotype (Figures 38f, g).

Bayerius ***peruvianus*** Warén & Bouchet, sp. nov.

(Figures 38h, 39c, 49d)

Type material: Holotype and 12 paratypes in MNHN.

Type locality: Peru, off Paita, NAUTIPERC PL 18, 10°01'S, 80°07'W, 5996–5385 m.

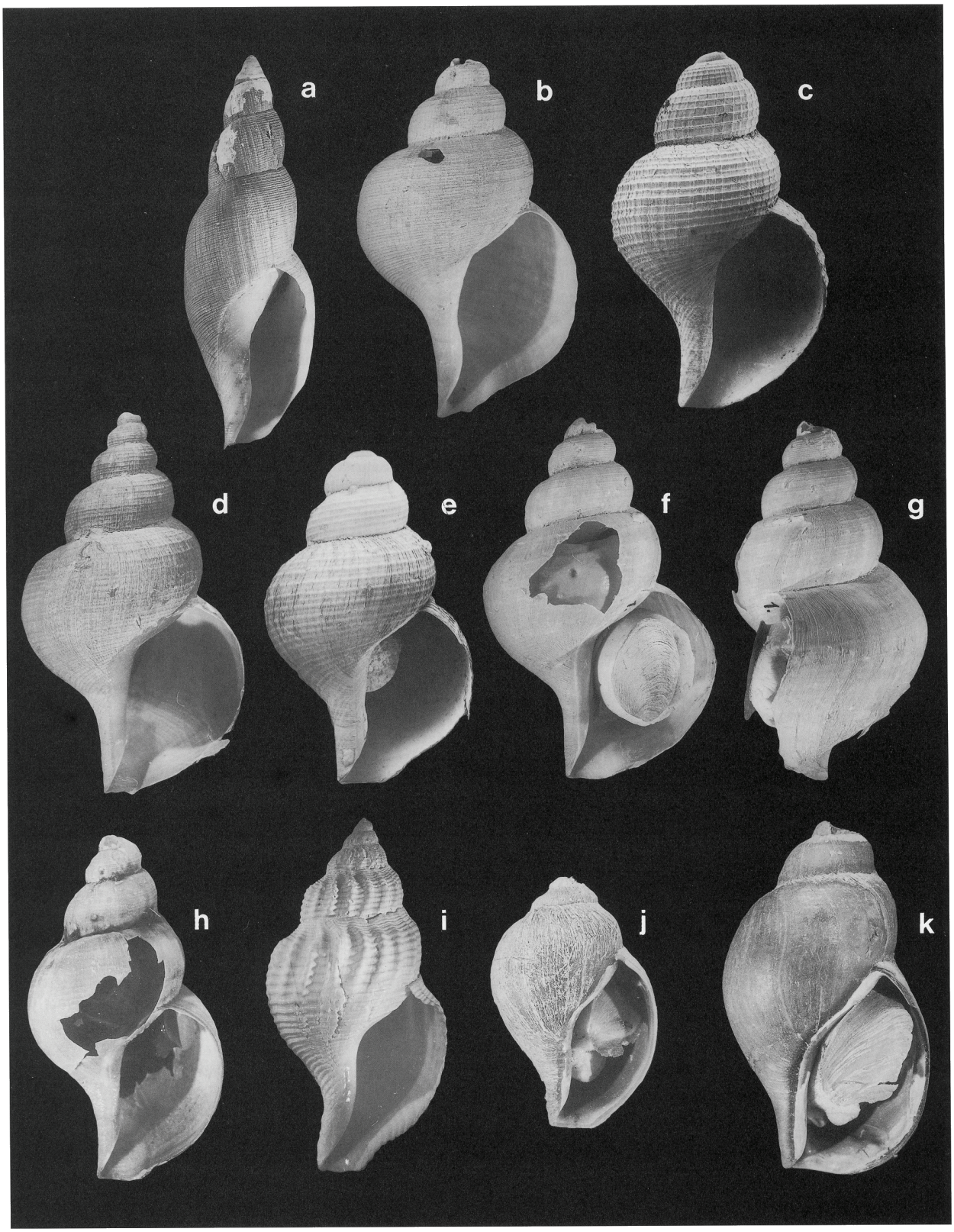
Material examined: Only known from the type series.

Distribution: Only known from the type locality.

Etymology: "*peruvianus*" after Peru.

Description: *Shell (Figure 38h).* Fusiform, extremely thin and fragile, with convex whorls and short siphonal canal. The protoconch is not known in any specimen, but the most apical whorl, of a diameter of 2.5–3 mm, has a uniform sculpture of 10–12 rounded spiral cords of equal size, and less than ½ a teleoconch whorl seems to be missing. At a diameter of 5–6 mm the axial sculpture starts to become more conspicuous and consists of growth lines only. On later whorls the spiral sculpture usually is less conspicuous and the growth lines may dominate. The periostracum is brownish green, thin, and forms very low lamellae at the growth lines, slightly higher close to the suture. The aperture is a little shorter than half the height of the shell; the outer lip is not thickened; in profile it is distinctly sigmoid with a shallow sinus occupying the apical ⅔; the siphonal canal is very short and open.

Dimensions. Maximum shell length (estimated) ca. 40 mm.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Radula (Figure 39c). The central tooth is low and has three cusps of equal size. The anterior and posterior margins are approximately parallel. The marginal plate has three strong cusps, the inner two slightly smaller.

Operculum (Figure 49d). Fan-shaped with nucleus corroded in all specimens. The shape is quite variable, from quite slender, as in the illustration, to about half the proportional length, i.e., ovate with lateral nucleus.

Remarks: This new species probably belongs to *Bayerius,* but it differs from the type species, *B. fragilissimus,* in being more stout with a shorter spire and more rapidly increasing diameter of the whorls. The sculpture of the present species is much weaker. The operculum of *B. fragilissimus* is not known, but Olsson (1971) figured the radula, which has tricuspidate laterals and a longer central plate than our species.

Baverius arnoldi (Lus, 1981)

(Figures 38b–e, 39b, 49c)

Tacita arnoldi Lus, 1981:140, figs. 1–4.

Type material: Holotype (Figure 38b) in the Institute of Oceanology, Moscow.

Type locality: "Vityaz" sta. 3575, north-eastern Pacific, 37°56'N, 146°24'E, 5471 m.

Material examined: The holotype and: - "Vityaz" sta. 5624, 45°26'N, 154°12'W, 5200 m, 12 spms. *Aleutian Trench:* - ROPOS 344, 1 spm; - TVG 24, 3 spms; - TVGKG 40, 1 adult spm with hydroids (SMF 311999), 15 shs, 5 spms (all young); - TVG 48, 2 spms (SMF 311997); - TVGKG 49, 7 shs (SMF 311998); - TVG 63, 1 adult spm.

Distribution: Japan, Kuril, and Aleutian Trenches, 6135–4800 m depth.

Redescription: *Shell (Figures 38b–e).* Of medium size for the family, *Neptunea*-like, greyish, very fragile. The protoconch (Figures 38c, e) is not demarcated, but starts smooth, then adds spiral ridges and sharp incremental lines after ca. 0.75 whorl. The teleoconch has ca. 12–15 rounded spiral ridges of uniform strength on the most apical whorls; 20 sharp threads, weaker and stronger ones alternating on the penultimate whorl. On the body whorl the sculpture extends across the base with the same appearance. The whorls are strongly and evenly convex; the suture deep. Our largest specimen has a little more than six whorls, but the apex is slightly corroded.

Dimensions. Largest good specimen 44.0 mm; maximum size 55 mm (estimated, spire broken).

Operculum (Figure 49c). Brownish, ovate, with about half a whorl and nucleus remaining.

Radula (Figure 39b). Normal for the genus.

Remarks: Our material was compared with the type in the Institute of Oceanology, Moscow. At 10 mm diameter, the holotype has seven stronger spiral cords which form small nodules at the intersections with the incremental lines; between these major cords there are three much smaller ones. In our specimens, at the same diameter, there are eight to nine major cords which hardly form any nodules, and there are only one or two spiral lines between them. Nevertheless, the shape and sculpture are close enough, and the specimens come from nearby localities so we believe them to be the same species.

Sahling (1997) assumed this species to be a predator on actinians which were common as epifauna on the clam *Calyptogena phaseoliformis* in the seeps.

The original description is in Russian and we have therefore redescribed *Bayerius arnoldi.*

Bayerius sp.

Material examined: *Mid America Trench, Jalisco Block Seeps at 20°N:* - NAUTIMATE PL 10, 1 sh.

Remarks: A single small shell (5 mm) differs from *B. arnoldi* in having taller and more slender whorls, but is too young for comparison with any of the more southern species of *Bayerius,* which are known only from large specimens with corroded apical whorls.

Buccinum Linnaeus, 1758

Buccinum Linnaeus, 1758:734.

Type species: *B. undatum* Linnaeus, 1758; by subsequent designation by Montfort (1810); northern Europe.

Remarks: The genus *Buccinum* is rich in species and taxonomic problems, due to a strong tendency to form local populations. The main distribution is northern and in shallow water, but scattered species occur down to about 2000 m depth. They are scavengers and predators.

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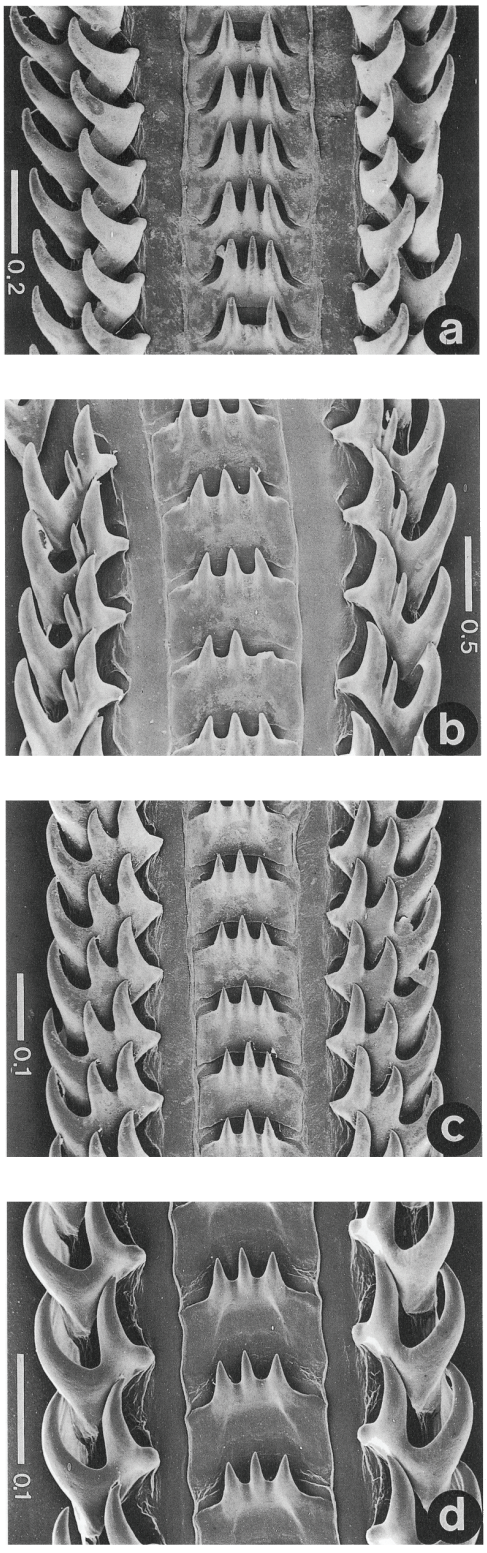
Figure 38. Neogastropod shells. *a. Tractolira sparta,* off Peru, 65 mm. *b–e. Bayerius arnoldi. b.* Holotype, 51 mm. *c.* Paratype, 13 mm. *d.* Aleutian Seeps, Edge site, 43 mm. *e.* Young specimen, Aleutian Seeps, Shumagin site, 12 mm. *f, g. Bayerius holosericeus,* holotype, 64 mm. *h. Bayerius* ***peruvianus*** Warén & Bouchet, sp. nov., holotype, 34 mm. *i. Eosipho canetae,* Bush Hill Seep, 52 mm. *j, k. Eosipho* ***auzendei*** Warén & Bouchet, sp. nov. *j.* Young specimen, 29 mm. *k.* Holotype, 62 mm.



Buccinum sp.

Records: *JdF, Endeavour Segment:* - ATV 50-1, High Rise vent field, 2 spms; - ROPOS #278, Main Field, 2 empty egg capsules, 2 capsules with 7–8 embryos each.

Remarks: The operculum is of normal *Buccinum* type, with concentric growth lines and the nucleus situated at the posterior 1/6, slightly over to the left side. The head-foot is unpigmented and the eyes are deeply subcutaneous and lack pigment. Species of *Buccinum* usually live in more shallow water and have pigmented eyes. Also those that live in quite deep water (500–1000 m) have eyes, which indicates that these specimens are not occasional guests in the deep-sea fauna.

This is probably the species reported as *Buccinum viridum* Dall, 1890, in various places at JdF. The type locality of that species is situated 10° farther south, off Santa Barbara, California, but no details about this locality (Albatross 1887-8, station 2839, ca. 750 m depth) are known. Cold seeps are, however, common all along the California coast (K. L. Smith, personal communication), and it is possible that the Albatross hit such a place. This identification is supported by the fact that *B. viridum* was described as having unpigmented eyes, which is rare in the genus. According to J. McLean (unpublished), populations of *Buccinum viridum* are common along the California coast in deep water, but the taxonomy is uncertain.

Eosipho Thiele, 1929

Eosipho Thiele, 1929:307.

Type species: *Chrysodomus* (*Sipho*) *smithi* Schepman, 1911; by original designation; Celebes Sea, ca. 1200 m depth.

Remarks: The genus *Eosipho* contains about half a dozen bathyal species of uncertain relation. Two species are now known from hydrothermal vents, both of which have a thick periostracum and a mainly smooth shell, while those from normal environment have well developed axial and spiral sculpture and thin periostracum. It is uncertain whether the two vent species really belong to *Eosipho,* but hypertrophy of the periostracum, as is the case with these two species compared with others, is common among vent gastropods and can change the appearance considerably. Anyhow, the two vent species are quite similar to each other and presumably closely related. Undescribed species of *Eosipho* have regularly been recovered from sunken pieces of driftwood from deep dredgings in the tropical western Pacific (Bouchet, unpub-

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Figure 39. Buccinid radulae. *a. Eosipho* ***auzendei*** Warén & Bouchet, sp. nov., paratype. *b. Bayerius arnoldi,* Aleutian Seeps, Shumagin site. *c. B.* ***peruvianus*** Warén & Bouchet, sp. nov., paratype. *d. E. canetae,* Bush Hill Seep. Scale bars in mm.

lished), and Harasewych (1990) reported the related *Manaria fusiformis* (Clench & Aguayo, 1941) from sunken wood.

Eosipho desbruyeresi Okutani & Ohta, 1993

Eosipho desbruyeresi Okutani & Ohta, 1993:217, figs. 1–5.

New records: *Lau Basin:* - BIOLAU PL04, 2 spms; - BIOLAU PL10, 1 juvenile spm.

Distribution: Lau and North Fiji Basins, in about 1750–2000 m depth.

Remarks: The top whorls, at a diameter of 7–8 mm and smaller, are axially ribbed, which is the normal sculpture of species of *Eosipho.*

Eosipho ***auzendei*** Warén & Bouchet, sp. nov.

(Figures 38j, k, 39a, 49a)

Type material: Holotype and 2 paratypes in MNHN.

Type locality: EPR at 17°S, Rehu site, 17°24.85'S, 113°12.15'W, 2578 m.

Material examined: The types and: *EPR at 17°S:* - NAUDUR PL19.1.2.b, site Rehu, 1 spm.

Etymology: Named after Jean-Marie Auzende, discoverer of many vent fields and expedition leader of NAUDUR.

Distribution: Only known from the type locality.

Description: *Shell (Figures 38j, k).* Large for the group, fusiform, smooth, brownish, with expanded peristome and very short canal. The uppermost whorls are lost by corrosion in all specimens. The most apical whorl in the young specimen has a diameter of about 6 mm and is sculptured with low, rather indistinct axial ribs which disappear on the subsequent whorls and are not present in any of the three adult specimens which have lost one more apical whorl. The shell is poorly calcified; ¼ whorl back from the outer lip its thickness is 0.5 mm of which the periostracum constitutes 0.2 mm. The periostracum has an outer layer of dense, soft axial lamellae, which probably wear off with time because they cover all the shell of the young specimen (Figure 38j), while they are restricted to the suture in adult specimens. Below this layer it is brown, smooth, and brittle. The suture is shallow, and rendered less conspicuous by the outer layer of the periostracum. The peristome is large, broad and expanded, especially in its lower part. The columella is covered by a well demarcated, thin, whitish calcareous layer. The outer lip is slightly thickened and reflected; its inside has a low rounded ridge paralleling the margin of the apical ⅔ of its height.

Operculum (Figure 49a). It is brown, a little longer than half the aperture, triangular to ovate with distinct growth lines, and its initial part is lost by abrasion. It is unusually soft and pliable and has a large semicircular, thinner attachment area bordered by a low ridge and a small callus below, at the left, inner part.

Radula (Figure 39a). The central plate is poorly demarcated, but has three strong cusps of equal size. The lateral tooth has two strong cusps, the inner one slightly smaller.

Soft parts. The foot is large and fleshy with demarcated propodium. The head is large with cephalic tentacles of a diameter of ⅓ of that of the proboscis. The eyes are half the diameter of the tentacle and situated at the outer side of these. The specimen used for radular examination was a female, and no other specimen was dissected, hence the presence of a penis could not be verified. The gill is large and its anterior half paralleled by a dark brown, bipectinate osphradium.

Remarks: The stomach was full of partly digested, unidentifiable flesh, and the species is a scavenger and predator.

Eosipho ***auzendei*** resembles *E. desbruyeresi,* but has a higher aperture, ⅔ of the height of the shell compared with half the height in *E. desbruyeresi. Eosipho desbruyeresi* also lacks the lamellar portion of the periostracum.

Eosipho canetae (Clench & Aguayo, 1944)

(Figures 38i, 39d, 49b)

Buccinum canetae Clench & Aguayo, 1944:64, fig. (not numbered).
"Buccinum" canetae: Warén & Bouchet, 1993:76, fig. 59 D.

New records: *Off Louisiana:* - Johnson Sealink dive 3129, 14 spms.

Distribution: From the Louisiana Slope to Surinam in 420–850 m depth.

Remarks: We transfer *Buccinum canetae* to *Eosipho,* based on similarities to the type species of *Eosipho* in shell, operculum, and radula. The animal lacks eyes. We figure the radula (Figure 39d) and operculum (Figure 49b), which agree well with other species of this genus (see Bouchet & Warén, 1986). The type species of *Eosipho, E. smithi,* differs in having no axial sculpture, but the shape of the aperture and the whorls, especially the slight constriction just below the suture make *B. canetae* fit better here than in any other of the deep water buccinid genera, and certainly much better than in *Buccinum* where it has been classified until now. *Eosipho canetae* is probably not an obligate member of the seep faunas since it was described from regular dredging, but it seems to be more common at the seeps.

Family VOLUTIDAE Rafinesque, 1815

Tractolira Dall, 1896

Tractolira Dall, 1896:12.

Type species: *T. sparta* Dall, 1896; by original designation; abyssal, off Central America.

Tractolira sparta Dall, 1896

(Figure 38a)

Tractolira sparta Dall, 1896:13.
Tractolira sparta: Dall, 1908b:299, pl. 2, fig. 7; Poppe & Goto, 1992:121, pl. 39, figs 7, 8 (holotype).

New records: *Off Peru, Paita area:* Between 5°34′ and 5°38′S, 81°54′ and 81°35′W, 5300–3100 m, 1 spm.

Distribution: Described from four localities between Acapulco, Mexico, to the Gulf of Panama, in 3043–4062 m, no further records known.

Remarks: This single specimen (67 mm high) had been brought back by an expedition to the Peruvian seeps with no indication of precise locality, but the species is poorly known and this record represents a considerable range extension, so we have included it. Poppe & Goto (1992) summarized the present knowledge about the genus.

Family CONIDAE Fleming, 1822

Remarks: The classification of the Turridae was recently reconsidered by Taylor et al. (1993) who transferred the subfamily Daphnellinae which contains the species below, to the Conidae. Their classification, however, was challenged by Rosenberg (1998), who considered that "malacologists will be justified in retaining the traditional classification, until more robust evidence for transfering [Daphnellinae] to Conidae is produced."

Conid type egg capsules are frequently found in vent environment, attached on rocks and shells. Two types were described by Gustafson et al. (1991), as "inflated triangular capsules" (from the Galapagos Rift) and "lenticular egg capsules" (from EPR at 21°N), but not assigned to genus, although the former type was convincingly assigned to the "Turridae."

We have egg capsules of the former type from the EPR (13°N) and MAR (Snake Pit) (Figures 40b, c), both from localities where species of *Phymorhynchus* are common. Regrettably they were empty or contained eggs only, so we have not been able to examine larvae with a shell. However, even if they had contained veligers with a shell and ready to hatch, protoconch 1 should probably not be specific enough in its sculpture to allow closer identification than the family Conidae. Furthermore, since we do not know the detailed sculpture of the protoconch 1 of any of the vent turrids, we could not have identified it by comparison with identified specimens. It seems, however, likely that the "inflated triangular capsules" (Gustafson et al., 1991) belong to *Phymorhynchus,* judging from the occurrence together with specimens of that genus, at three widely separate localities. Also the "lenticular egg capsules" have most likely been deposited by a conoid species as suggested by Gustafson et al. (1991), perhaps a different species of *Phymorhynchus,* judging from the large size.

We want to take this occasion to draw the attention to another type of egg capsules that we frequently have received, identified as "belonging to gastropods." Turbellarians of the family Fecampidae (Rhabdocoela) produce capsules very similar to those of gastropods and of a similar size (Figures 40a, c). For further information about these, see Möller Christensen (1981).

We have noticed that the radular teeth of species of *Phymorhynchus* change shape and size with the size of the specimen (Figures 43b–d). The length of the teeth increases more slowly than the height of the shell and the shape of the teeth may change. This has previously not been recognized, but should be considered when the radula is used for identification or phylogenetic work.

Phymorhynchus Dall, 1908

Pleurotomella (*Phymorhynchus*) Dall, 1908b:258.

Type species: *Pleurotomella* (*Phymorhynchus*) *castanea* Dall, 1908; by original designation; deep water east of Galapagos.

Remarks: Dall (1908b) described several species of *Phymorhynchus* from 1500–4000 m depth from the tropical eastern Pacific. These, however, are all more slender than the species described below from the EPR.

The species of *Phymorhynchus* from hydrothermal vents are all quite similar to each other, more so than to any of the species from non-vent environments that we have examined (Bouchet & Warén, 1980) or those described by Dall (1908b). The species from the ambient deep-sea have more developed axial ribs and the spiral cords are more distinctly differentiated in size and appearance by the fact that the more apical ones are stronger and separated by wider interspaces than the abapical ones. The genus can be recognized by the large rhynchodeum, large size, presence of mainly spiral sculpture, and total absence of subsutural (anal) sinus in the shell (except in very small specimens).

Sysoev & Kantor (1995) described the anatomy of the head-foot of *P. moskalevi* and *P. wareni.* We figure a critical-point dried specimen of *P. **ovatus*** to show the huge funnel-shaped rhynchostome (Figure 40d), actually formed from the head and the area around the proboscis opening. The real proboscis is small and usually everted in the bottom of the funnel. The cephalic tentacles are small, cylindrical, and situated far apart on the head. None of the species we have examined have eyes. Almost all specimens have a penis at some stage of development,

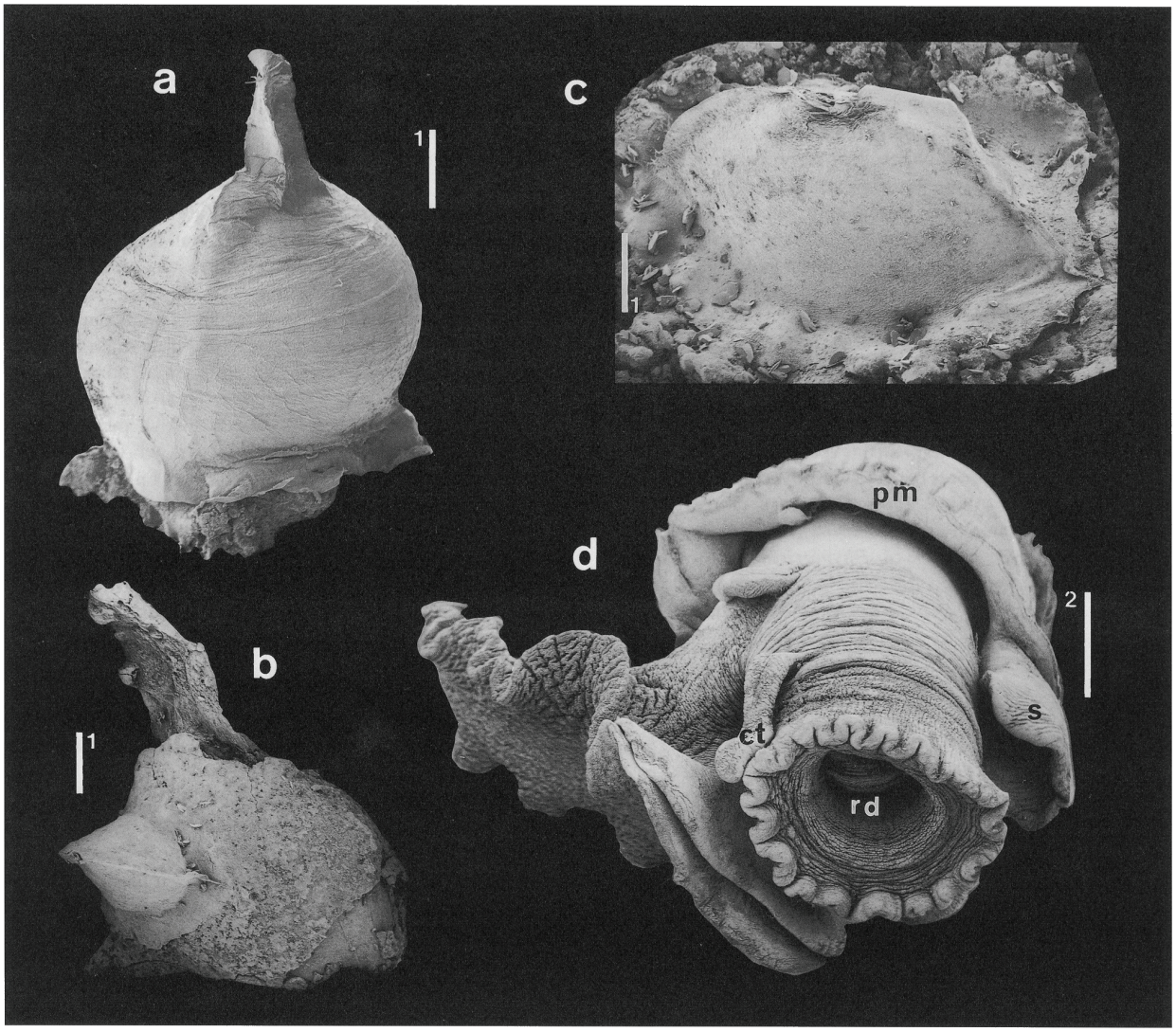


Figure 40. *a.* Turbellarian (Rhabdocoela) egg capsule, MAR, Lucky Strike, height 5.7 mm. *b, c. Phymorhynchus* sp., egg capsule, MAR, Lucky Strike. *b.* On turbellarian egg capsule. *c.* On a rock. *d. Phymorhynchus* sp., MAR, Lucky Strike. ct - cephalic tentacle; pm - pallial margin; rd - rhynchodaeum; s - siphon. Scale bars in mm.

from a small wart behind and below the right cephalic tentacle, to a large, flat structure with an apical papilla. This may be present in combination with a pallial oviduct, independently of sex and size of the specimen. It seems more to be a case of "imposex" than actual hermaphroditism, but this needs verification by histological examination of the gonad. (If this is a case of imposex, it does not seem likely that it is caused by tributyl tin, since these localities are as far from sources for those compounds as one can get. It seems more likely to be caused by effluents from the vents.) The right edge of the siphonal canal continues as a skin fold inside the pallial margin, where it turns abruptly to the right and forms a drape hanging from the pallial roof, closing the space between the back of the snail and its pallial skirt, and directing the outflow of respiratory water to the right ¼ of the cavity. This curtain was noticed in all species listed below.

A specimen of *Phymorhynchus* sp. from the EPR had eaten *Neomphalus fretterae* (Warén & Bouchet, 1991), and two specimens of *P. **ovatus*** from the MAR had eaten *Bathymodiolus,* two had remains of a worm-shaped animal (not a polychaete) in their esophagus. M. Segonzac (personal communication) has seen a specimen eating a fresh shrimp, *Rimicaris exoculata,* at the Snake Pit site, but did not know if the snail had caught it alive or found it dead.

No protoconchs have been available, except some brown remains in the smallest specimens (Figure 42a) which unambiguously show that the species have planktotrophic larval development. A single young specimen from MICROSMOKE PL 20, 2.6 mm high, had one complete whorl left of protoconch 2, maximum diameter 0.8 mm. Judging from this remaining whorl, it closely resembles the protoconch we (Bouchet & Warén, 1980, fig. 238) assumed to be *P. alberti,* but perhaps slightly lower, and a height of 0.7 mm above the teleoconch suture seems likely. In young specimens, up to 4–8 mm teleoconch height, the anal sinus is more conspicuous, and below 4–5 mm the spiral sculpture is quite weak.

Species of *Phymorhynchus* should probably make a suitable object for molecular study of vent species with planktotrophic development: they are common and easy to identify to genus, there are several species, they are often collected because of their large size, which also makes it possible to save enough material of each specimen for regular taxonomic work.

Four additional species of *Phymorhynchus,* not discussed below, have been described: *P. starmeri* Okutani & Ohta, 1993, and *P. hyfifluxi* Beck, 1996, from the North Fiji Basin, *P. wareni* Sysoev & Kantor, 1995, from the Edison Seamount, and *P. buccinoides* Okutani, Fujikura & Sasaki, 1993 from seeps at the Hatsushima site in Sagami Bay.

Phymorhynchus ***ovatus*** Warén & Bouchet, sp. nov.

(Figures 41e–g, 42a, b, 43b–d)

Type material: Holotype and 6 paratypes in MNHN.

Type locality: MAR at Logatchev site, MICROSMOKE PL 20, Irina site, 14°45.10′N, 44°48.60′W, 3005 m.

Material examined: The types and: *MAR, Lucky Strike:* - DIVA 2: 02, 1 spm; - ALVIN dive 2607, 2 spms. *Snake Pit:* - HYDROSNAKE PL 10 (Les Ruches), 11 spms; - GRAVINAUT PL 01-2 (Les Ruches), 1 spm; - ALVIN dive 2615 (Elan), 1 spm, crushed; - ALVIN dive 2619 (Elan/Ruches), 3 spms, 1 young, 8 egg capsules on rocks and on a turbellarian egg capsule; - ALVIN dive 2620 (Elan/Ruches), 4 spms; - ALVIN dive 2621 (Elan), 2 spms, 1 young; in trap, 13 spms; - MICROSMOKE PL 08, Ruches site, in trap, 10 spms; - MICROSMOKE PL 14, 1 spm; - MICROSMOKE PL 16, 3 spms; - MICROSMOKE PL 17, Elan, 5 spms. *MAR 14°45′N:* - MICROSMOKE PL 21 (Irina), 1 spm.

Distribution: MAR, from Lucky Strike to Logatchev site, in 1600–3500 m depth.

Etymology: From "*ovatus*" (Latin), shaped like an egg.

Description: *Shell (Figures 41e–g).* Large, colorless, fragile, buccinoid, with uniform spiral sculpture, brown periostracum, and rounded aperture. The apex and protoconch are not known in detail, but the shells in Figures 42a, b probably belong here. The teleoconch has had about 4.5 whorls (estimated; ± 0.5 whorls) of rapidly increasing diameter. The sculpture consists of spiral cords, 18 on the last whorl close to the outer lip, four to five on the penultimate whorl, and four on the whorl before. More apically no trace remains of them because of corrosion. The cords are evenly rounded, much broader than the interstices, covered by 15–20 fine, undulating lines, and increase in size toward the apical part of the whorls. The incremental sculpture is visible mainly on the last half whorl of the shell and consists of numerous irregular, weak lines and scattered stronger scars. The outermost layer of the shell and the brownish periostracum are usually worn off or corroded on the whole shell, except sometimes in the interspaces between the ribs and close to the lip. The whorls are evenly convex and the suture very shallow. The aperture is high and elongate, its outer lip not thickened, in profile unusually straight and without a trace of a labial sinus. The relation between the total height of the shell and the maximum diameter of the peristome varies individually between 1.34 to 1.39 (15 specimens between 13 and 67 mm shell height). The siphonal canal is very short, and the lower part of the outer lip projects below the end of the columella.

Dimensions. Height of holotype 49 mm, largest specimen 67 mm.

Soft parts. As in the genus, operculum absent. The penis is flat, apically truncated with a smooth flat surface surrounding a papilla. The anterior edge is finely wrinkled, the posterior, apical third has a folded glandular area.

Radula (Figures 43b–d). Length of teeth 270 μm in a specimen of 55 mm shell height, 220 μm at 39 mm, 130 μm at 10 mm.

Remarks: Two specimens from ALVIN dive 2620 had disgorged their partly digested prey, which still was firmly anchored in the rhynchostome. It was identified, from the gills, paired pedal retractors, and paired gonads, as remains of mytilids. Two specimens from ALVIN dive 2621 had vomited wormlike animals, and one had thrown up a mass of flesh.

Phymorhynchus ***ovatus*** is not always easy to distinguish from *P. moskalevi* but the ovoid shape and the evenly curved profile of the whorls help. At a size of 13–30 mm, *P.* ***ovatus*** has four rather distinct furrows at the end of the penultimate whorl; when adult it has five (rarely six) of them. *P. moskalevi* has indistinctly shouldered whorls and a relation between maximum diameter of peristome and shell height varying between 1.47 and 1.60 (10 specimens in the size range 10–40 mm). They have a subsutural zone with indistinct spiral furrows and below these six to seven spiral furrows at the end of the pen-

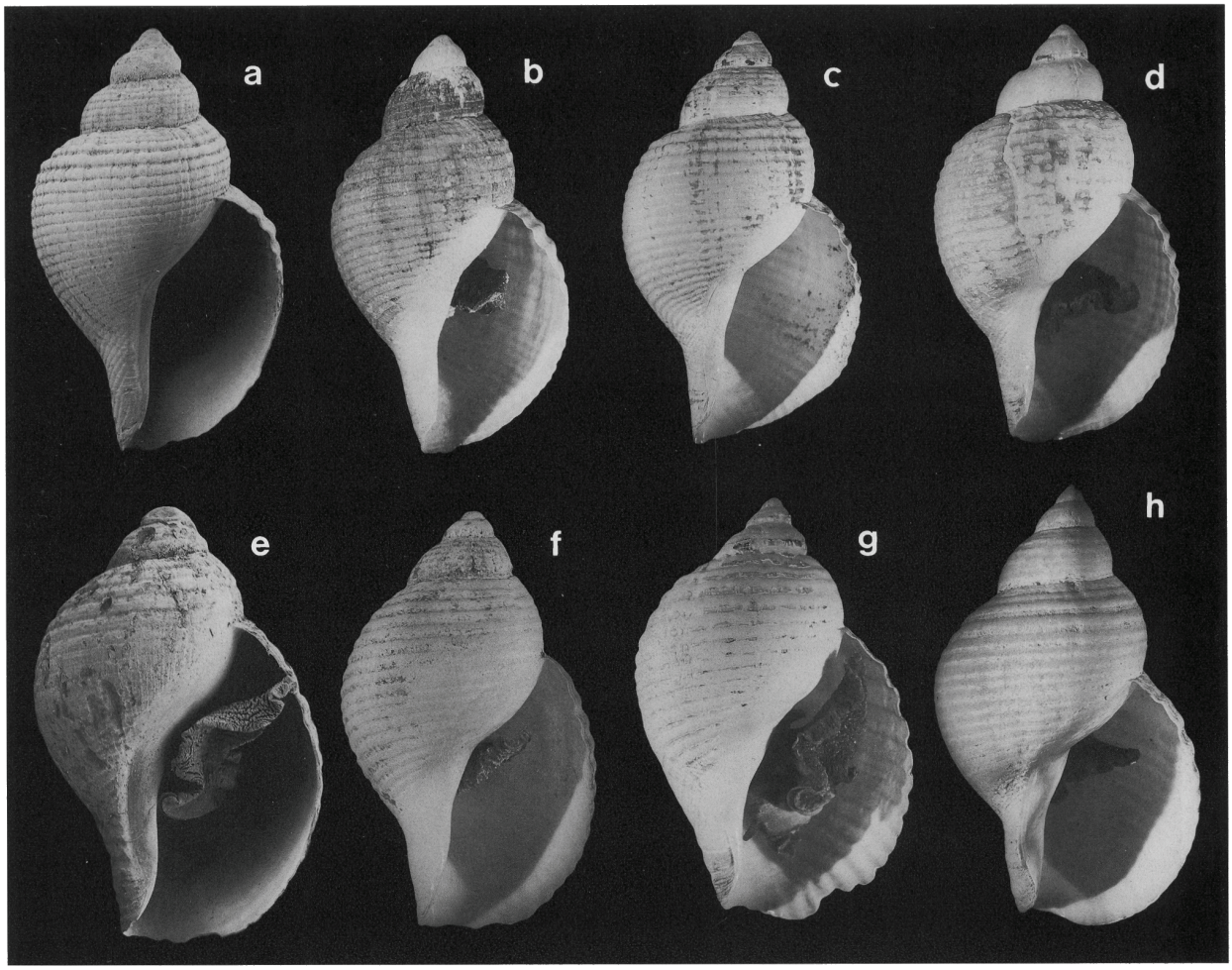


Figure 41. *Phymorhynchus* spp. *a–d. P. moskalevi. a.* Young specimen, MAR, Snake Pit, 10.3 mm. *b.* Subadult, MAR, Snake Pit, 28.4 mm. *c.* Adult, MAR, TAG field, 39 mm. *d.* Adult, MAR, Snake Pit, 38.5 mm. *e–g. P. **ovatus*** Warén & Bouchet, sp. nov. *e.* Young specimen, MAR, Snake Pit, 13.5 mm. *f.* Adult specimen, MAR, Lucky Strike, 38.5 mm. *g.* Large specimen, MAR, Logatchev site, 49 mm. *h. P. **major*** Warén & Bouchet, sp. nov., holotype, EPR, 13°N, 71.5 mm.

ultimate whorl. The radular teeth have a tendency to be slightly thicker in *P. **ovatus,*** but this was not perfectly clear from examination of four adult radulae of each.

Phymorhynchus moskalevi Sysoev & Kantor, 1995

(Figures 41a–d, 43e, f)

Phymorhynchus moskalevi Sysoev & Kantor, 1995:22, figs. 1H–I, 4, 5D–F.

New records: *TAG:* - Kremlin site, 2 spms (Tyler). *Snake Pit:* - MICROSMOKE PL 08 in a trap at the Ruches site, 75 spms; - MICROSMOKE PL 14 (Elan), 1 spm.

Distribution: MAR between 26 and 23°N, in 3400–3700 m depth.

Remarks: For differences from *P. **ovatus,*** see under that species.

*Phymorhynchus **carinatus*** Warén & Bouchet, sp. nov.

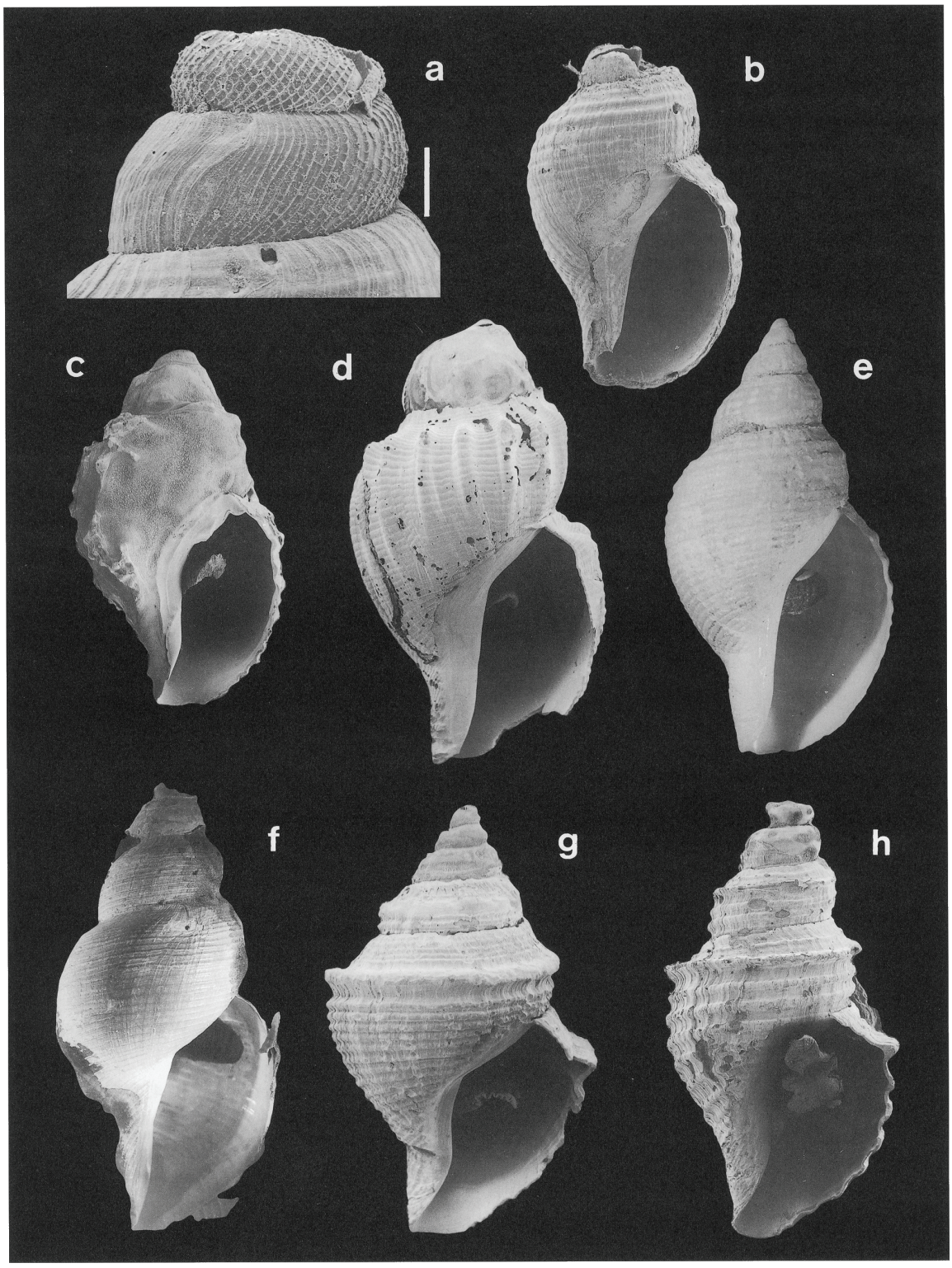
(Figures 42g, h, 43g–i)

Phymorhynchus sp. 2: Warén & Bouchet, 1993:79.

Type material: Holotype and 5 paratypes in MNHN.

Type locality: MAR at the Logatchev site: MICROSMOKE PL 20, 14°45'N, 44°59'W, 3040 m, Irina.

Material examined: The types and the two specimens from Snake Pit, recorded by Warén & Bouchet (1993).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Distribution: Snake Pit and Logatchev site, ca. 3000–3500 m depth.

Etymology: "*carinatus,*" Latin, meaning keeled.

Description: *Shell (Figures 42g, h).* Small for the genus, colorless, fragile, fusiform, with uniform spiral sculpture, a strong peripheral keel, and rounded aperture. The apex and protoconch are not known in detail, all specimens are badly corroded apically, and only traces of an apparently normal, brownish yellow planktotrophic type protoconch can be seen in the holotype (Figure 42g). The teleoconch has had about five whorls (± 0.5 whorls) of slowly increasing diameter. The sculpture consists of spiral cords, five above the strong peripheral keel on the last whorl, 18 below the keel; two or three above and one or two below at the beginning of the penultimate whorl. More apically no trace remains of them. The cords are evenly rounded, much broader than the interstices and twice as wide and high below the keel as above. The incremental sculpture is indistinct and irregular. The whorls are not very convex and the suture very shallow. The aperture is high and slender, with a distinct internal, V-shaped furrow corresponding to the peripheral keel, its outer lip is not thickened, unusually straight and without a trace of a labial sinus. The siphonal canal is very short, and the lower part of the outer lip projects below the canal.

Dimensions. Height of holotype 10.9 mm, largest specimen 15 mm.

Soft parts. As in the genus, operculum absent. A penis was not present in any of the two specimens we examined for this. The snout is inconspicuous in specimens of 8–11 mm shell height, normally developed at 14–15 mm.

Radula (Figures 43g–i). Length of teeth 75 μm in a specimen of 5.6 mm, 90–100 μm in the holotype, and 140 μm in a large specimen of 15 mm.

Remarks: As shown by Figures 42g–h, *P.* ***carinatus*** is quite variable in shell shape, but these two specimens represent the extremes. We have selected a subadult specimen as holotype (Figure 42g), because this specimen has much better preserved sculpture than adult(?) ones. One of the specimens from Logatchev site had thrown up some half digested prey, which seems to be the pedal retractor muscles of a *Bathymodiolus.*

Phymorhynchus ***major,*** sp. nov.

(Figures 41h, 43a)

Phymorhynchus sp.: Warén & Bouchet, 1989:95, figs. 115–116.

Type material: Holotype (dry), one complete and one crushed paratype in alcohol (MNHN).

Type locality: EPR at 09°50'N, HERO 91 PL 09, 09°50.20'N, 104°17.40'W, 2505 m, Worm Barbecue site.

Material examined: The types and specimens reported by Warén & Bouchet (1989).

Distribution: Known from the EPR at 13° and 09°50'N, at a depth of ca. 2500–2600 m. See remarks.

Etymology: "*major*" Latin, from its large size.

Description: *Shell (Figure 41h).* Large, colorless, fragile, *Buccinum*-like in shape, with uniform spiral sculpture and rounded aperture. The apex and protoconch are not known, all specimens are badly corroded apically. The teleoconch has had about six whorls (estimated; ± 0.5 whorls) of rapidly increasing diameter. The sculpture consists of spiral cords, 25 on the last whorl close to the outer lip, nine on the penultimate whorl, and eight on the whorl before. More apically no trace remains of them. The cords are evenly rounded, much broader than the interstices and increase in size toward the apical part of the whorls. There is no incremental sculpture visible except a few lines close to the outer lip, but the outermost layer of the shell and the thin brownish periostracum have been worn off or corroded on the whole shell, except in the interspaces between the ribs, close to the lip. The whorls are not very convex and the suture very shallow. The aperture is short and rounded, its outer lip not thickened, unusually straight and without a trace of a labial sinus. The siphonal canal is very short, and the lower part of the outer lip projects below the canal.

Dimensions. Height of holotype (largest specimen) 72 mm.

Soft parts. As in the genus, operculum absent. The penis is flat, apically truncate with a smooth flat surface surrounding a papilla. The anterior edge is finely wrinkled, the posterior, apical third has a folded glandular area.

Radula (Figure 43a). Length of teeth 330 μm (in a 55 mm male).

Remarks: Species of *Phymorhynchus* seem to be regularly occurring at the EPR sites, judging from video recordings, but have not been collected very frequently. This may be because they are too large and rare to be included in sediment and vestimentiferan samples, and because their shells are fragile and break when collected with the mechanical arms of the submersibles.

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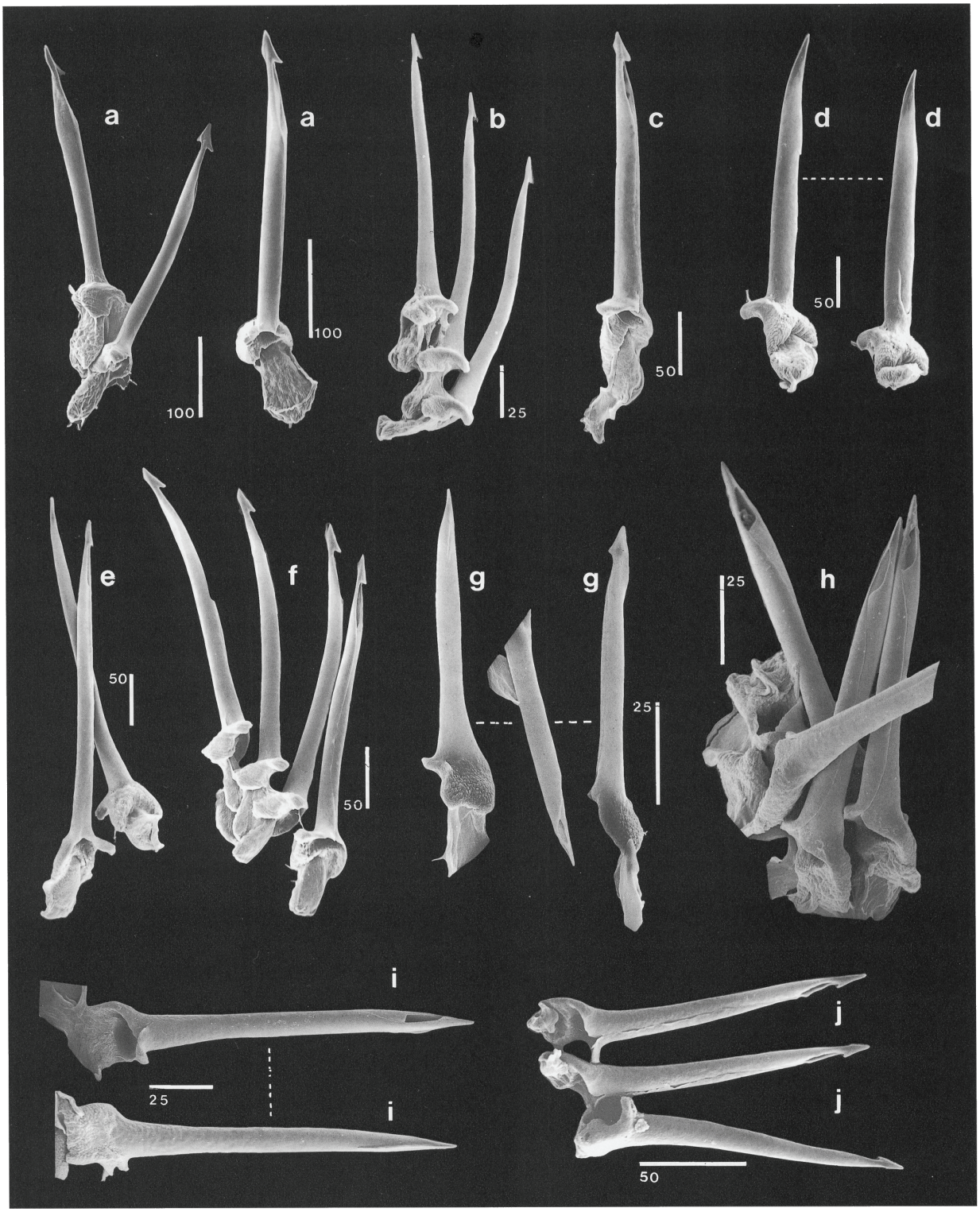
Figure 42. Conidae, shells. *a, b. Phymorhynchus* ***ovatus*** Warén & Bouchet, sp. nov., MAR, Logatchev site, scale bar 0.2 mm, height 3.5 mm. *c. Gymnobela* sp. B, MAR, Snake Pit, 13.3 mm. *d. Gymnobela* sp. A, EPR, 13°N, 12 mm. *e. P.* aff. *alberti,* End of Barbados Prism, 26.3 mm. *f. Bathybela* ***papyracea*** Warén & Bouchet, sp. nov., off Jalisco, height 95 mm. *g, h. P.* ***carinatus*** Warén & Bouchet, sp. nov., MAR, Logatchev site. *g.* 10.9 mm. *h.* Young specimen, 5.4 mm.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Phymorhynchus aff. *alberti* (Dautzenberg & Fischer, 1906)

(Figure 42e)

Phymorhynchus alberti Dautzenberg & Fischer, 1906:16, pl. 1 figs. 8–10.
Phymorhynchus alberti: Bouchet & Warén, 1980:27, figs. 40, 72–73, 239.

New records: *Barbados:* - MANON PL 06 (north of Barbados), 3 broken spms; - DIAPISUB 10-4 (Orenoque), 1 spm.

Distribution: Known from the north-eastern Atlantic between 16°N and 47°N, in ca. 1850–4800 m depth.

Remarks: One male from MANON had a simple, fingerlike, penis, tapering into a small apical papilla. A second specimen had a very small fingerlike process only. The identification of our specimens is doubtful. The MANON specimens are badly corroded, slightly broken, and unusually tall-spired; that one from DIAPISUB is not adult. It is therefore uncertain if these records are misidentifications or a westward extension of the range of *P. alberti.* The records are, however, of interest to show the presence of the genus also in seeps in the Atlantic Ocean.

Gymnobela Verrill, 1884

Gymnobela Verrill, 1884:157.

Type species: *G. engonia* Verrill, 1884; by subsequent designation by Cossmann (1896:63); bathyal North Atlantic.

Remarks: The genus has never been thoroughly revised and our use of this name is more a consequence of recent usage of the name for a number of Atlantic and West Pacific deep-sea species (e.g., Bouchet & Warén 1980, Sysoev, 1997), than based on a systematic selection among the ca. 900 generic names available for the Conoidea. The three species *G. extensa* (Dall, 1881), *G. sagamiana* (Okutani & Fujikura, 1992) (***comb. nov.***), and *G.* sp. A are quite similar in shell characters and have the same type of radula. We therefore believe this to be a group of species adapted to vent environment. They differ from *Phymorhynchus* in having very small snout and comparatively large cephalic tentacles. All three species lack eyes. Possibly also *Gymnobela* sp. B, from the MAR, belongs here, but it is in too poor condition for more than a guess.

Gymnobela extensa (Dall, 1881)

Gymnobela extensa: Warén & Bouchet, 1993:78, fig. 59A–C.

New records: *Off Louisiana:*-Johnson Sealink dive 3129, 17 spms.

Distribution: From the Yucatan Channel to off Louisiana in 512–1463 m depth.

Gymnobela sp. A

(Figure 42d)

Material examined: *EPR at 13°N:* - HERO 91 PL 11, 1 spm; - HERO PL 12, 8 spms; - HERO PL 21, 1 spm; - HERO 92 dive 2523, 8 spms.

Distribution: Only known from the EPR at 13°N.

Remarks: The specimens are too corroded to be described, but are probably conspecific.

Gymnobela sp. B

(Figure 42c)

Material examined: *MAR, Snake Pit:* - MICROSMOKE PL 07 (Elan), 1 badly corroded spm.

Remarks: The specimen above is too corroded for meaningful attempts of identification; it is included more as an example of how badly many specimens (and often all specimens of certain species) get corroded in these environments.

Bathybela Kobelt, 1905

Bathybela Kobelt, 1905:275.

Type species: *Thesbia nudator* Locard, 1897; by subsequent designation by Dall (1918b); abyssal, North Atlantic.

Remarks: The Atlantic type species, *Bathybela nudator* resembles ***B. papyracea,*** but the new species is larger, much more fragile, has a proportionally lower aperture, fewer whorls, and weaker axial sculpture. The general shape resembles some of the non-vent species described in *Phymorhynchus* from the East Pacific, but they have a coarser sculpture and no trace of color pattern on the columella. As far as known, this is the largest West American turrid.

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Figure 43. Turrid radular teeth. *a. Phymorhynchus* ***major*** Warén & Bouchet, sp. nov., EPR, 13°N, specimen 55 mm high. *b–d. P.* ***ovatus*** Warén & Bouchet, sp. nov. *b.* Young specimen, 10 mm, MAR, Snake Pit. *c.* Subadult specimen, 38 mm, MAR, Lucky Strike. *d.* Large specimen, 55 mm, MAR, Lucky Strike. *e, f. P. moskalevi. e.* Young specimen, 12 mm, MAR, Lucky Strike. *f.* Adult, 38 mm, MAR, TAG field. *g–i. P.* ***carinatus*** Warén & Bouchet, sp. nov. *g.* Young specimen, 5.6 mm, MAR, Snake Pit. *h.* Holotype. *i.* Large specimen, 15 mm, paratype. *j. Gymnobela* sp. A, EPR, 13°N. Scale bars in μm.

Bathybela ***papyracea*** Warén & Bouchet, sp. nov.

(Figure 42f)

Type material: Holotype in MNHN (in alcohol).

Type locality: *Mid America Trench.* Jalisco Block Seeps at 20°N: - NAUTIMATE PL 18, 20°05'N, 106°18'W, 3662 m.

Material examined: The holotype.

Distribution: Only known from the type locality.

Etymology: "*papyracea*" refers to the thin shell.

Description: *Shell (Figure 42f).* Tall, slender, fusiform, fragile, finely spirally striated, slightly shiny and pale beige in color. The first few whorls are lost by corrosion; the diameter of the most apical, partially lost one is 10.5 mm. 3.5 evenly convex teleoconch whorls of rapidly increasing diameter remain. The subsutural zone occupies slightly more than ⅓ of the height of the whorls. This zone is demarcated only by the incremental lines being concave, instead of convex. The zone is sculptured by about a dozen raised spiral lines of variable strength but weaker than on the adjacent part of the whorl. Below the zone the whorls carry 10 additional, raised ribs, stronger toward the abapical suture, alternating with three to five much smaller ones in each interspace. The body whorl has 20 additional, more basal spiral cords. The axial sculpture consists only of incremental lines, more distinct in the apical part of the subsutural zone, almost disappearing below the zone. The aperture is high, the outer lip almost semicircular, thin, and fragile. The columella and parietal wall are covered by a thin glaze, following the shape of the underlying spiral ribs. The central part of the columella is darker brown than the rest of the shell, a color pattern also visible at the columella of the broken, most apical whorl.

Dimensions. Height of the holotype 98 mm.

Remarks: The shell is very fragile and it seems impossible to extract the soft parts without breaking the shell. Also drying the specimen in order to detach the columellar muscle was judged dangerous, since it probably should have cracked the shell by the contraction of the soft parts. We therefore have no information about the soft parts, except that there is no operculum.

The classification in the genus *Bathybela* is based on similarity in shell characters, and direct comparison with the type species.

The shell was carrying several specimens of a sea-anemone.

Subclass HETEROBRANCHIA

Family HYALOGYRINIDAE Warén & Bouchet, 1993

Remarks: Several species of this group live in the vents and seeps of the northeastern Pacific, from the Aleutian seeps to those in the Galapagos Rift vents. They have been found in sediment samples and on rocks. The gut is filled with sediment.

The systematic position of the Hyalogyrinidae is uncertain; the affinity to some of the "lower heterobranchs" (*sensu* Ponder, 1991) is supported by the heterostrophic protoconch, the sculpture of its initial whorl and the very unusual structure of the jaw, but is seemingly contradicted by the rhipidoglossate radular type (not bilobed at the initial part!), which is shared by *Hyalogyrina, Hyalogyra,* and *Xenoskenea* among the heterobranchs (See Warén et al., 1993).

Hyalogyrina Marshall, 1988

Hyalogyrina Marshall, 1988:982.

Type species: *H. expansa* Marshall, 1988; by original designation; on sunken, bathyal driftwood off New Zealand.

Remarks: In addition to the species discussed here, a few specimens were found at the Oregon seeps (TVG 18, shells in SMF), but were too poor to allow identification. The generic position was confirmed by examination of radula and jaw.

Hyalogyrina ***umbellifera*** Warén & Bouchet, sp. nov.

Figures 37e, g; 44h–j; 45a–d; 47d; 48a, b; 49i)

Type material: Holotype SMF 311986 and 125 paratypes, SMF 311987. 125 paratypes in MNHN.

Type locality: Aleutian Trench, Shumagin site, TVGKG 40, 54°18.17'N, 157°11.82'W, 4808 m.

Material examined: The type material and: *Aleutian Trench:* - TVGKG 49, 19 shs and spms (SMF 311988).

Distribution: Only known from the material above, Aleutian Trench, Shumagin site, in 4800 m.

Etymology: "*umbellifera,*" Latin, the one who carries an umbrella, referring to the set of large flat tentacles on top of the head.

Description: *Shell (Figures 44h–j).* Large for the group, tall-spired, rather sturdy, smooth, greyish white with a very thin, slightly iridescent periostracum. The protoconch (Figures 37e, g) consists of about 0.8 whorls, diameter 280 μm, with a very small initial part sculptured by small, crowded pits, diameter 4–5 μm, to some extent spirally arranged and fused. Where this sculpture ends, the diameter starts to increase rapidly and the shell becomes perfectly smooth. The peristome of the protoconch is slightly constricted and its width is three times the width of the whorl where the sculpture stops. The teleoconch consists of about 3.5 almost perfectly smooth whorls; the precise number of an adult specimen cannot

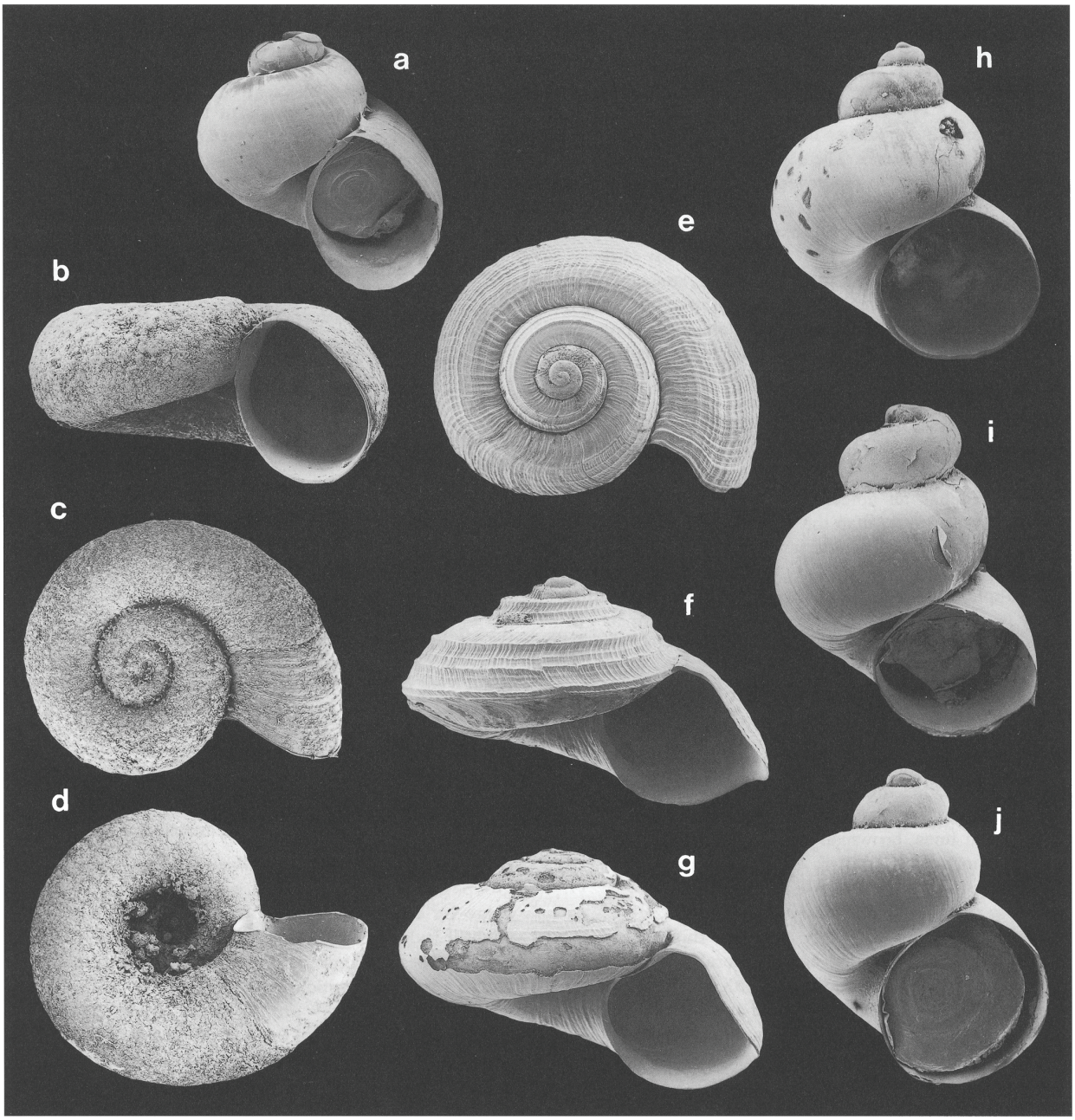

Figure 44. Heterobranchia, shells. *a. Hyalogyrina* ***globularis*** Warén & Bouchet, sp. nov., holotype, height 2.05 mm. *b–d. Xylodiscula* ***analoga*** Warén & Bouchet, sp. nov., holotype, diameter 1.7 mm. *e–g.* ***Lurifax vitreus*** Warén & Bouchet, gen. & sp. nov., MAR, Menez Gwen. *e.* Diameter 2.37 mm. *f.* Diameter 2.04 mm. *g.* Diameter 2.48 mm. *h–j. H.* ***umbellifera*** Warén & Bouchet, sp. nov., paratypes, height 3.2 mm, 3.2 mm and young specimen, 1.86 mm (j).

be given because all half-grown and larger specimens have lost the apex by corrosion. The suture is deep and the whorls not very firmly adjoining the preceding one. The entrance to the umbilicus is quite oblique and its width in a basal view corresponds to $\frac{1}{20}$ of diameter of the shell. The peristome is prosocline, more tangential than radial, not thickened, and not indented by the preceding whorl. The cross section of the whorls is almost circular, except for the part of the inner lip which borders the umbilicus; this is almost straight.

Dimensions. Maximum height ca. 3.4 mm.

Soft parts (Figures 45a–d). The foot is very large, broad, and flat, posteriorly rounded with a shallow notch, anteriorly shallowly bilobed, and lacking a demarcated propodium. An epipodial ridge starts at the anterior part of the operculum, continues forward and reaches the base of the cephalic tentacles. The cephalic tentacles are about as long as the snout in preserved specimens, and are ciliated along the edges. At the central side each has large skinfolds, attached along its proximal half and to the basal part of the snout. The right tentacle has two of these, an upper one which is flat, distally broader, attached more basally and has four small digits and a lower one, which is partly covered by the upper one, is attached along the basal, central half of the tentacle. The left cephalic tentacle has a basally attached, fan-shaped fold, which also is fused to the basal part of the more ventral fold from the right tentacle. Together these folds form a complete cover over most of the snout. The snout is almost cylindrical, strongly transversally folded, slightly expanded distally, and has an apical-ventral mouth. The slender buccal mass is longer than the snout, has salivary glands opening to the buccal cavity, jaws composed of apically denticulate rodlets, and a short "rhipidoglossate" radula with simple, rounded end of the radular sac. The pallial cavity is rather deep, half a whorl; and the bipectinate gill is situated in the middle of its depth. The pallial margin is distinctly thickened and has a densely ciliated tentacle at its right corner. The inner, posterior half of the cavity is filled by invaginated pallial roof, with a loop of the large intestine. The stomach and intestine contain grey sediment; in the intestine the fecal rod is partly split by a deep longitudinal furrow.

Operculum (Figure 49i). Round, multispiral, with distinct growth lines, brownish flesh colored. The width of the last whorl, at the growth zone, corresponds to ⅕ of the diameter.

Radula (Figures 47d, 48a, b). Ca. 15 - 1 - 1 - 1 - ca 15, short, 3–3.5 times as long as broad, rhipidoglossate, with marginal teeth folded across laterals and centrals. The central tooth is low and broad with projecting lateral supports, a triangular, finely serrated apical plate and distinct "wings" behind the lateral support. The lateral tooth is low and broad, its central half forms a triangular plate with finely serrated central side and a more coarsely denticulate outer side with irregularly scattered larger denticles. Its outer half is simple, and lacks dentation. The first marginal is flattened, with a dorsal, regular comb of small denticles, an apical finely serrated truncation, and an equally fine ventral serration. The basal ⅔ of its length lacks serration. The second marginal is longer, more slender, and both sides of the apical half are denticulate. Toward the side, the teeth become slightly shorter, more slender, and oar-shaped.

Jaw. Bipartite and consists of numerous rods in a tilelike arrangement, each equipped with three to five denticles at their free (inner) end.

Remarks: *Hyalogyrina* ***umbellifera*** has the tallest shell of the species of this genus, and is also characterized by the development of the cephalic tentacles. The protoconch and radula seem to be identical in all species.

Hyalogyrina ***globularis*** Warén & Bouchet, sp. nov.

(Figures 37f, 44a, 46a, 47e, f)

Type material: Holotype and one paratype (FMNH 279656 and 280923).

Type locality: JdF, Endeavour Segment, Clam Bed Vent Field, ROPOS HYS 351, 47°57.780'N, 129°05.493'W, 2200–2250 m, 3 spms (1 used for critical-point drying and radular preparation).

Material examined: *JdF, Endeavour Segment:* - ALVIN dive 2409, 1 young spm from a piece of flange (MNHN); - ROPOS HYS 364, 3 spms (V. Tunnicliffe ref. coll.); - Main Vent Field, 1 spm (FMNH 229661). *Middle Valley:* - ROPOS 149, 1 spm; - ALVIN dive 3146, 3 spms (FMNH 280952).

Distribution: Only known from the Endeavour segment, 2200–2250 m depth.

Etymology: "*globularis,*" Latin, meaning globular.

Description: *Shell (Figure 44a).* Medium-sized for the group, globular, rather fragile, smooth, slightly yellowish beige by transparency of soft parts, with a very thin, slightly iridescent periostracum. The protoconch (Figure 37f) consists of about 0.8 whorls, diameter ca. 260 μm, with a very small initial part sculptured by small, crowded pits, diameter 4–5 μm, to some extent spirally arranged and fused. Where this sculpture ends, the diameter starts to increase rapidly and the shell becomes perfectly smooth. The outer lip of the protoconch is slightly constricted and its radial width is three times the width of the whorl where the sculpture stops. The teleoconch consists of about 2.5 almost perfectly smooth whorls; the precise number cannot be given because the half-grown and larger specimens have lost the apex by corrosion. The

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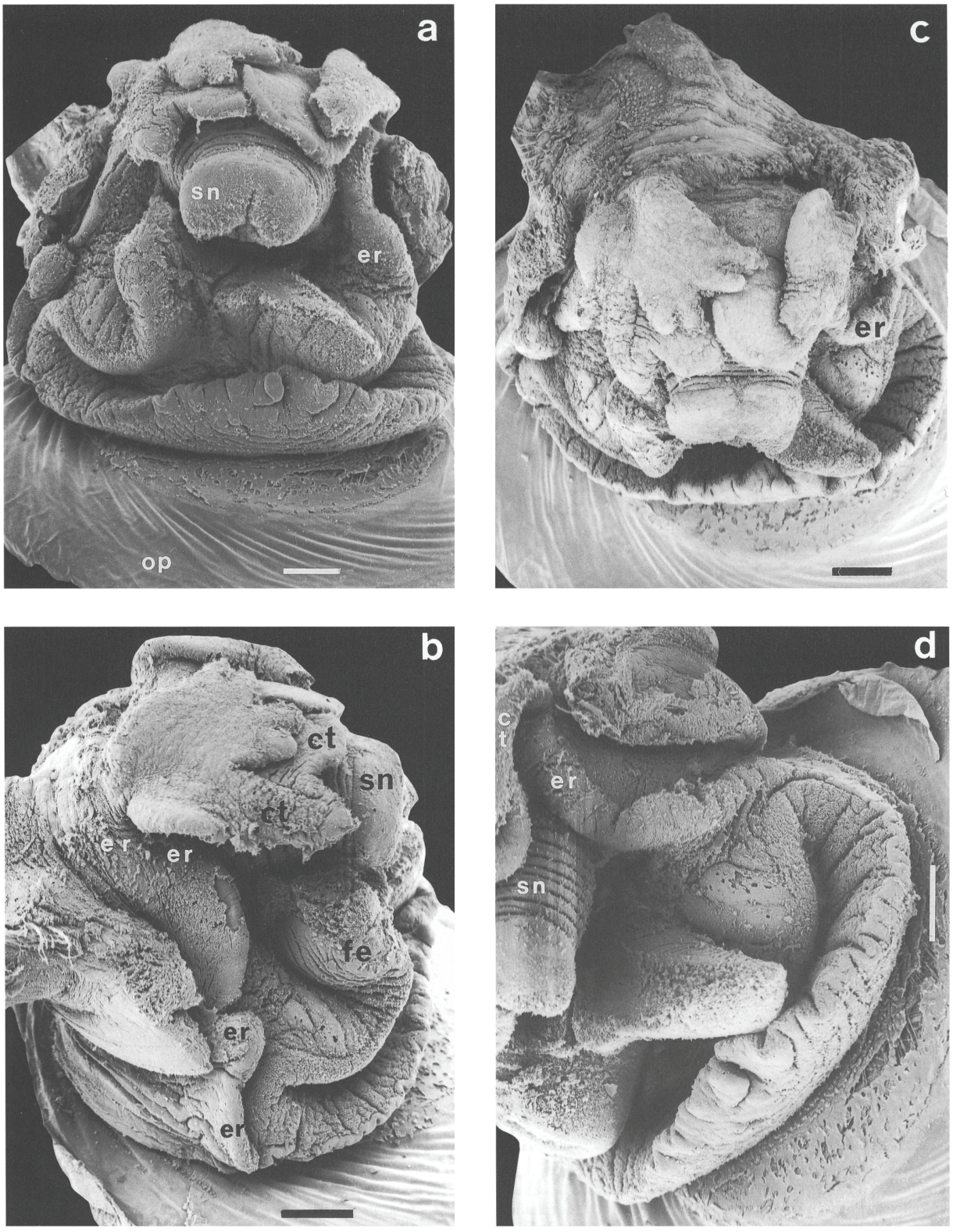
Figure 45. *Hyalogyrina* ***umbellifera*** Warén & Bouchet, sp. nov., critical-point dried, Aleutian Seeps, Shumagin site. *a.* Frontal view. *b.* Right side of head-foot. *c.* Dorsal view of head-foot. *d.* Left side of head-foot. ct - cephalic tentacle; er - epipodial ridge; fe - edge of foot; op - operculum; sn - snout. Scale bars 0.2 mm.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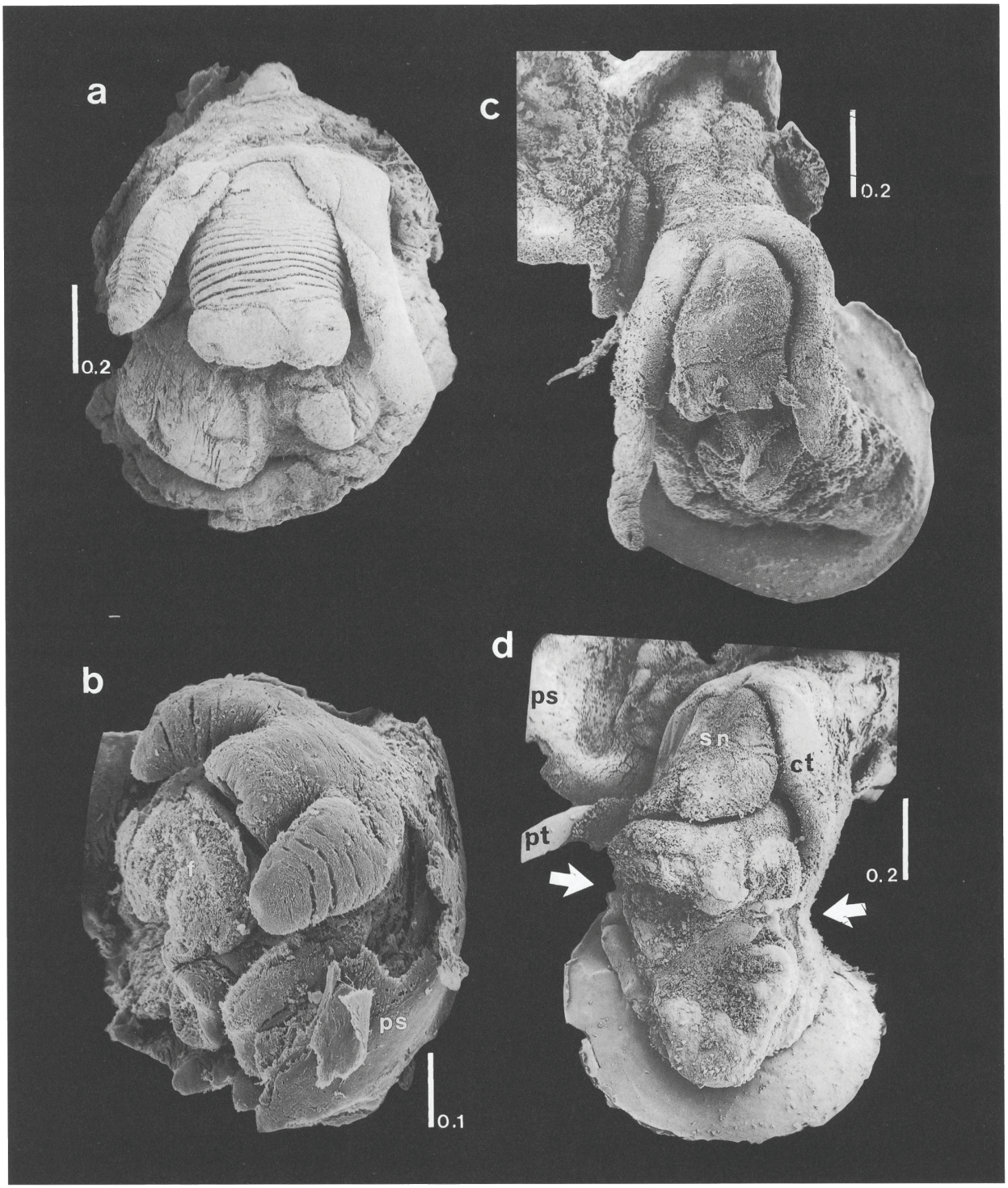

Figure 46. Critical-point dried soft parts. *a. Hyalogyrina* ***globularis*** Warén & Bouchet, sp. nov., paratype, FMNH. *b. Peltospira lamellifera,* EPR, 13°N. *c, d.* ***Lurifax vitreus*** Warén & Bouchet, gen. & sp. nov., paratypes. *c.* Dorsal view. *d.* Anterior view, foot partly autotomized, arrows indicate position of autotomy. ct - cephalic tentacle; f - foot; ps - pallial skirt; sn - snout; pt - pallial tentacle. Scale bars in mm.

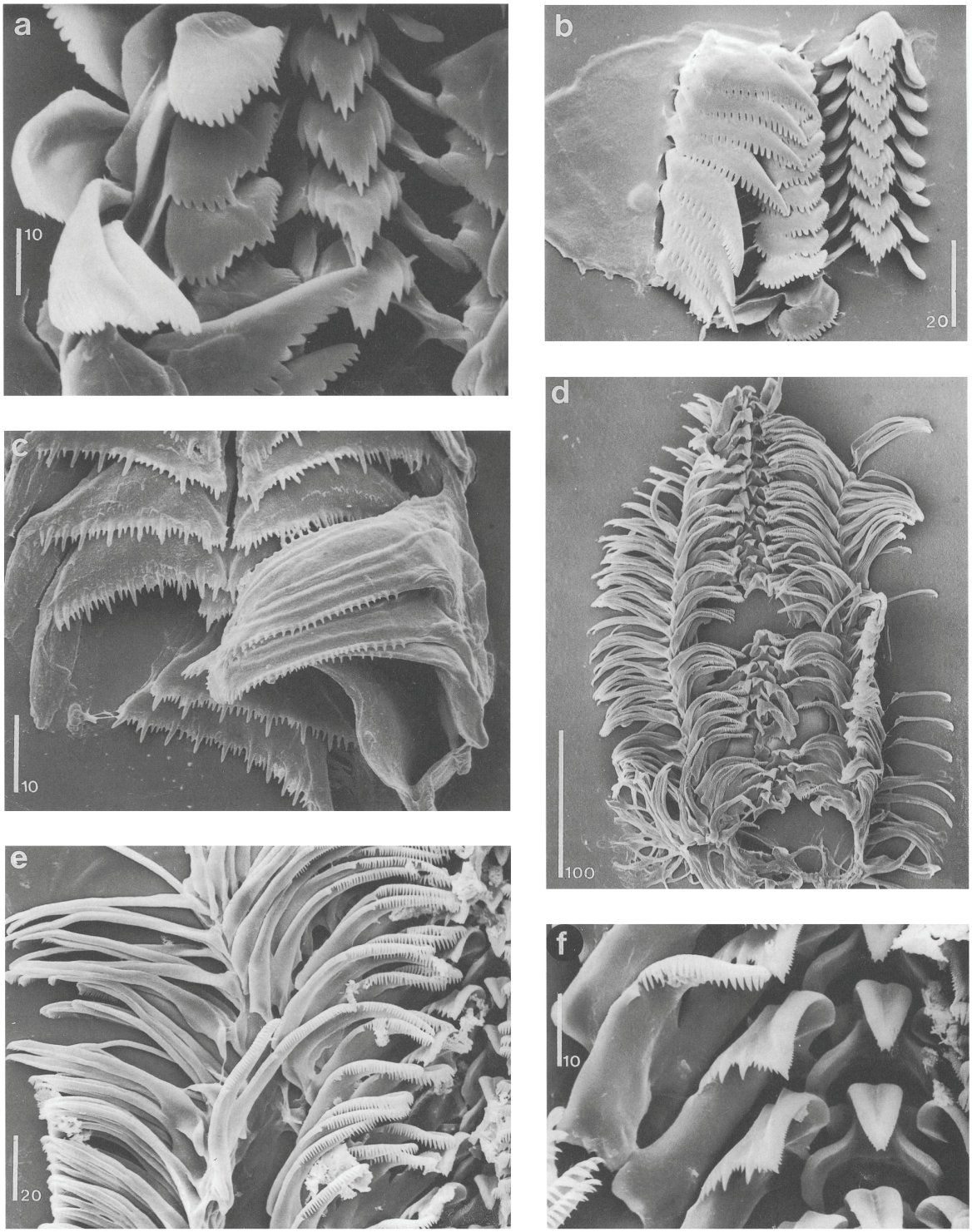

Figure 47. Heterobranchia, radulae. *a, b.* ***Lurifax vitreus*** Warén & Bouchet, gen. & sp. nov., paratype. *a.* Detail of central and lateral teeth. *b.* About half the length of the radula, laterals missing at right side. *c. Xylodiscula* ***analoga*** Warén & Bouchet, sp. nov., paratype. *d. Hyalogyrina* ***umbellifera*** Warén & Bouchet, sp. nov., Aleutian Seeps, Shumagin site, complete radula (see also Figures 48a–b). *e, f.* ***H. globularis*** Warén & Bouchet, sp. nov. *e.* Half width of radula. *f.* Detail of central and lateral tooth. Scale bars in μm.

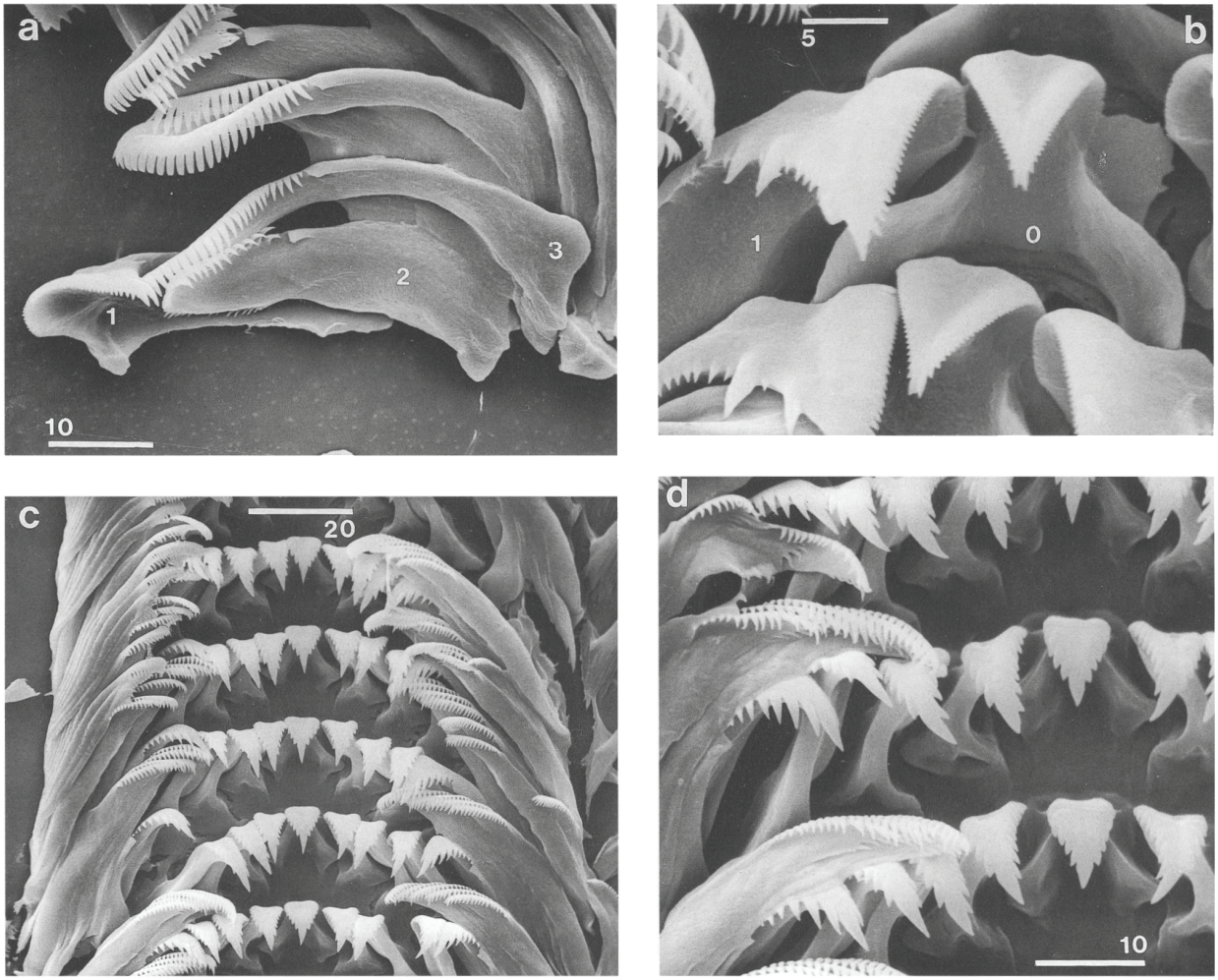

Figure 48. Radulae. Teeth numbered sequentially with central tooth as 0. *a, b. Hyalogyrina* ***umbellifera*** Warén & Bouchet, sp. nov., Aleutian Seeps, Shumagin site. *a.* First and second laterals, first marginal tooth. *b.* Central tooth and first lateral. *c, d. Peltospira lamellifera,* EPR, 13°N. *c.* Whole width. *d.* Detail of central field and inner marginals. Scale bars in μm.

suture is deep and the whorls not very firmly adjoined. The entrance to the umbilicus is quite oblique, and its width in a ventral view corresponds to $1/15$ of the diameter of the shell. The peristome is prosocline, more tangential than radial, not thickened, and not indented by the preceding whorl. The cross section of the whorls is almost circular.

Dimensions. Maximum height ca. 1.9 mm (holotype).

Soft parts (Figure 46a). The foot is large, broad and flat, posteriorly rounded, anteriorly shallowly bilobed, and lacking a demarcated propodium. The anterior corners are drawn out to short tentacles. An epipodial ridge starts at the anterior part of the operculum, continues forward and reaches the base of the cephalic tentacles. No epipodial tentacles. The cephalic tentacles are about as long as the snout in preserved specimens, and seem to be smooth. They are connected by a small skin fold across the base of the snout. The right tentacle has a low, dorsal ridge at its basal $1/5$. The left cephalic tentacle has a similar ridge at its central side. The snout is almost cylindrical, strongly transversally folded, slightly expanded and ciliated distally, and has an apical-ventral mouth. The slender buccal mass is longer than the snout, with salivary glands opening to the buccal cavity, jaws composed of apically denticulate rodlets, and a short "rhipidoglossate" radula with simple, rounded end of the radular sac. The pallial cavity is rather deep, half a whorl, and the bipectinate gill is attached only at its basal part, behind the ctenidial leaflets. It is situated just in front of the intestinal coils, with the very low, ridgelike leaflets paralleling line of attachment. A large afferent vessel, is possibly connected to the rectal sinus. The afferent mem-

brane is attached just in front of rectum, the efferent one over in the far left part of pallial cavity. The pallial margin is distinctly thickened and has a densely ciliated tentacle at its right corner. The inner, posterior half of the cavity is filled by invaginated pallial roof, with a loop of the large intestine. The stomach and intestine contain grey sediment; in the intestine the fecal rod is partly split by a deep longitudinal furrow.

Operculum. Transparent, colorless; round, multispiral, with distinct growth lines. The width of the last whorl, at the growth zone, corresponds to 1/5 of the diameter.

Radula (Figures 47e–f). Ca. 15 - 1 - 1 - 1 - ca. 15, short, 3–3.5 times as long as broad, rhipidoglossate, with marginal teeth folded across laterals and central. The central tooth is low and broad with projecting lateral supports, a triangular, finely serrated apical plate and distinct "wings" behind the lateral support. The lateral tooth is low and broad, its central half forms a triangular plate with finely serrated central side and a more coarsely denticulate outer side with irregularly scattered larger denticles. Its outer half is simple, and lacks dentation. The first marginal is flattened, with a dorsal regular comb of small denticle, an apical finely serrated truncation, and an equally fine ventral serration. The basal 2/3 of its length lacks serration. The second marginal is longer, more slender, and both sides of the apical half are denticulate. Laterally the teeth become slightly shorter, more slender, and lose the denticles.

Jaw. Bipartite and consists of numerous rods in a tilelike arrangement and equipped with three to five denticles at their free (inner) end.

Remarks: *Hyalogyrina* ***globularis*** resembles *H. grasslei* Warén & Bouchet, 1993, from the Guaymas Basin, but has a more globular shape, more slowly increasing diameter of the whorls, and the shell has a proportionally larger aperture. We do not know if the poor development of the cephalic tentacles (compared with *H.* ***umbellifera***) is because our specimens are young, or if there is much variation in this character within the group. *Hyalogyrina grasslei* has the same arrangement of the cephalic tentacles as *H.* ***globularis.***

Family ORBITESTELLIDAE Iredale, 1917

Remarks: The genus *Orbistestella* Iredale, 1917, contains mainly shallow water species, usually living under rocks (Ponder, 1990; Bosch et al., 1995; own observations). A second genus, *Microdiscula* Thiele, 1912, is restricted to shallow water in the temperate parts of Australia and off Antarctica in deeper water. (The third genus, *Boschitestella* Moolenbeek, 1994, is very similar to *Orbitestella,* and we feel uncertain about the necessity for it.)

The new species below shares some shell characters with *Orbitestella* (*Microdiscula* has a smooth shell), but is three times as large as the average species of *Orbitestella.* The protoconch of ***Lurifax*** shows no trace of heterostrophy despite being multispiral, and the shape of the shell differs from orbitestellids by having a distinct spire (not planispiral). The sculpture consists of fine spiral and axial cords, not mainly broad, rounded axial ridges. The radula, however, is indistinguishable from that of *Orbitestella* and *Microdiscula,* and we feel sure about the family assignment.

Lurifax Warén & Bouchet, gen. nov.

Type species: ***Lurifax vitreus,*** sp. nov.

Diagnosis: Orbitestellids with unusually tall-spired and large shell with fine sculpture of spiral ribs and keels of variable strength and radiating flexuous incremental lines. Umbilicus deep. Protoconch of 1.5 smooth whorls. Radula normal for family.

Etymology: "lurifax," Swedish, a person who tries to deceive, referring to the confusing shell morphology. Gender masculine.

Remarks: The name of this new genus and species is well deserved; at the first sorting, specimens with poorly developed spiral sculpture fooled the senior author that they were a species of *Leptogyra* Bush, 1897 (Vetigastropoda), those with developed spiral sculpture that they belonged to *Cyclostremiscus* Pilsbry & Olsson, 1945 (Neotaenioglossa).

A very similar species was reported by Lewis & Marshall (1996) from a seep off New Zealand as *Pterolabrella* sp. The latter genus is based on a New Zealand Tertiary fossil species, most likely belonging to the Vitrinellidae. The specimens from New Zealand do, however, fit better in ***Lurifax*** (Marshall, personal communication).

Lurifax ***vitreus*** Warén & Bouchet, sp. nov.

(Figures 37c, d, 44e–g, 46c, d, 47a, b)

Type material: Holotype and 55 paratypes in MNHN.

Type locality: MAR, Menez Gwen, DIVA 2 PL 11, 37°50.54'N, 31°31.30'W, 860–870 m, on mussels.

Material examined: *MAR, Menez Gwen:* - DIVA 1 PL 13, on an active chimney, 9 spms; - DIVA 1 PL 14, on sulfide rock with Hydrozoa, 12 spms; - DIVA 1 PL 16, on base of a black smoker, 12 spms; on chimney, 2 spms; - DIVA 2 PL 14, suction sample among mussels, 1 spm; - DIVA 2 PL 16, 1 spm; - MARVEL PL1202, 850 m, retrieval box, 1 spm; - MARVEL PL1203, 850 m, retrieval box, 2 spms; - MARVEL PP46, particle trap, 1 spm. *Lucky Strike:* - DIVA 1 PL 04, in baited trap, 2 spms; with mussels and polychaetes, 4 spms; on inactive chimney among Hydrozoa and sponge *Cladorhiza,* 32 spms; - DIVA 1 PL 08, on a rock, 1 sh; - DIVA 1 PL 17, among

mussels, 5 spms; - DIVA 1 PL 19, among mussels, 1 spm; - DIVA 2 PL 02, 6 spms; - DIVA 2 PL 03, 10 spms; - DIVA 2 PL 04, 5 spms; suction sample among mussels in shimmering water, 3 spms; - DIVA 2 PL 07, 31 spms; 2 suction samples among mussels and hydrothermal sediments, 8 and 8 spms; - DIVA 2 PL 08, retrieval box, 3 spms; - DIVA 2 PL 09, 14 spms; - DIVA 2 PL 10, 13 spms; on a rock, 8 spms; retrieval box, 189 spms; - DIVA 2 PL 19, 3 spms; - DIVA 2 PL 20, 2 spms; - DIVA 2 PL 21, 1 spm; - DIVA 2 PL 26, 1 spm; - ALVIN dive 2604, 1 spm; - ALVIN dive 2607, 21 spms; - LUSTRE Exp., Tour Eiffel, on mussels, 1 spm; - MARVEL PL1193, Tour Eiffel, retrieval box, 4 spms; - MARVEL PL1194, Tour Eiffel, retrieval box, 5 spms.

Distribution: MAR, from Menez Gwen to Lucky Strike, ca. 850–1800 m depth, seems to be epifaunal.

Etymology: "*vitreus,*" Latin, referring to the transparent shell in well preserved specimens.

Description: *Shell (Figures 44e–g).* Large for its family, vitrinellidlike, depressed conical, rather fragile, vitreous, often covered by thick crusts of rust. The protoconch (Figure 37c, d) consists of ca. 1.5 perfectly smooth whorls of slowly increasing diameter, sculptured by faint incremental lines, without a trace of heterostrophy, diameter 300–310 μm. The teleoconch has up to 3.5 whorls of slowly increasing diameter, sculptured by collabral, sharp, dense, and flexuous incremental lines. The spiral sculpture consists of numerous spiral striae of which those between the shoulder and periphery may develop into stronger ribs and give the shell a keeled appearance. The aperture is rounded-rhombic, distinctly broader than high, the peristome is not thickened. The umbilicus is broad and deep.

Dimensions. Maximum diameter 2.8 mm.

Soft parts (Figures 46c, d). The foot is long and slender, anteriorly truncated, posteriorly tapering, with well demarcated propodium. There are no appendages except the metapodial lobes. The head has a pair of simple cylindrical cephalic tentacles, each with a well developed eye dorsally in the base. Pallial margin with at least one well developed, ciliated pallial tentacle attached just inside the right corner.

Operculum. Multispiral with about six whorls, central nucleus, weak incremental lines, stiff, almost transparent.

Radula (Figures 47a, b). 1 - 1 - 1 - 1 - 1. The central tooth has an apical, rhombic, serrated plate and widely diverging antero-lateral supports. The lateral tooth has an ovate, irregularly serrated plate with an antero-lateral basal process. The marginal tooth consists of a long, triangular plate with short base and anteriorly serrated margin.

Jaw. Not examined in detail, consisting of numerous small elements.

Remarks: ***Lurifax vitreus*** often autotomizes the posterior part of its foot when being preserved (Figure 46d). This is not known for shallow water species of *Orbitestella,* but may be a response to predators grabbing the foot.

The shell of ***Lurifax vitreus*** is amazingly similar to species of *Cyclostremiscus,* a genus of the neotaenioglossate (Caenogastropoda) family Vitrinellidae, but the radula and soft parts convincingly show that it belongs to the Orbitestellidae.

Family XYLODISCULIDAE Warén, 1992

Xylodiscula Marshall, 1988

Xylodiscula Marshall, 1988:988.

Type species: *X. vitrea* Marshall, 1988; by original designation; deep water off New South Wales, on sunken drift wood.

Remarks: The genus now includes seven species. Two are known from hydrothermal vents, three, perhaps four (Hasegawa, 1997) from sunken drift wood, and two from accumulations of *Posidonia* fibers (Warén & Bouchet, 1993). The two species from hydrothermal vents differ by being about twice the size of those from non-vent localities.

Xylodiscula ***analoga*** Warén & Bouchet, sp. nov.

(Figures 44b–d, 47c, 49h)

Type material: Holotype in MNHN.

Type locality: MAR, Lucky Strike, ALVIN dive 2607, 37°17.50'N, 32°16.47'W, 1628 m, Sintra site.

Material examined: *MAR, Menez Gwen:* - MARVEL PL1201, 850 m, 5 spms; - MARVEL PL1202, 850 m, retrieval box, 2 spms; - MARVEL PL1203, 850 m, retrieval box, 1 spm; - MARVEL PP46, particle trap, 1 young. *Lucky Strike:* - DIVA 1 PL 19, among mussels, 2 spms; - DIVA 2 PL 07, 1 spm.

Distribution: Only known from the material above, MAR from Menez Gwen to Lucky Strike, 850–1728 m depth.

Etymology: From "analogos" (Greek), meaning similar.

Description: *Shell (Figures 44b–d).* Large for the genus, fragile, with a thick yellowish, brownish periostracum, subplanispiral, with whorls of round cross section and rapidly increasing diameter. Protoconch not seen, corroded in all specimens. The teleoconch has about 2.5 whorls of round cross section, not indented by preceding whorl and sculptured only by collabral incremental lines. The aperture is subradial and slightly prosocline, slightly flexuous in profile. The umbilicus is deep and wide.

Dimensions. Maximum diameter of holotype 1.7 mm, maximum diameter examined ca. 3 mm.

Operculum (Figure 49h). Thin and transparent, round, smooth, multispiral with central nucleus.

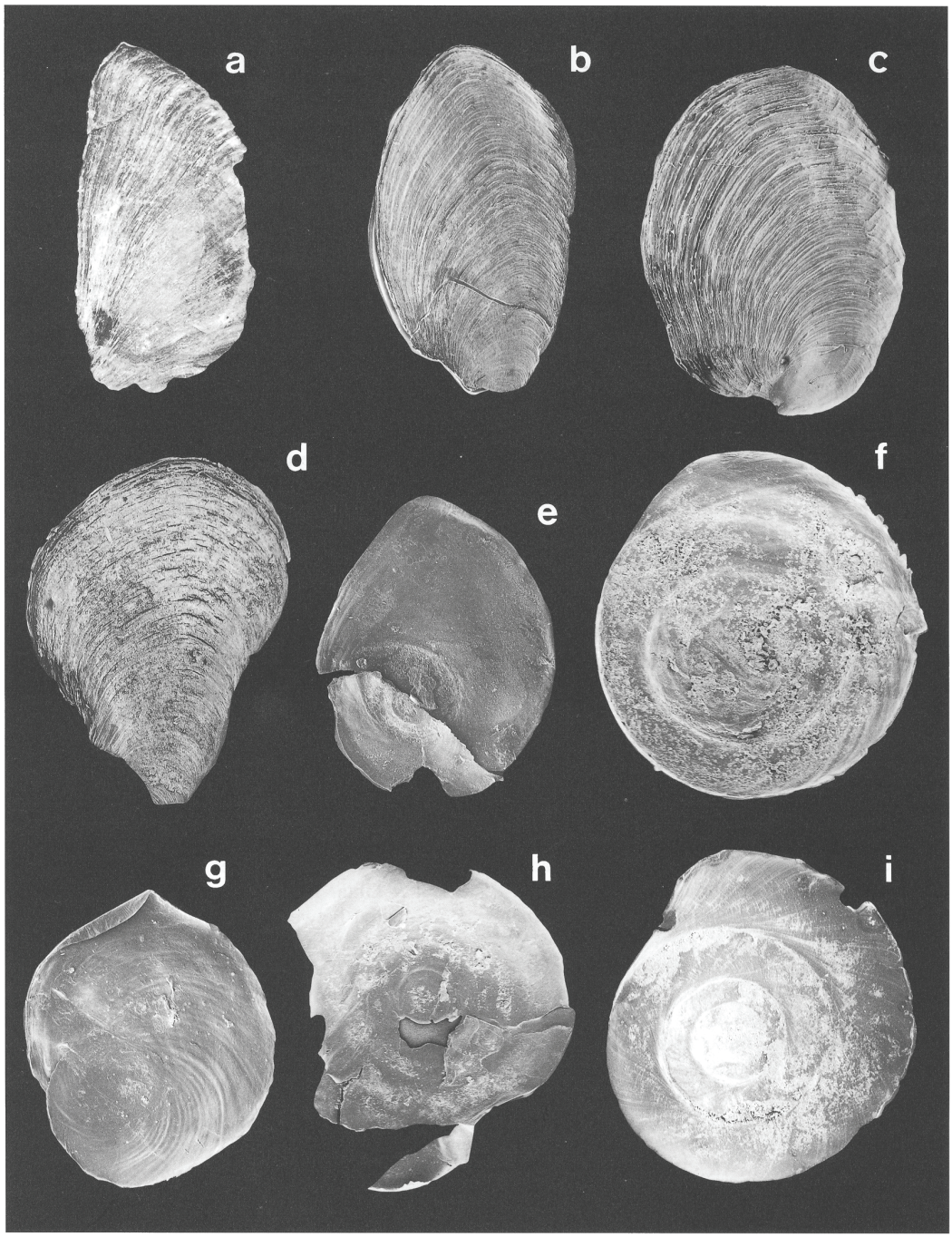

Figure 49. Opercula. *a. Eosipho* ***auzendei.*** Warén & Bouchet, sp. nov., paratype, diameter 18 mm. *b. E. canetae,* Bush Hill Seep, diameter 11.4 mm. *c. Bayerius arnoldi,* Aleutian Seeps, Edge site, diameter 7.5 mm. *d. B.* ***peruvianus*** Warén & Bouchet, sp. nov., paratype, diameter 7.7 mm. *e. Laeviphitus* ***desbruyeresi*** Warén & Bouchet, sp. nov., MAR, Lucky Strike, diameter 0.7 mm. *f.* ***Neusas*** Warén & Bouchet, gen. nov., *marshalli,* MAR, Menez Gwen, diameter 0.55 mm. *g.* ***Speculator cariosus*** Warén & Bouchet, gen. & sp. nov., holotype, diameter 1.6 mm. *h. Xylodiscula* ***analoga*** Warén & Bouchet, sp. nov., paratype, diameter 0.8 mm. *i. Hyalogyrina* ***umbellifera*** Warén & Bouchet, sp. nov., Aleutian Seeps, Shumagin site, diameter 1.0 mm.

Radula (Figure 47c). 1 - 1 - 0 - 1 - 1, short and broad with about 20 transverse rows of teeth. The marginal teeth are roughly triangular, long, and finely serrated along the anterior edge. The lateral teeth are broadly triangular with a projecting lateral support; their anterior edge is serrated with nine or 10 larger, cylindrical and pointed denticles with irregular interspaces and one to four much smaller ones between each pair of the larger ones.

Remarks: *Xylodiscula major* Warén & Bouchet, 1993, the other species of this genus known from hydrothermal vents, has a flatter shell with whorls of more slowly increasing diameter, its radula has much more slender marginal teeth, and the serration of the laterals consists of teeth of uniform size.

DISCUSSION

Tunnicliffe et al. (1998) presented a thorough discussion of the biogeography and related topics of the hydrothermal vent fauna. We have previously discussed several aspects of the gastropod fauna of the vent and seep environments (Warén & Bouchet, 1989, 1993) and will here restrict these discussions to a few comments on the vent environment. The mollusk fauna of the seeps is intermediate between the faunas of vents and those of the surrounding deep-sea (Warén & Bouchet, 1993; Tunnicliffe et al., 1998) with a few large, endemic, chemosynthetically nourished animals that constitute the majority of the biomass, for example species of *Bathymodiolus* or vesicomyids (Bivalvia) or Vestimentifera (Sahling, 1997; Carney, 1994; Jollivet et al., 1990; Suess & Bohrmann, 1997).

The aspects for which we feel that the new information is sufficient to complete earlier discussions are distribution, endemism, and age of the fauna of the hydrothermal vents.

Distribution. Appendix 1 updates Warén & Bouchet's (1993) list of seep and vent localities from which gastropods have been reported. It also gives a summary of the fauna of each locality. From these lists it is very clear that each of the three well documented areas, JdF, EPR, and MAR, has a fauna of its own with no overlap. The following comments are needed:

MAR. A uniform fauna with 15 species occurs from 38°N to 14°45′N along the MAR. We have identified some species from Menez Gwen, the northernmost of the sites, with a main distribution outside the vents. Most of these are well known from normal bathyal environments, but three species (***Neusas marshalli*** (1 record), *Alvania stenolopha* nine records) and *Rokopella* ***segonzaci*** (one record)) are of uncertain status. These are not included in the 15 spp.

JdF Ridge system. The Gorda Ridge off northern California (41°N) still is poorly known (six spp. identified), but seems to resemble the northern localities much more than the EPR (see Warén & Bouchet, 1993:87). Three species of the main system (44–50°N), *Provanna laevis, P. variabilis,* and *Pyropelta musaica* are also known from the seeps off Oregon and the Guaymas Basin. *Buccinum viridum* Dall, 1890, was described from (seeps?) off Santa Barbara, California, but no details about this locality are known, and the identification of the specimens from JdF is uncertain (McLean, personal communication). No other species out of the 14 species known from JdF are known elsewhere, although the Oregon seeps are nearby.

EPR and Galapagos Rift. A very uniform fauna with about 35 endemic species occurs along the EPR, from 21°N to 17°S. Of 16 species collected at 17°S, 14 are known also at the more northern localities. The Galapagos rift fauna has 11 species of gastropods of which *Lacunoides exquisitus* is not known from other localities; otherwise the species are known also from the EPR. There is no overlap with the seep fauna of the Guaymas Basin, or the seeps off Peru. Three additional species (*Moelleriopsis* sp., *Sinezona* sp., *Falsimargarita* ***nauduri***), are known from a single specimen each and may be occasional intruders.

Western Pacific vents. These are more difficult to compare with each other since the Japanese vents have been less thoroughly reported from a biological point of view, and few gastropods have been reported from more than a single locality. The same is true for the Edison Seamount vents (ca. six spp. known; Tunnicliffe, 1994; Beck, 1996; Warén & Bouchet, herein). The Manus Back Arc Basin has been more investigated (Beck, 1992a, b, 1993; Galkin, 1993). The Mariana Back Arc Basin is represented by six species of which four are known from there only. The North Fiji and Lau Basins are better known, with altogether 30 species (Warén & Bouchet, 1993; Okutani & Ohta, 1993; Beck, in press). About 50% of these are shared between the two localities. Three species are shared between at least two of the Manus, Mariana, and Fiji basins: *Lepetodrilus schrolli, Alviniconcha hessleri,* and *Ifremeria nautilei.* In some further cases there are closely resembling species in two or three of these localities:

Symmetromphalus hageni (Manus), *regularis* (Mariana) and *macleani* (Fiji)

Shinkailepas conspira (Fiji), *tufari* (Manus)

Pyropelta ovalis (Fiji), *bohlei* (Lihir)

Pseudorimula leisei (Fiji), *marianae* (Mariana)

In the case of *Alviniconcha* genetic differences between the populations in the Lau and North Fiji Basins were reported by Denis et al. (1993), but considering that the specimens are morphologically inseparable we find it premature to assume that two species are involved, and in any case the similarity must indicate recent connections between the localities.

We therefore assume that there is more faunal relationship between the western Pacific vent systems than with other vent systems.

An analysis of the genus level relations between the four major vent systems shows that a few genera like *Provanna* (absent from MAR), *Lepetodrilus* (present at all), and *Phymorhynchus* (present at all?) are quite widely dispersed. Other genera may occur at widely scattered localities: *Pseudorimula* (WP - MAR), *Shinkailepas* (WP - MAR), *Peltospira* (EPR - MAR), *Fucaria* (JdF - WP; also seeps off Florida), ***Lurifax*** (MAR and seeps off New Zealand). This disjunct distribution may be a result of missing information, but it may also indicate that the gastropods have a good dispersal capacity.

Some genera have a rather restricted distribution at vents and seeps:

Buccinum, Neptunea, and *Oenopota* occur at North Pacific vents and seeps, but have their main distribution in shallow, non-vent environments.

Gorgoleptis (three spp. EPR), *Nodopelta* (three spp. EPR), and *Desbruyeresia* (three spp. WP) have a few species each, they are restricted to a single vent system, and may represent local radiations.

Endemism. Knowledge on the extent to which the hydrothermal vent fauna is restricted to the vents is severely hampered by lack of knowledge on the normal deep-sea fauna, especially that of the bathyal and abyssal rocky bottoms and in the Pacific basins. There is also a problem with the vent fauna in general in that less than 25% of the species are known from more than one site (Tunnicliffe et al., 1998). The corresponding figure for gastropods is 55% known from more than one site. Nevertheless, some conclusions may be drawn, especially based on the fauna of the MAR vents, since the gastropod fauna of the surroundings there is much better known than in the Pacific.

Endemism at Species Level. Our knowledge on the gastropod fauna of the three well known localities at the MAR (Table 1; Menez Gwen, Lucky Strike, and Snake Pit) is based on 70 dives during which 1–10 samplings were made. Three such samples at Menez Gwen contained nine specimens and shells of six species well documented from non-vent environments (DIVA 1 PL 13-6; DIVA 2 PL 11, DIVA 2 PL 13). This shall be contrasted with ca. 500 specimens of eight species known from vents only in the same samples. It seems thus quite obvious that these samplings touched areas less affected by hydrothermal effluents, where conditions allowed species not acclimatized to vent life, to enter. Two subsamplings from Menez Gwen (DIVA 2 PL 11: *Pseudosetia azorica* and *Rokopella* ***segonzaci:*** DIVA 2 PL 26: ***Neusas*** *marshalli*) gave six specimens of three species; we do not know if they are a part of the vent fauna or not.

The most common and regularly occurring not endemic species at the MAR vents is *Protolira thorvaldssoni.* It was described from two specimens found on a piece of whale bone in a few hundred meters depth, south of Iceland. The shell is simple, the radula variable, and the external morphology of the soft parts is not known in the type material. Therefore there is some uncertainty in the identification, but at least the whale bone and vent specimens are closer to each other than to any other specimens we have seen.

Table 1.

List of species from MAR.

Species	Number of specimens
Paralepetopsis ***ferrugivora,*** sp. nov.	24
Protolira valvatoides	8895
Protolira thorvaldssoni	3855
Sutilizona ***pterodon,*** sp. nov.	17
Lepetodrilus ***atlanticus,*** sp. nov.	41,477
Pseudorimula midatlantica	257
Peltospira ***smaragdina,*** sp. nov.	766
Lirapex ***costellata,*** sp. nov.	45
Shinkailepas ***briandi,*** sp. nov.	1632
Laeviphitus ***desbruyeresi,*** sp. nov.	63
Alvania stenolopha	49
Phymorhynchus ***ovatus,*** sp. nov.	53
Phymorhynchus moskalevi	78
Phymorphynchus ***carinatus,*** sp. nov.	8
Lurifax vitreus, sp. nov.	492
Xylodiscula ***analoga,*** sp. nov.	13
Total	57,724

A second case is *Alvania stenolopha.* About 50 specimens, from Menez Gwen and Lucky Strike, were found among 57,000 specimens of gastropods from the MAR.

No other species from the MAR vent fauna is suspected to occur also outside the vent environment.

Our material from the EPR at 13°N, the best known locality, includes ca. 35 species represented by about 325,000 specimens. Of these a single specimen each of three species does not belong to the vent fauna.

This can be summarized as species numbers: About 125 species of gastropods have now been identified from hydrothermal vent localities in the Atlantic and Pacific oceans. Six of these species are also known from localities outside the vents: *Alvania stenolopha* (MAR) and one species of *Buccinum* (*viridum*?, JdF) are known from undefined (non-vent?) environments. Four further species are known from hydrocarbon seeps (*Provanna laevis* and *Neolepetopsis gordensis*) and whale bone (*Pyropelta musaica* [Guaymas Basin and off Oregon] and *Protolira thorvaldssoni* [MAR]). These six species are regular component of the fauna, each known from a few to several records in vent environments. However, four of the six species are in one way or another connected with taxonomic problems and it is only *Alvania stenolopha* and *Provanna laevis* for which we are convinced that the records outside hydrothermal vents are conspecific.

This means that 95–98% of the fauna is endemic at species level. That is a slightly higher figure than given

by Tunnicliffe et al. (1996), 93% for the fauna in general, in the vent environment.

Genus Level. About 57 genera of gastropods are known from hydrothermal vents; 31 (54%) are endemic; eight further genera occur also in various kind of seeps, but are not known from non-chemosynthetic environments. If these are included, 70% of the genera in hydrothermal vents are endemic to chemosynthetic environments.

Family Level. Among the families, Peltospiridae (nine genera, 17 species) and Sutilizonidae (three genera, six species) are endemic; Neomphalidae (nine genera, 15 species [one in seeps, ***Retiskenea diploura***]) and Lepetodrilidae (four genera, 20 species [one in seeps, *Lepetodrilus guaymasensis*]) are almost endemic to vents. The families Provannidae (four genera, 12 species in vents, eight in seeps, one in both) and Neolepetopsidae (three genera, six species in vents, two in seeps and one in both) are also taxa that have their main distribution in vents. Together these families have an average of 5.3 genera and almost 12 species per family living in the vents. This shall be compared to 1.3 genera and 2.4 species per family among the ca. 25 (23–27 depending on family concept) families mainly known from outside the vents. From these figures it is obvious that the families which have their main distribution in the vents also have undergone a considerable radiation there. These are also the families that exhibit many morphological adaptations and of which the relations are difficult to recognize. This problem directly leads to the next question, the "age" of the vent fauna.

Age and Origin of Vent Gastropod Fauna. It has been suggested that the hydrothermal vents have acted as refugia for Palaeozoic-Mesozoic faunas, and that the vents have been quite isolated since the time they were first inhabited. For non-mollusk taxa, the first evidence of antiquity of vent animals was given for a stalked barnacle (Newman, 1979), which was considered intermediate between a genus known only from the Upper Triassic and another known from Jurassic until Recent. Newman (1985) elaborated this idea and discussed further invertebrates, among them also gastropods, and considered the higher endemic taxa (families etc.) to be relicts of Palaeozoic and Mesozoic age. These opinions have then been supported by Král (1995), Tunnicliffe (1991), Tunnicliffe & Fowler (1996), Tunnicliffe et al. (1996), Tunnicliffe et al. (1998), McArthur & Tunnicliffe (1998).

McLean has in several papers emphasized a Palaeozoic to Lower Mesozoic origin of endemic gastropod families: Lepetodrilidae (1988), Peltospiridae (1989b), Neomphalidae (1990b) and Neolepetopsidae (1990a), but this has only in the case of Neolepetopsidae been supported by direct reference to a similar fossil taxon, assumed to be related at superfamily level. Also Beck (1992a, b, 1993, 1996) has in several, more cursory comments suggested an ancient origin of vent gastropods.

The mollusks in general and especially the marine gastropods have an excellent fossil record compared with other groups of invertebrates. This helps to give some ideas about the age of many of the major taxa of gastropods. On the other hand, the richness of fossils also gives good opportunities for erroneous conclusions because of convergence in shell characters. This is especially obvious with simplified shells, like many of the species of the vent fauna.

Table 2 summarizes the present knowledge on the earliest appearance of families or reliably identified lower taxa from hydrothermal vents. Most information here is of little value; many of the taxa consist of small species with featureless shells and may occur unnoticed in earlier deposits. For others, e.g., Fissurellidae, Trochidae, and Turbinidae, the table gives a more reliable idea of the earliest appearance of the taxon, but nothing is known about when the vent-inhabiting subtaxon entered hydrothermal vents. The families Conidae and Buccinidae are, however, more informative. These two families (with 13 species and five genera in vents) go back to the Late Cretaceous only. The species were then large and common, but cannot be recognized in Early Cretaceous deposits. In the case of the genus *Buccinum,* with two species, one in vents and one in seeps, an even more recent and precise maximum age can be given since the oldest species is from the Late Oligocene (Golikov, 1980). For *Neptunea* (one species at the Kaikata Seamount vents) a Late Eocene age has been given (Strauch, 1972). The case is similar for *Phymorhynchus*; the earliest appearance of its subfamily is Eocene. This clearly shows that some immigration into the hydrothermal vents has taken place in quite recent time, Late Cretaceous to Eocene; for *Buccinum* even Late Oligocene, and that the vent environment is not completely isolated.

Among the four major endemic vent radiations, Neolepetopsidae, Lepetodriloidea, Peltospiridae, and Neomphalidae, the three latter taxa show considerable variation in their morphology, which has been used as evidence that they have lived isolated in the vent environment for a long time (back to Late Palaeozoic or Early Mesozoic). This assumption is contradicted by the fact that within each of these taxa, there is virtually no variation in protoconch characters (Lepetodriloidea, see Warén, in press; Peltospiridae and Neomphalidae, see Warén & Bouchet, 1989, 1993, and herein). All other non-vent vetigastropod families and subfamilies show a considerable variation in this character, often also within a genus. Warén (in press), based on an analysis of the Lepetodriloidea and related non-vent groups, suggested a maximum age of Late Triassic for this superfamily. The radiation may, however, as well be of Late Mesozoic or Caenozoic origin, since the tree could not be resolved between Scissurellidae, Haliotidae, and Lepetodriloidea. The sister taxa Scissurellidae and Haliotidae go back to the Jurassic and Late Cretaceous respectively. McArthur (1999) suggested "at least mid-Mesozoic" origin for Neomphalina (Peltospir-

Table 2.

Fossil record of gastropod taxa from hydrothermal vents. Data mainly from Tracey et al. (1993), Moore (1960) and Wenz (1938–1944), supplemented by more recent information when available.

Taxon	Earliest known fossil record//Recent distribution
Cocculiniformia	Eocene//mainly bathyal biogenic substrata
Hyalogyrinidae	Oligocene (Lozouet, 1997)//bathyal to shallow biogenic substrates
Orbitestellidae	Eocene (Ducasse et al., 1973)//bathyal to shallow
Xylodisculidae	Late Eocene? (Warén & Bouchet, 1993:53)// bathyal to shallow biogenic substrates
Cerithiopsidae	Jurassic (Dogger) (Gründel, 1980)//sponge feeders
Elachisinidae	Paleocene//shallow water
Provannidae	Late Jurassic (Campbell, unpublished), Late Eocene (Squires, 1995)//in seeps and on driftwood
Rissoidae	(Jurassic?) Cretaceous//all abyssal to littoral environments
Vitrinellidae	Cretaceous//all bathyal to littoral environments
Conidae	Cretaceous//all abyssal to littoral environments
Buccinidae	Cretaceous//all abyssal to littoral environments
Buccinum	Late Oligocene//north Pacific, Atlantic and Arctic, bathyal to littoral
Neptunea	Late Eocene//north Pacific, Atlantic and Arctic, bathyal to littoral
Neomphalina	Late Eocene seeps, Warén & Bouchet herein//endemic to vents and seeps
Neritoidea	Late Triassic//Recent non-vent species in shallow, marine to fresh water environments
Acmaeidae	Mid Triassic//mainly in shallow water
Neolepetopsidae	no fossils known, compared to Lepetopsidae (Permian-Triassic) (McLean, 1989)
Peltospiridae	no fossils known (McLean, 1990b); Late Jurassic-Early Cretaceous (? Campbell, pers. comm.)//endemic to vents and seeps
Fissurellidae	Triassic (Bandel, pers. comm.)//all abyssal to littoral environments
Lepetodrilidae	no fossils known, McLean (1988)//endemic to vents and seeps
Sutilizonidae	Not known as fossil//endemic to vents
Skeneidae	Cretaceous(?)//all abyssal to littoral environments
Trochidae	Triassic(?)//all abyssal to littoral environments
Turbinidae	Triassic(?) (Permian???)//all bathyal to littoral environments

idae + Neomphalidae) based on molecular information, but their comparison included almost no freeliving possible relatives.

The ages given in Table 2 do not differ drastically from those that would be obtained for any other marine gastropod assemblage, and groups like Neritimorpha, Fissurellidae, Trochidae, and Acmaeidae (all of Triassic origin) are common in many non-vent environments (quoting some of the oldest ones).

Fossil hydrothermal vents are well known back to the earliest Palaeozoic times (Little et al., 1997, 1998), but it is rare that they contain fossils well enough preserved to allow any conclusions about the inhabitants. This is largely a result of the vent environment, with an outflow of hydrothermal fluids with a pH of 2–6, and richness of decaying organic material. Almost all empty shells of gastropods recovered from modern vents consist mainly of periostracum, and even adult living specimens are often severely attacked (Figure 42c).

Fossil vents with "identifiable" animal remains have been described back to the Silurian (Little et al., 1997, 1998, 1999a, b), and gastropods have been tentatively identified as members of the family Nododelphinulidae in the Jurassic (Little et al., 1999a) and as cerithioids and epitoniids in the Cretaceous (Little et al., 1999b). Apart from these attempts, it has generally not been possible to identify gastropods to family level. Deposits from seep communities are better known, and gastropods have been identified, in some cases belonging to genera known from modern vents and seeps (Moroni, 1966; Squires & Goedert, 1991; Goedert & Squires, 1990; Taviani, 1994; *?Sahlingia:* Squires & Goedert, 1996 [as *Thalassonerita*]; *Provanna:* Squires, 1995; and its relative *Abyssochrysos:* Goedert & Kaler, 1996; *Retiskenea,* Goedert & Benham, 1999).

The bivalves also show a similar pattern. Campbell & Bottjer (1993, 1995) showed that during the Late Jurassic bivalves of the families Vesicomyidae, Mytilidae, Lucinidae, Thyasiridae, and Solemyidae began to replace brachiopods in seeps and vents, to become dominant in the Early Cretaceous. The genera *Vesicomya* and *Calyptogena* (Vesicomyidae) which dominate many seeps and vents are known as fossil back to the Late Eocene in methane seeps (Goedert & Squires, 1990). (Earlier reports about Silurian vesicomyids [Kuznetsov et al., 1993] were based on misidentified brachiopods (!) [Little et al., 1997]). In Eocene and Miocene seeps there were mussels more similar to *Modiolus* (Moroni, 1966; Squires & Goedert, 1991), instead of the genus *Bathymodiolus,* which now often dominates in vents and seeps.

We therefore favor a view that throughout the times during which vents have existed, there has been a continuous immigration of new taxa from more shallow water, often via seeps and biogenic substrates, with concomitant extinction of taxa already living in the vents. A result of this model is that the taxa of the vent (and seep) fauna will be slightly older than those of shallow water, but from there to a relict fauna of Palaeozoic-Mesozoic origin, there is a long step.

A consequence of this view is that it is likely that some

of the palaeontologically "old" taxa with few and rare species in vents, like the grazing species of *Puncturella* may be the last surviving "dinosaurs" in the process of losing the competition with the presumed more efficient, and presumably more recently evolved gastropods (e.g., lepetodriloids), which combine grazing with filter-feeding or bacterial symbiosis. It seems unlikely that, confronted with an inflow of taxa with newly evolved functional specializations, the old and original immigrants should have resisted competition throughout 400 million years.

Acknowledgments. A.-M. Alayse, J.-M. Auzende, J. Bourgois, D. Desbruyères, J. Dubois, A. Fiala, J.-P. Foucher, F. Gaill, R. Hékinian, C. Mével, J.-C. Faugères, S. Lallemant, B. Mercier de Lépinay, F. Michaud, X. Le Pichon, D. Prieur, C. van Dover were leaders for the French expeditions, the material of which forms the backbone of this report. The MARVEL cruise, led by D. Desbruyères and A.-M. Alayse, was part of the European Commission MAST III programme AMORES (MAST3 CT 950040) and supported by IFREMER. We also want to thank M. Segonzac, P. Briand, and J. Galeron of IFREMER, who have tremendously facilitated our work in sending the material to us, well sorted and uniformly labeled.

Other material and information were contributed by: K. A. Campbell (now University of Auckland, New Zealand); R. S. Carney (investigations funded by National Underwater Research Program, University of North Carolina at Wilmington, and Minerals Management Service); C. L. Van Dover (Fairbanks); H. Sahling (Kiel); J. H. Slapcinsky & J. Voight (FMNH); V. Tunnicliffe (Victoria); and P. Tyler (Southampton).

C. Hammar worked in the photolab and assisted in preparing the plates; K. Rigneus helped with counting and sorting gastropods; and F. Pleijel helped with identification of symbiontic polychaetes (all at SMNH). Y. Kantor (Moscow) helped localizing Russian type material; J. Le Renard and P. Lozouet (MNHN) assisted with palaeontological information. We also thank O. Israelsson (SMNH) for sharing unpublished information on "archaeogastropod," especially neomphaline, anatomy. We thank P. Chevaldonné for permission to use Figure 1 of Desbruyères & Segonzac (1997).

J. McLean (LACM), M. Segonzac (IFREMER) and V. Tunnicliffe read and commented on the manuscript.

LITERATURE CITED

Aartsen, J. J. van, C. Bogi & F. Giusti. 1989. Remarks on genus *Benthonella* (Rissoidae) in Europe. La Conchiglia 246–249: 19–22.

Andrews, E. A. 1935. The egg capsules of certain Neritidae. Journal of Morphology 57:31–54.

ASHES Expedition. 1986. Pisces submersible exploration of a high-temperature vent field in the caldera of Axial Volcano, Juan de Fuca Ridge. EOS 67:1027.

Auzende, J.-M., M. Tanahashi, V. Bendel, K. Fujikura, P. Geistdoerfer, E. Gracia-Mont, M. Joshima, K. Kisimoto, K. Mitsuzawa, M. Murai, Y. Nojiri, H. Ondreas, C. Pratt & E. Ruellan. 1992. Résultats préliminaires des plongées du Shinkai 6500 sur la dorsale du Bassin Nord-Fidjien (SW Pacifique) - Programme STARMER. Compte-Rendus de l'Académie des Sciences de Paris, Sér. II, 314:491–498.

Bandel, K. 1982. Morphologie und Bildung der frühontogenetischen Gehäuse bei conchiferen Mollusken. Facies 7:1–198.

Beck, L. A. 1992a. *Symmetromphalus hageni,* a new neomphalid gastropod (Prosobranchia: Neomphalidae) from hydrothermal vents at the Manus Back Arc Basin (Bismarck Sea, Papua New Guinea). Annalen des Naturhistorisches Museums, Wien 93B:243–257.

Beck, L. A. 1992b. Two new neritacean limpets (Gastropoda: Prosobranchia: Neritacea: Phenacolepadidae) from active hydrothermal vents at Hydrothermal Field 1 "Wienerwald" in the Manus Back Arc Basin (Bismarck Sea, Papua New Guinea). Annalen des Naturhistorisches Museums, Wien 93B:259–275.

Beck, L. A. 1993. Morphological and anatomical studies on a new leptodrilacean limpet (Gastropoda, Prosobranchia) from hydrothermal vents at the Manus Back-Arc Basin (Bismarck Sea, Papua New Guinea). Annalen des Naturhistorisches Museums, Wien 94/5B:167–179.

Beck, L. A. 1996a. Morphology and anatomy of new species of neolepetopsid, acmaeid, fissurellid and pyropeltid limpets from Edison Seamount off Lihir Islands (West Pacific). Archiv für Molluskenkunde 125:87–103.

Beck, L. A. 1996b. Systematic position and relationship of *Phymorhynchus hyfifluxi* n. sp., a further new turrid gastropod species associated with hydrothermal vent sites in the North Fiji Basin. Archiv für Molluskenkunde 126:109–115.

Beck, L. In press. Limpets from Lau and N Fiji.

Bosch, D. T., S. P. Dance, R. Moolenbeek & P. G. Oliver. 1995. Seashells of Eastern Arabia. Motivate Publishing: Dubai. 296 pp.

Bouchet, P. & A. Waren. 1980. Revision of the North-East Atlantic bathyal and abyssal Turridae (Mollusca, Gastropoda). Journal of Molluscan Studies, Suppl. 8:1–119.

Bouchet, P. & A. Waren. 1986. Mollusca Gastropoda: taxonomical notes on tropical deep-water Buccinidae with descriptions of new taxa. Mémoires du Muséum d'Histoire Naturelle, Paris, Sér. A, Zool. 133:457–517.

Bouchet, P. & A. Waren. 1993. Revision of the northeast Atlantic bathyal and abyssal Mesogastropoda. Bollettino Malacologico, Suppl. 3:579–840.

Campbell, K. A. & D. J. Bottjer. 1993. Fossil cold seeps. National Geographic Magazine, Research and Exploration 9: 326–343.

Campbell, K. A. & D. J. Bottjer. 1995. Brachiopods and chemosymbiontic bivalves in Phanerozoic hydrothermal vent and cold seep environments. Geology 23:321–324.

Canadian American Seamount Expedition. 1985. Hydrothermal vents on an axis seamount of the Juan de Fuca Ridge. Nature 313:212–214.

Carney, R. S. 1994. Consideration of the oasis analogy for chemosynthetic communities at Gulf of Mexico hydrocarbon vents. Geo-Marine Letters 14:149–159.

Chevaldonne, P., A. Godfroy, P. Guezennec, F. Lesongeur, Y. Fouquet, G. Barbier & D. Desbruyeres. 1995. Preliminary description of the micro-scale ecology of a hydrothermal vent chimney at 9°50'N on the East Pacific Rise. InterRidge News 4(1):15–16.

Clarke, A. H. 1989. New mollusks from under-sea oil seep sites off Louisiana. Malacology Data Net 2:122–134.

Clench, W. J. & C. G. Aguayo. 1944. A new tropical *Buccinum* from Cuba. Revista de la Sociedad Malacologica Carlos de la Torre 2:67–68.

Colaco, A., D. Desbruyeres, T. Comtet & A.-M. Alayse. 1998. Ecology of the Menez Gwen hydrothermal vent field (Mid-Atlantic Ridge/Azores Triple Junction). Cahiers de Biologie Marine 39:237–240.

Cossmann, M. 1896. Essais de Paléoconchologie comparée. 2. Published by the author: Paris.

CRADDOCK, C., R. A. LUTZ & R. C. VRIJENHOEK. 1997. Patterns of dispersal and larval development of archaeogastropod limpets at hydrothermal vents in the eastern Pacific. Journal of Experimental Marine Biology and Ecology 210:37–51.

CROSSE, H. 1885. Bibliographie. Journal de Conchyliologie 33: 139–142.

DALL, W. H. 1896. Diagnoses of new species of mollusks from the west coast of America. Proceedings of the U.S. National Museum 18:7–20.

DALL, W. H. 1908a. Descriptions of new species of mollusks from the Pacific coast of the United States with notes on other mollusks from the same region. Proceedings of the U.S. National Museum 34:245–257.

DALL, W. H. 1908b. Report on the dredging operations off the west coast of Central America. . . . . The Mollusca and the Brachiopoda. Bulletin of the Museum of Comparative Zoology 43:205–487.

DALL, W. H. 1918a. Description of new species of shells chiefly from Magdalena Bay, Lower California. Proceedings of the Biological Society of Washington 31:5–8.

DALL, W. H. 1918b. Notes on the nomenclature of the mollusks of the family Turritidae. Proceedings of the U.S. National Museum 54:313–333.

DAUTZENBERG, P. & H. FISCHER. 1906. Mollusques provenants des dragages effectués à l'ouest de l'Afrique. Résultats des Campagnes Scientifiques. . . Albert 1er 32:1–125.

DELANEY, J. R., V. ROBIGOU, R. E. MCDUFF, & M. K. TIVEY. 1992. Geology of a vigorous hydrothermal system on the Endeavour Segment, Juan de Fuca Ridge. Journal of Geophysical Research 97 B13:19, 663–679, 682.

DELL, R. K. 1990. Antarctic Mollusca with special reference to the fauna of the Ross Sea. Bulletin of the Royal Society of New Zealand 27:1–311.

DENIS, F., D. JOLLIVET, & D. MORAGA. 1993. Genetic separation of two allopatric populations of hydrothermal snails *Alviniconcha* spp. (Gastropoda) from two south western Pacific Back-Arc basins. Biochemical Systematics and Ecology 21: 431–440.

DESBRUYERES, D. 1995. Biological studies at the ridge crest. InterRidge News 4(2):6–10.

DESBRUYERES, D. 1998. Temporal variations in the vent communities on the East Pacific Rise and Galapagos Spreading Centre: a review of present knowledge. Cahiers de Biologie Marine 39:241–244.

DESBRUYERES, D. & M. SEGONZAC (EDS). 1997. Handbook of Deep-Sea Hydrothermal Vent Fauna. Brest: IFREMER. 279 pp.

DESBRUYERES, D., A.-M. ALAYSE, E. ANTOINE, G. BARBIER, F. BARRIGA, M. BISCOITO, P. BRIAND, J.-P. BRULPORT, T. COMTET, L. CORNEC, P. CRASSOUS, P. DANDO, M.-C. FABRI, H. FELBECK, F. LALLIER, A. FIALA-MEDIONI, J. GONÇALVES, F. MENARD, J. KERDONCUFF, J. PATCHING, L. SALDANHA & P.-M. SARRADIN. 1994a. New information on the ecology of deep-sea vent communities in the Azores triple junction area: Preliminary results of the DIVA 2 cruise (May 31–July 4, 1994). InterRidge News 3(2):18–19.

DESBRUYERES, D., A.-M. ALAYSE-DANET & S. U. OHTA. 1994b. Deep-sea hydrothermal communities in south-western Pacific back-arc basins (the North Fiji and Lau basins): composition, microdistribution and food-web. Marine Geology 116:227–242.

DUCASSE, O., M. LABRACHERIE, A. MAGNE & A.-M. VERGNEAU-SAUBADE. 1973. Le gisement stampien de Bruges (Gironde). Bulletin de l'Institut Géologique du Bassin Aquitanien 14: 111–116.

ECKELBARGER, K. J. & C. M. YOUNG. 1997. Ultrastructure of the ovary and oogenesis in the methane-seep mollusc *Bathynerita naticoidea.* (Gastropoda: Neritidae) from the Louisiana slope. Invertebrate Biology 116(4):299–312.

EMBLEY, R. W., W. W. CHADWICH, I. R. JONASSON, D. A. BUTTERFIELD & E. T. BAKER. 1995. Initial results of the rapid response to the CoAxial 1993 event: relationships between hydrothermal and volcanic events. Geophysical Research Letters 22:143–146.

FISCHER, P. 1875. Sur l'anatomie des *Neritopsis.* Journal de Conchyliologie, 23:197–204.

FOUQUET, Y., J.-L. CHARLOU, I. COSTA, J.-P. DONVAL, J. RADFORD-KNOERY, H. PELLE, H. ONDREAS, N. LOURENÇO, M. SEGONZAC & M. K. TIVEY. 1994. A detailed study of the Lucky Strike hydrothermal site and discovery of a new hydrothermal site: Menez Gwen; Preliminary results of the DIVA 1 Cruise (5-29 May 1994). InterRidge News 3(2):14–17.

FRETTER, V. 1984. The functional anatomy of the neritacean limpet *Phenacolepas omanensis* Biggs and some comparison with *Septaria.* Journal of Molluscan Studies 50:8–18.

FRETTER, V. 1988. New archaeogastropod limpets from hydrothermal vents; superfamily Lepetodrilacea. II. Anatomy. Philosophical Transactions of the Royal Society of London B318:33–82.

FRETTER, V. 1990. The anatomy of some new archaeogastropod limpets (Order Patellogastropoda, Suborder Lepetopsina) from hydrothermal vents. Journal of Zoology, London 222: 529–555.

FUJIOKA, K. & R. P. VON HERZEN. 1994. Shinkai-Yokosuka MODE '94 Leg 2 cruise summary: Studies of an active hydrythermal mound at the TAG area on the Mid-Atlantic Ridge. InterRidge News 3(2):21–22.

FUSTEC, A., D. DESBRUYERES & K. JUNIPER. 1987. Deep-sea hydrothermal vent communities at 13°N on the East Pacific Rise: microdistribution and temporal variations. Biological Oceanography 4:121–164.

GALKIN, S. V. 1990. Hydrothermal fauna of the Mid-Atlantic Ridge. Oceanology 30:624–627.

GALKIN, S. V. 1993. The benthic fauna of hydrothermal vents in the Manus Basin. Oceanology 32:768–784.

GEBRUK, A. V., L. I. MOSKALEV, P. CHEVALDONNE, M. SUDAROKOV & E. S. CHERNYAEV. 1997. Hydrothermal vent fauna of the Logatchev area (14°45'N): preliminary results from the first Mir and Nautile dives in 1995. InterRidge News 6(2):10–14.

GEISTDOERFER, P., J. M. AUZENDE, R. BATIZA, D. BIDEAU, M.-H. CORMIER, Y. FOUQUET, Y. LAGABRIELLE, J. SINTON & P. SPADEA. 1994. Hydrothermalisme et communautés animales associées sur la dorsale du Pacifique oriental entre 17°S et 19°S (Campagne Naudur, décembre 1993). Compte Rendus de l'Académie des Sciences de Paris, Sér. II, 320:47–54.

GOEDERT, J. L. & S. R. BENHAM. 1999. A new species of *Depressigyra*? (Gastropoda: Peltospiridae) from cold-seep carbonates in Eocene and Oligocene rocks of western Washington. The Veliger 42:112–116.

GOEDERT, J. L. & K. L. KALER. 1996. A new species of *Abyssochrysos* (Gastropoda: Loxonematoidea) from a Middle Eocene cold-seep carbonate in the Humptulips Formation, Western Washington. The Veliger 39:65–70.

GOEDERT, J. L. & R. L. SQUIRES. 1990. Eocene deep-sea communities in localized limestones formed by subduction-re-

lated methane seeps, Southwestern Washington. Geology 18: 1182–1185.

GOLIKOV, A. N. 1980. Fauna of the USSR, Mollusca 5: 2, Mollusca, Buccininae, of the World Oceans. Nauka. 465 pp.

GRASSLE, J. F. 1986a. Animals at Mid-Atlantic Ridge hydrothermal vents. EOS 67:1022.

GRASSLE, J. F. 1986b. The ecology of deep-sea hydrothermal vent communities. Advances in Marine Biology 23:301–362.

GRASSLE, J. F. 1989. Species diversity in deep-sea communities. Trends in Ecology and Evolution 4:12–15.

GRÜNDEL, J. 1980. Bemerkungen zur Überfamilie Cerithiopsacea H. & A. Adams, 1854 (Gastropoda) sowie zur Fassung einiger ihrer Gattungen. Zoologische Anzeiger 204:209–264.

GUINOT, D. & M. SEGONZAC. 1997. Description d'un crabe hydrothermal nouveau du genre *Bythograea* (Crustacea, Decapoda, Brachyura) et remarques sur les Bythograeidae de la dorsale du Pacifique oriental. Zoosystema 19:117–145.

GUSTAFSON, R. G., D. T. J. LITTLEWOOD & R. A. LUTZ. 1991. Gastropod egg capsules and their contents from deep-sea hydrothermal vent environments. Biological Bulletin 180: 34–55.

GUSTAFSON, R. G. & R. A. LUTZ. 1994. Molluscan life history traits and deep-sea hydrothermal vents and cold methane/sulphide seeps. Pp. 76–97 in C. M. Young, & K. J. Eckelbarger (eds), Reproduction, Larval Biology, and Recruitment of the Deep-Sea Benthos. Columbia University Press: New York.

HARASEWYCH, M. G. 1990. Studies on bathyal and abyssal Buccinidae (Gastropoda: Neogastropoda). I. *Metula fusiformis* Clench & Aguayo, 1941. The Nautilus 104:120–129.

HASEGAWA, K. 1997. Sunken-wood associated gastropods collected from Suruga Bay, Pacific side of the Central Honshu, Japan, with descriptions of 12 new species. National Science Museum Monographs Tokyo 12:59–123.

HASEGAWA, K., K. FUJIKURA & T. OKUTANI. 1997. Gastropod fauna associated with hydrothermal vents in the Mariana Back-Arc Basin: summary of the results of 1996 "Shinkai 6500" dives. JAMSTEC Journal of Deep Sea Research 13:69–83.

HASHIMOTO, J., S. OHTA, T. TANAKA, H. HOTTA, S. MUTSUZAWA & H. SAKAI. 1989. Deep-sea communities dominated by the giant clam, *Calyptogena soyoae,* along the slope foot of Hatsushima Island, Sagami Bay, Central Japan. Paleogeography, Paleoclimatology, Paleobiology 71:179–192.

HASHIMOTO, J., OHTA, S. FUJIKURA, K. & T. MIURA. 1995. Microdistribution pattern and biogeography of the hydrothermal vent communities of the Minami-Ensei Knoll in the Mid-Okinawa Trough, Western Pacific. Deep-Sea Research I 42:577–598.

HASHIMOTO, J., S. OHTA, A. FIALA-MEDIONI, J.-M. AUZENDE, S. KOJIMA, M. SEGONZAC, Y. FUJIWARA, J. C. HUNT, K. GENA, T. MIURA, T. KIKUCHI, T. YAMAGUCHI, T. TODA, H. CHIBA, S. TSUCHIDA, J. ISHIBASHI, K. HENRY, M. ZBINDEN, A. PRUSKI, A. INOUE, H. KOBAYASHI, J.-L. BIRRIEN, J. NAKA, T. YAMANAKA, C. LAPORTE, K. NISHIMURA, C. YEATS, S. MALAGUN, P. KIA, M. OYAIZU & T. KATAYAMA, 1999. Hydrothermal vent communities in the Manus Basin, Papua New Guinea: Results of the BIOACCESS cruises '96 and '98. InterRidge News 8(2):12–18.

HASZPRUNAR, G. 1988. On the origin and evolution of major gastropod groups, with special reference to the Streptoneura. Journal of Molluscan Studies 54:367–441.

HASZPRUNAR, G. 1989a. The anatomy of *Melanodrymia aurantiaca* Hickman, a coiled archaeogastropod from the East Pacific hydrothermal vents. Acta Zoologica 70:175–186.

HASZPRUNAR, G. 1989b. New slit-limpets (Scissurellacea and Fissurellacea) from hydrothermal vents. Part II. Anatomy and relationships. Contributions in Science, Los Angeles County Museum of Natural History 408:1–17.

HERZIG, P., M. HANNINGTON, B. MCINNES, P. STOFFERS, H. VILLINGER, R. SEIFERT, R. BINNS & T. LIEBE. 1994. Submarine volcanism and hydrothermal venting studied in Papua New Guinea. EOS 75:513–516.

HERZIG, P., E. SUESS & P. LINKE. 1997. RV Sonne, Cruise Report SO109. Geomar Report, Kiel 50:1–250.

HESSLER, R. R. 1985. Spatial and temporal variation of giant clams, tube worms and mussels at deep sea hydrothermal vents. Bulletin of the Biological Society of Washington 6: 411–428.

HESSLER, R. R. & V. A. KAHARL. 1995. The deep-sea hydrothermal vent community: An overview. Geophysical Monographs 91:72–84.

HESSLER, R. R. & P. F. LONSDALE. 1991a. Biogeography of Mariana Trough hydrothermal vent communities. Deep-Sea Research 38:185–199.

HESSLER, R. R. & P. F. LONSDALE. 1991b. The biogeography of the Mariana Trough hydrothermal vents. Pp. 165–182 in J. Mauchling & T. Nemoto (eds), Marine Biology, Its Accomplishment and Future Prospect. Hokusen-cha.

HESSLER, R. R. & W. M. SMITHEY. 1983. The distribution and structure of megafauna at the Galapagos Rift hydrothermal vents. Pp. 735–770 in P. A. Rona, K. Boström, L. Laubier & K. L. Smith (eds), Hydrothermal Processes at Sea-Floor Spreading Centres. NATO Conference Series 4(12).

HICKMAN, C. S. 1984. A new archaeogastropod (Rhipidoglossa, Trochacea) from hydrothermal vents on the East Pacific Rise. Zoologica Scripta 13:19–25.

HICKMAN, C. S. & J. H. MCLEAN. 1990. Systematic revision and suprageneric classification of trochacean gastropods. Science Series, Natural History Museum of Los Angeles County 35: 1–169.

HUMPHRIS, S. E., P. M. HERZIG & J. MILLER. 1995. TAG hydrothermal field. JOIDES 21:8–15.

ISRAELSSON, O. 1998. The anatomy of *Pachydermia laevis* (Archaeogastropoda: "Peltospiridae"). Journal of Molluscan Studies 64:93–109.

ISRAELSSON, O. In press. Anatomy and phylogeny of *Cyathermia naticoides* ("Archaeogastropoda", Neomphalina). Journal of Molluscan Studies.

JEFFREYS, J. G. 1883. On the Mollusca procured during the Lightning and Porcupine expeditions. VI. Proceedings of the Zoological Society of London (1883):88–115.

JOHNSON, H. P. 1993. Processes associated with ocean crustal formation: the Juan de Fuca Ridge. Geophysical Research Letters 20:1847–50.

JOLLIVET, D. 1993. Distribution et évolution de la faune associée aux sources hydrothermales profondes à 13°N sur la dorsale du Pacifique oriental: le cas particulier des polychètes Alvinellidae. Thesis, Université de Bretagne Occidentale, Brest. 353 pp.

JOLLIVET, D., J. HASHIMOTO, J.-M. AUZENDE, E. HONZA, E. RUELLAN, S. PUTT, Y. IWABUCHI, P. JARVIS, M. JOSHIMA, T. KAWAI, T. KAWAMOTO, K. KIOIMOTO, Y. LAFOY, T. MATSUMOTO, K. MITSUZAWA, T. NACANUMA, J. NAKA, K. OTSUKA, A. OTSUKI, B. RAO, M. TANAHASHI, T. TANAKA, J. S. TEMAKON, T. URABE, T. VEIVAU & T. YOKOKURA. 1989. Premières observations de communautés animales associées à l'hydrothermalisme arrière-arc du bassin nord-Fidjien.

Compte Rendus de l'Académie des Sciences de Paris, sér. III 309:301–308.

JOLLIVET, D., J. C. FAUGERES, R. GRIBOULARD, D. DESBRUYERES & G. BLANC. 1990. Composition and spatial organization of a cold seep community on the South Barbados accretionary prism: tectonic, geochemical and sedimentary context. Progress in Oceanography 24:25–45.

JUNIPER, K., C. FISHER & J. DELANEY. 1996. Report on ROPOS operations on the R/V Thomas G. Thompson Cruise: 12–27 August 1996. InterRidge News 5(2):25–26.

KASE, T. & I. HAYAMI. 1992. Unique submarine cave mollusc fauna: composition, origin and adaptation. Journal of Molluscan Studies 58:446–449.

KOBELT, W. 1905. Iconographie der schalentragenden europäischen Meeresconchylien. Vol. 3. Kreidel: Wiesbaden. 406 pp.

KOJIMA, S. & S. OHTA. 1997. Bathymetrical distribution of the species of the genus *Calyptogena* in the Nankai Trough, Japan. Venus 56:293–297.

KRAL, J. 1995. Marine ecosystems based on chemoautotrophic and methylotrophic bacteria as possible refuge for living fossils. GeoLines (Praha) 3:21–26.

KUZNETSOV, A. P., V. V. MASLENNIKOV & V. V. ZAYKOV. 1993. Near-hydrothermal fauna of the silurian Palaeozoic in the South Urals. Izvestija RAN, ser. Biol. 4:20–32.

LALLEMANT, S. E., G. GLAÇON, A. LAURIAT-RAGE, A. FIALA-MEDIONI, J.-P. CADET, C. BECK, M. SIBUET, J. T. IIYAMA, H. SAKAI & A. TAIRA. 1992. Seafloor manifestations of fluid seepage at the top of a 2000-meter-deep ridge in the eastern Nankai accretionary wedge.: long-lived venting and tectonic implications. Earth and Planetary Science Letters 109:333–346.

LE PICHON, X., J.-P. FOUCHER, J. BOULEGUE, P. HENRY, S. LALLEMANT, M. BENEDETTI, F. AVEDIK & A. MARIOTTI. 1990. Mud volcano field seawards of the Barbados accretionary complex: a submersible survey. Journal of Geophysical Research 95(B6):8931–8943.

LEWIS, K. B. & B. A. MARSHALL. 1996. Seep faunas and other indicators of methane-rich dewatering on New Zealand convergent margins. New Zealand Journal of Geology and Geophysics 39:181–200.

LINNAEUS, C. 1758. Systema Naturae, ed. 10. Holmiae. 824 pp.

LITTLE, C. T. S., R. J. HERRINGTON, V. V. MASLENNIKOV, N. J. MORRIS & V. V. ZAYKOV. 1997. Silurian hydrothermal-vent community from the southern Urals, Russia. Nature 385: 146–148.

LITTLE, C. T. S., R. J. HERRINGTON, V. V. MASLENNIKOV & V. V. ZAYKOV. 1998. The fossil record of hydrothermal vent communities. Pp. 259–270 in R. A. Mills & K. Harrison (eds), Modern Ocean Floor Processes and the Geological Record. Geological Society, London, Special Publications 148.

LITTLE, C. T. S., R. J. HERRINGTON, R. M. HAYMON & T. DANIELAN. 1999a. Early Jurassic hydrothermal vent community from the Franciscan Complex, San Rafael Mountains, California. Geology 27:167–170.

LITTLE, C. T. S., J. R. CANN, R. J. HERRINGTON & M. MORISSEAU. 1999b. Late Cretaceous hydrothermal vent communities from the Troodos ophiolite, Cyprus. Geology 27:1027–1030.

LOZOUET, P. 1997. Le domaine atlantique européen au Cénozoïque moyen: diversité et évolution des gastéropodes. Thesis, Paris. 309+52 pp.

LUS, V. J. 1971. A new genus and species of gastropod molluscs (family Buccinidae) from the ultra-abyssal of Kurile-Kamchatka Trench. Trudy Instituta Okeanologia P. P. Shirshov 92:61–72. [in Russian]

LUS, V. J. 1981. New species of *Tacita* (Prosobranchia Buccinidae) with wide distribution in the north-western part of the Pacific Ocean. Trudy Instituta Okeanologia P. P. Shirshov 115:140–154. [in Russian]

LUS, V. J. 1989. The most deep-water gastropod mollusks among Buccinacea (Neogastropoda: Buccinacea s.l.). Trudy Instituta Okeanologia P. P. Shirshov 123:151–164. [in Russian]

LUTZ, R., R. VRIJENHOEK, G. LEVAI, T. SHANK, E. SUESS, P. LINKE, G. BOHRMANN, H. SAHLING, N. V. MIRBACH, J. GREINERT, D. ORANGE, N. MAHER & C. MOYER. 1996. Biological communities and geological features associated with methane/sulphide seepage at 4960 m in the Aleutian Subduction Zone: a video presentation. EOS, Suppl. 77:F405.

MACEY, D. J., L. R. BROOKER, J. WEBB & T. G. STPIERRE. 1997. Structural organisation of the radular teeth of the chiton *Plaxiphora albida.* Acta Zoologica 77:287–294.

MARSHALL, B. A. 1988. Skeneidae, Vitrinellidae, and Orbitestellidae (Mollusca: Gastropoda) associated with biogenic substrata from bathyal depths off New Zealand and New South Wales. Journal of Natural History 22:949–1004.

MARSHALL, B. A. 1991. Mollusca Gastropoda: Seguenziidae from New Caledonia and the Loyalty Islands. Mémoires du Muséum national d'Histoire naturelle, Paris A150:41–109.

MARSHALL, B. A. 1995. Calliostomatidae (Gastropoda: Trochoidea) from New Caledonia, the Loyalty Islands, and the northern Lord Howe Rise. Mémoires du Muséum national d'Histoire naturelle, Paris 167:381–458.

MCARTHUR, A. G. 1996. Molecular investigation of the evolutionary origins of hydrothermal vent gastropods. Thesis, University of Victoria, Canada.

MCARTHUR, A. G. 1999. Partial 28S rDNA sequences and the antiquity of hydrothermal vent endemic gastropods. Molecular Phylogenetics and Evolution. 13:255–274.

MCARTHUR, A. G. & V. TUNNICLIFFE. 1998. Relics and antiquity revisited in the modern vent fauna. Pp. 271–291 in R. A. Mills & K. Harrison (eds), Modern Ocean Floor Processes and the Geological record. Geological Society, London, Special Publications 148.

MCINNES, B. (1998, May). Submarine volcanoes. Available via *http://www.syd.dem.csiro.au/research/hydrothermal/brent/Edison_volcano.htm l.*

MCLEAN, J. H. 1981. The Galapagos Rift limpet *Neomphalus:* relevance to understanding the evolution of a major Paleozoic-Mesozoic radiation. Malacologia 21:291–336.

MCLEAN, J. H. 1988. New archaeogastropod limpets from hydrothermal vents: Superfamily Lepetodrilacea. I. Systematic descriptions. Philosophical Transactions of the Royal Society of London B319:1–32.

MCLEAN, J. H. 1989a. New slit limpets (Scissurellacea and Fissurellacea) from hydrothermal vents. Part 1. Systematic descriptions and comparisons based on shell and radular characters. Contributions in Science, Los Angeles County Museum of Natural History 407:1–29.

MCLEAN, J. H. 1989b. New archaeogastropod limpets from hydrothermal vents: new family Peltospiridae, new superfamily Peltospiracea. Zoologica Scripta 18:49–66.

MCLEAN, J. H. 1990a. Neolepetopsidae, a new docoglossate limpet family from hydrothermal vents and its relevance to patellogastropod evolution. Journal of Zoology, London 222: 485–528.

MCLEAN, J. H. 1990b. A new genus and species of neomphalid limpet from the Mariana vents with a review of current un-

derstanding of the relationships among Neomphalacea and Peltospiracea. The Nautilus 104:77–86.

McLEAN, J. H. 1992a. A new species of *Pseudorimula* (Fissurellacea: Clypeosectidae) from hydrothermal vents of the Mid-Atlantic Ridge. The Nautilus 106:115–118.

McLEAN, J. H. 1992b. Cocculiniform limpets (Cocculinidae and Pyropeltidae) living on whale bone in the deep-sea off California. Journal of Molluscan Studies 58:401–414.

McLEAN, J. H. 1993. New species and records of *Lepetodrilus* (Vetigastropoda: Lepetodrilidae) from hydrothermal vents. The Veliger 36:27–35.

McLEAN, J. H. & G. HASZPRUNAR. 1987. Pyropeltidae, a new family of cocculiniform limpets from hydrothermal vents. The Veliger 30:196–205.

McLEAN, J. H. & J. F. QUINN. 1987. *Cataegis,* a new genus of three new species from the continental slope (Trochidae: Cataeginae new subfamily). The Nautilus 101:111–116.

MEVEL, C., J.-M. AUZENDE, M. CANNAT, J.-P. DONVAL, J. DUBOIS, Y. FOUQUET, P. GENTE, D. GRIMAUD, J. A. KARSON, M. SEGONZAC & M. STIEVENARD. 1989. La ride du Snake Pit (dorsale médio-Atlantique, 23°22′N): résultats préliminaires de la campagne HYDROSNAKE. Compte Rendus de l'Académie des Sciences de Paris, sér. 2, 308:545–552.

MÖLLER CHRISTENSEN, A. 1981. *Fecampia abyssicola* n.sp. (Turbellaria, Rhabdocoela) and five cocoon types of undescribed species of Fecampidae from the deep sea. Galathea Report 15:69–77.

MONTEROSATO, T. A. DI 1884. Nomenclatura generica e specifica di alcune conchiglie Mediterranee. Virzi: Palermo. 152 pp.

MONTFORT, D. DE 1810. Conchyliologie Systématique. Schoell: Paris. 676 pp.

MOORE, R. C. (ED.) 1960. Treatise on Invertebrate Paleontology, Part I, Mollusca 1. University of Kansas Press. 351 pp.

MORONI, M. A. 1966. Malacofauna dei "calcare a Lucine" di S. Sofia - Forli. Paleontographica Italica 60:69–87.

MULLINEAUX, L. S., S. L. KIM, A. POOLEY & R. A. LUTZ. 1996. Identification of archaeogastropod larvae from a hydrothermal vent community. Marine Biology 124:551–560.

MURTON, B. J., C. VAN DOVER & E. SOUTHWARD. 1995. Geological setting and ecology of the Broken Spur hydrothermal vent field 29°10′N on the Mid-Atlantic Ridge. Pp. 32–41 in L. M. Parson, C. L. Walker & C. R. Dixon (eds), Hydrothermal Vents and Processes. Geological Society of London, Special Publication 87.

NAGANUMA, T., H. WADA & K. FUJIOKA. 1996. Biological community and fatty acids associated with the deep-sea whale skeleton at the Torishima Seamount. Journal of Oceanography 52:1–15.

NAGANUMA, T., C. J. MEISEL, H. WADA, Y. KATO, A. TAKEUCHI, K. FUJIKURA, J. NAKA & K. FUJIOKA. 1999. Seafloor fissures, biological communities and sediment fatty acids of the northern Okushiri Ridge, Japan Sea: implications for possible methane seepage. The Island Arc 8:232–244.

NEVILL, G. 1885. Hand List of the Mollusca in the Indian Museum, Calcutta. Part II. Government Printer: Calcutta.

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 19:153–167.

NEWMAN, W. A. 1985. The abyssal hydrothermal vent fauna: a glimpse of antiquity? Bulletin of the Biological Society of Washington 6:231–242.

OKUTANI, T. 1990. Two new species of *Provanna* (Gastropoda: Cerithiacea) from "Snail Pit" in the hydrothermal vent site at the Mariana Back-Arc Basin. Venus 49:19–24.

OKUTANI, T. & K. FUJIKURA. 1992. A new turrid gastropod associated with metachromatic seabed near the *Calyptogena*-community in Sagami Bay. Venus 51:1–7.

OKUTANI, T. & S. OHTA. 1993. New buccinid and turrid gastropods from North Fiji and Lau basins. Venus 52:217–221.

OKUTANI, T., H. SAITO & J. HASHIMOTO. 1989. A new neritacean limpet from a hydrothermal vent site, near Ogasawara Islands, Japan. Venus 48:223–230.

OKUTANI, T., E. TSUCHIDA & K. FUJIKURA. 1992. Five bathyal gastropods living within or near the *Calyptogena*-community of the Hatsuchima Islet, Sagami Bay. Venus 51:137–148.

OKUTANI, T., K. FUJIKURA & T. SASAKI. 1993. New taxa and new distribution records of deep-sea gastropods collected from or near chemosynthetic communities in the Japanese waters. Bulletin of the National Science Museum, Tokyo, ser. A 19(4):123–143.

OLSSON, A. A. 1971 [March]. Mollusks from the Gulf of Panama, collected by R/V John Elliott Pillsbury, 1967. Bulletin of Marine Science 21:35–92.

OLU, K., A. DUPERRET, M. SIBUET, J.-P. FOUCHER & A. FIALA-MEDIONI. 1996a. Structure and distribution of cold-seep communities along the Peruvian active margin: relationship to geological and fluid patterns. Marine Ecology Progress Series 132:109–125.

OLU, K., M. SIBUET, F. HARMEGNIES, J.-P. FOUCHER & A. FIALA-MEDIONI. 1996b. Spatial distribution of diverse cold seep communities living on various diapiric structures of the southern Barbados prism. Progress in Oceanography 38: 347–376.

OLU, K., S. LANCE, M. SIBUET, P. HENRY, A. FIALA-MEDIONI & A. DINET. 1997. Cold seep communities as indicators of fluid expulsion patterns through mud volcanoes seaward of the Barbados accretionary prism. Deep-Sea Research I 44:811–841.

ORANGE, D. L., N. MAHER, G. BOHRMANN, E. SUESS, P. LINKE, H. SAHLING, N. V. MIRBACH, A. DAEHLMANN, J. GREINERT, R. LUTZ, G. LEVAI & C. MOYER. 1996. Fluid seepage at the toe of the Aleutian accretionary complex—Observations from the longest and deepest ROPOS dive yet. EOS, Suppl. 77:F323.

PONDER, W. F. 1990. The anatomy and relationships of the Orbitestellidae (Gastropoda: Heterobranchia). Journal of Molluscan Studies 56:515–532.

PONDER, W. F. 1991. Marine valvatoidean gastropods - implications for early heterobranch phylogeny. Journal of Molluscan Studies 57:21–32.

PONDER, W. F. 1994. The anatomy and relationships of three species of vitrinelliform gastropods (Caenogastropoda: Rissooidea) from Hong Kong. The malacofauna of Hong Kong and southern China 3:243–281.

PONDER, W. F. & D. R. LINDBERG. 1997. Towards a phylogeny of gastropod molluscs: an analysis using morphological characters. Zoological Journal of the Linnean Society 119: 83–265.

POPPE, G. T. & Y. GOTO. 1992. Volutes. L'Informatore Piceno: Ancona. 348 pp.

POWELL, A. W. B. 1951. Antarctic and Subantarctic Mollusca: Pelecypoda and Gastropoda. Discovery Reports 26:47–196.

RISBEC, J. 1935. Biologie et ponte de mollusques gastéropodes néo-calédoniens. Bulletin de la Société Zoologique de France 60:387–416.

RISSO, A. 1826. Histoire naturelle des principales productions de l'Europe méridionale et particulièrement de Nice et des Alpes Maritimes. Vol. 4. Paris.

RONA, P. A. 1986. Black smokers on the Atlantic Sea-floor. Deep-Sea Newsletter 12:10–11.

ROSENBERG, G. 1998. Reproducibility of results in phylogenetic analysis of mollusks: a reanalysis of the Taylor, Kantor, and Sysoev (1993) data set for conoidean gastropods. American Malacological Bulletin 14:219–228.

SAHLING, H. 1997. Untersuchungen an cold seep assoziierten Organismen im NE-Pazifik. Diplomarbeit der Christian Albrechts Universität. vii + 89 pp.

SALDANHA, L., M. BISCOITO & D. DESBRUYERES. 1996. The Azorean deep-sea hydrothermal ecosystem: Its recent discovery. Pp. 383–388 in F. Uiblein, J. Ott & M. Stachowitsch (eds), Deep-Sea and Extreme Shallow-Water Habitats: Affinities and Adaptations. Biosystematics and Ecology Series 11.

SEGONZAC, M. 1992. Les peuplements associés à l'hydrothermalisme océanique du Snake Pit (dorsale médio-atlantique; 23°N, 3480 m): composition et microdistribution de la mégafaune. Compte Rendus de l'Académie des Sciences de Paris, sér. III 314:593–600.

SEGUENZA, G. 1876. Studii stratigrafici sulla formazione pliocenica dell'Italia meridionale. Bollettino del Reale Comitato Geologico d'Italia 7:7–15.

SQUIRES, R. L. 1995. First fossil species of the chemosynthetic-community gastropod *Provanna:* Localized cold-seep limestones in Upper Eocene and Oligocene rocks, Washington. The Veliger 38:30–36.

SQUIRES, R. L. & J. L. GOEDERT. 1991. New Late Eocene mollusks from localized limestone deposits formed by subduction-related methane seeps, southwestern Washington. Journal of Paleontology 65:412–416.

SQUIRES, R. L. & J. L. GOEDERT. 1996. A new species of *Thalassonerita*? (Gastropoda: Neritidae?) from a middle Eocene cold-seep carbonate in the Humptulips Formation, western Washington. The Veliger 39:270–272.

STAROBOGATOV, YA. I. & L. I. MOSKALEV. 1987. Systematics of the Monoplacophora. Vsesojuznoe soveshchanie po izucheniju molljuskov, 8 [8th Meeting on the investigation of Molluscs, Leningrad]: 7–11. [in Russian]

STRAUCH, F. 1972. Phylogenese, Adaptation und Migration einiger nordischer Molluskengenera (*Neptunea, Panomya, Cyrtodaria* und *Mya*). Abhandlungen der Senckenbergischen naturforschende Gesellschaft 531:1–211.

SUESS, E. 1994. FS Sonne, Fahrtbericht SO-97, KODIAK Vent. GEOMAR Report, Kiel 29:1–220.

SUESS, E. & G. BOHRMANN. 1997. RV Sonne, Cruise Report SO110. GEOMAR Report, Kiel 59; 1–181.

SUESS, E., B. CARSON, S. D. RITGER, J. C. MOORE, M. L. JONES, L. D. KULM & G. R. COCHRANE. 1985. Biological communities at vent sites along the subduction zone off Oregon. Bulletin of the Biological Society of Washington 6:475–484.

SUESS, E., G. BOHRMANN, P. LINKE, R. W. COLLIER & M. TORRES. 1996. Gas hydrates and fluid venting from the Cascadia accretionary margin. EOS, Suppl. 77:F321.

SYKES, E. R. 1925. On the Mollusca procured during the "Porcupine" Expeditions, 1869–70. Supplemental notes, part V. Proceedings of the Malacological Society of London 16: 181–193.

SYSOEV, A. V. 1997. New deep-water turrid gastropods (Conoidea) from eastern Indonesia. Mémoires du Muséum national d'Histoire naturelle 172:325–355.

SYSOEV, A. V. & Y. I. KANTOR. 1995. Two new species of *Phymorhynchus* (Gastropoda, Conoidea, Conidae) from the hydrothermal vents. Ruthenica 5:17–26.

TAVIANI, M. 1994. The "Calcari a *Lucina*" macrofauna reconsidered: deep-sea faunal oases from Miocene-age cold vents in the Romagna Apennine, Italy. Geo-Marine Letters 14: 185–191.

TAYLOR, J. D., Y. I. KANTOR & A. V. SYSOEV. 1993. Foregut anatomy, feeding mechanisms, relationships and classification of the Conoidea (= Toxoglossa) (Gastropoda). Bulletin of the Natural History Museum, London, Zoology 59:125–170.

THIELE, J. 1929. Handbuch der systematischen Weichtierkunde. 1. G. Fischer: Jena.

TRACEY, S., J. A. TODD & D. H. ERWIN. 1993. Mollusca: Gastropoda. Pp. 131–167 in M. J. Benton (ed.), The Fossil Record 2. Chapman & Hall: London.

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 des österreischischen geologischen Gesellschaft 82:183–210.

TUNNICLIFFE, V. 1988. Biogeography and evolution of hydrothermal vent fauna in the eastern Pacific Ocean. Proceedings of the Royal Society of London, Ser. B, 233:347–366.

TUNNICLIFFE, V. 1991. The biology of hydrothermal vents: ecology and evolution. Oceanography and Marine Biology, Annual Review 29:319–407.

TUNNICLIFFE, V. 1994. What to do with the slimy stuff? InterRidge News 3(1):12.

TUNNICLIFFE, V. & A. R. FONTAINE. 1987. Faunal composition and organic surface encrustations at hydrothermal vents on the southern Juan de Fuca Ridge. Journal of Geophysical Research 92:11303–11314.

TUNNICLIFFE, V. & C. M. R. FOWLER. 1996. Influence of sea-floor spreading on the global vent fauna. Nature 379:531–533.

TUNNICLIFFE, V., K. S. JUNIPER & M. E. DE BURGH. 1985. The hydrothermal vent community on Axial Seamount, Juan de Fuca Ridge. Bulletin of the Biological Society of Washington 6:453–464.

TUNNICLIFFE, V., M. BOTROS, M. E. DE BURGH, A. DINET, H. P. JOHNSON, S. K. JUNIPER & R. M. MCDUFF. 1986. Hydrothermal vents of Explorer Ridge, northeast Pacific. Deep-Sea Research 33:401–412.

TUNNICLIFFE, V., C. M. R. FOWLER & A. G. MCARTHUR. 1996. Plate tectonic history and hot vent biogeography. Pp. 225–238 in C. J. MacLeod (ed.), Tectonic, Magmatic, Hydrothermal and Biological Segmentation of Mid-Oceanic Ridges. Geological Society, Special Publication 118.

TUNNICLIFFE, V., A. G. MCARTHUR & D. MCHUGH. 1998. A biogeographical perspective of the deep-sea hydrothermal vent fauna. Advances in Marine Biology 34:353–442.

TURNER, R. D., R. A. LUTZ & D. JABLONSKI. 1985. Modes of molluscan larval development at deep-sea hydrothermal vents. Bulletin of the Biological Society of Washington 6: 167–184.

VALDES, Á. & P. BOUCHET. 1998. Naked in toxic fluids: a nudibranch mollusc from hydrothermal vents. Deep-Sea Research II 45:319–327.

VAN DOVER, C. L. 1995. Ecology of Mid-Atlantic Ridge hydrothermal vents. Pp. 257–294 in L. M. Parson, C. L. Walker & C. R. Dixon (eds), Hydrothermal Vents and Processes. Geological Society of London, Special Publication 87.

VAN DOVER, C. L., D. DESBRUYERES, M. SEGONZAC, T. COMTET, L. SALDANHA, A. FIALA-MEDIONI & C. LANGMUIR, C. 1996.

Biology of the Lucky Strike hydrothermal vent field. Deep-Sea Research 43:1509–1529.

VAN DOVER, C. L., J. TRASK & J. SCHURMEIER. 1997. Biological diversity at hydrothermal vents. Preliminary results form the LUSTRE (LUcky STRike Exploration) '96 Cruise. InterRidge News 6(1):9–12.

VERRILL, A. E. 1884. Second catalogue of Mollusca, recently added to the fauna of the New England coast and the adjacent parts of the Atlantic, consisting mostly of deep-sea species, with notes on others previously recorded. Transactions of the Connecticut Academy of Arts and Science 6:139–294.

WAREN, A. 1991. New and little known molluscs from Iceland and Scandinavia. Sarsia 76:53–124.

WAREN, A. 1996. New and little known mollusca from Iceland and Scandinavia. Part 2. Sarsia 81:197–245.

WAREN, A. In press. Phylogeny of the hydrothermal vent lepetodriloids and "slit-limpets" (Archaeogastropoda): macroevolution in progress. Zoologica Scripta.

WAREN, A. & P. BOUCHET. 1986. Four new species of *Provanna* Dall (Prosobranchia, Cerithiacea?) from East Pacific hydrothermal sites. Zoologica Scripta 15:157–164.

WAREN, A. & P. BOUCHET. 1989. New gastropods from East Pacific hydrothermal vents. Zoologica Scripta 18:67–102.

WAREN, A. & P. BOUCHET. 1993. New records, species, genera and a new family of gastropods from hydrothermal vents and hydrocarbon seeps. Zoologica Scripta 22:1–90.

WAREN, A. & S. GOFAS. 1997. A new species of Monoplacophora, redescription of the genera *Veleropilina* and *Rokopella,* and new information on three species of the class. Zoologica Scripta 25:215–232.

WAREN, A. & W. F. PONDER. 1991. New species, anatomy, and systematic position of the hydrothermal vent and hydrocarbon seep gastropod family Provannidae fam. n. (Caenogastropoda). Zoologica Scripta 20:27–56.

WAREN, A., F. CARROZZA & R. ROCCHINI. 1990. *Elachisina versiliensis,* a new Mediterranean species of the family Elachisinidae (Prosobranchia, Truncatelloidea). Bollettino Malacologico 25:335–339.

WAREN, A. & S. GOFAS & C. SCHANDER. 1993. Systematic position of three European heterobranch gastropods. The Veliger 36:1–15.

WENZ, W. 1938–44. Gastropoda. Teil 1. In Schindewolf (ed.), Handbuch der Paläozoologie, Band 6. 1639 pp.

ZANDE, J. M. 1994. Feeding and life history of the gastropod *Bathynerita naticoidea* from Gulf of Mexico hydrocarbon seeps. Thesis, Louisiana State University, Department of Oceanography and Coastal Sciences. 97 pp.

Note Added in Proof

While this paper was in press, several papers were published that affect the discussion on age, origin, and distribution of the fauna.

Based on sequences of mtDNA of *Alviniconcha* from four different populations, Kojima et al. (1998) expanded the results of Denis et al. (1993), based on allozyme frequencies, and concluded that three species are present in the western Pacific back-arc basins: *A. hessleri,* restricted to the Mariana Trough, *Alviniconcha* sp. A, in the Manus and North Fiji Basins, and *Alviniconcha* sp. B, in the North Fiji and Lau Basins. Possibly, a finer morphometric re-analysis of the shells is needed.

Bandel & Kiel (2000) have described *Desbruyeresia antiqua* from the Campanian (Late Cretaceous) of Spain. They rejected a position of Provannidae in the Loxonematoidea because *Loxonema* Phillips, 1842, is "most probably" a member of the Archaeogastropoda, and instead place the family in the superfamily Cerithioidea. Even if this is the case, the similarities in protoconch morphology between Provannidae and Pseudozygopleuridae remain, and we hypothesize that the relationship of Provannidae is with Zygopleuroidea rather than with Cerithioidea. The Zygopleuroidea are considered paraphyletic by Nützel (1998) and represent a grade rather than a clade. The Abyssochrysidae were tentatively considered modern zygopleuroids by Nützel.

The ecology of the MAR Logatchev site is described by Gebruk et al. (2000), who present a fauna inventory with 11 species of gastropods, all except two (*Pseudorimula* sp. [most probably *P. midatlantica* of our list] and *Phymorhynchus moskalevi* [not listed by us from Logatchev]) not identified beyond family level.

BANDEL, K. & S. KIEL. 2000. Earliest known (Campanian) members of the Vermetidae, Provannidae and Litiopidae (Cerithioidea, Gastropoda), and a discussion of their possible relationships. Mitteilungen der Geologisch–Paläontologischen Institut, Universität Hamburg, 84:209–218.

GEBRUK, A. V., P. CHEVALDONNE, T. SHANK, R. A. LUTZ & R. C. VRIJENHOEK. 2000. Deep-sea hydrothermal vent communities of the Logatchev area (14°45'N, Mid-Atlantic Ridge): diverse biotopes and high biomass. Journal of the Marine Biological Association of the United Kingdom 80:383–393.

KOJIMA, S., S. OHTA, Y. FUJIWARA, K. FUJIKURA & J. HASHIMOTO. 1998. Speciation of gastropods of the genus Alviniconcha in the South Western Pacific. JAMSTEC Journal of Deep-Sea Research 74:501–505.

NÜTZEL, A. 1998. Über die Stammesgeschichte der Ptenoglossa (Gastropoda). Berliner geowissenschaftliche Abhandlungen, ser. E, 26:1–229.

APPENDIX 1

List of localities with hydrothermal vents, sulphide and methane seeps from which gastropods have been reported (updated from Warén & Bouchet, 1993). The localities are listed from north to south in this order: Mid Atlantic, western Atlantic, East Pacific, and West Pacific (Figure 50). The gastropod fauna is listed by alphabetical order of genus name.

Mid-Atlantic Ridge: Menez Gwen

Position. Ca. 37°50'N, 31°31'W, 850 m.

Expedition 1. DIVA 1, May 1994, chief scientist Y. Fouquet.

Samplings. DIVA 1 PL 13 (37°50'N, 31°31'W, 844-1013 m), DIVA 1 PL 14 (37°50.46'N, 31°31.35'W, 840–870 m), DIVA 1 PL 16 (37°50.47'N, 31°31.20'W, 840 m).

Expedition 2. DIVA 2, June 1994, chief scientists D. Desbruyères & A.-M. Alayse.

Samplings. DIVA 2 PL 11, DIVA 2 PL 12, DIVA 2 PL 13, DIVA 2 PL 14, DIVA 2 PL 16, DIVA 2 PL 26 (all same position, 37°50.54'N, 31°31.30'W, 860–870 m).

Expedition 3. MARVEL, August 1997, chief scientists D. Desbruyères & A.-M. Alayse.

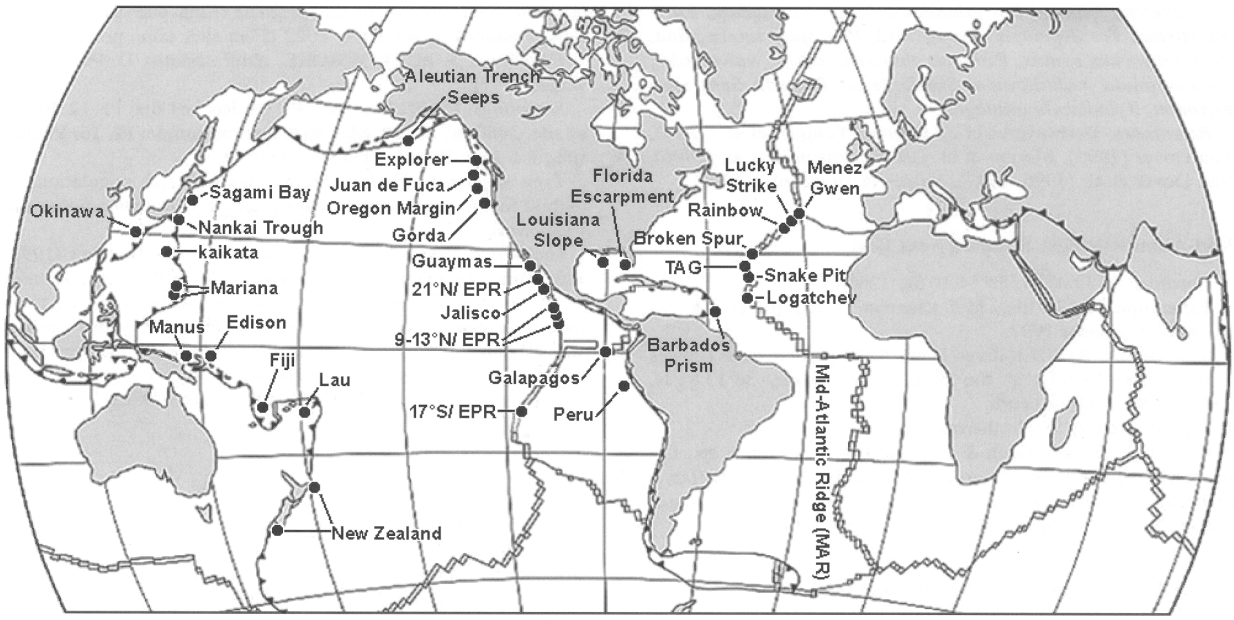

Figure 50. Localities with hydrothermal vents, sulfide and methane seeps from which gastropods have been reported. (Modified from Desbruyères & Segonzac, 1997, with permission).

Samplings. NAUTILE dives 1201 (850 m); 1202 (850 m); 1203 (850 m); 1208 (850 m); particle traps PPS 20, 24, 46, 49, 50, at the foot of a "translucid smoker" 37°50.52'N, 31°31.23'W, 845 m.

Type of locality. Area with hydrothermal vents situated at the peak of a young volcano and covering 200 m². Sulfide mounds in the area are covered by mussels. Shrimps (Alvinocarididae) common. Normal bathyal fauna is abundant at the periphery of the site.

Gastropod fauna. Warén & Bouchet herein: *Alvania stenolopha, Lepetodrilus* ***atlanticus, Lurifax vitreus,*** *Peltospira* ***smaragdina,*** *Protolira thorvaldssoni, P. valvatoides, Shinkailepas* ***briandi***, *Laeviphitus* ***desbruyeresi,*** *Xylodiscula* ***analoga*** [*Amphissa acuticostata* (Philippi, 1844), *Anatoma* sp., *Calliostoma obesula* (Locard, 1896), *Emarginula* sp., ***Neusas*** *marshalli, Pedicularia* sp., *Pseudosetia azorica, Strobiligera brychia* (Bouchet & Guillemot, 1988)]; species within brackets are not vent fauna, but occurred in samplings that also yielded vent species).

References. Colaco et al. (1998), Desbruyères et al. (1994a), Saldanha et al. (1996).

Mid-Atlantic Ridge: Lucky Strike

Position. Ca. 37°17'N, 32°17'W, 1620–1720 m.

Expedition 1. ALVIN dives May–June 1993, chief scientist C. Langmuir.

Samplings. ALVIN dive 2604 (37°20'N, 32°17'W, 1636 m); Dives 2605 and 2606 (37°17.55'N, 32°16.47'W, 1628 m, Statue de la Liberté); Dive 2607 (37°17.50'N, 32°16.47'W, 1628 m, Sintra site); Dive 2608 (Tour Eiffel).

Expedition 2. DIVA 1, May 1994, chief scientist Y. Fouquet.

Samplings. DIVA 1 PL 01 (37°17.49'N, 32°16.60'W, 1681–1729 m), DIVA 1 PL 03 (37°17.55'N, 32°16.47'W, 1624 m), DIVA 1 PL 04 (37°17.32'N, 32°16.51'W, 1685–1703 m), DIVA 1 PL 08 (37°17.30'N, 32°16.70'W, 1680–1728 m), DIVA 1 PL 09 (37°17.40'N, 32°16.50'W, 1622–1683 m), DIVA 1 PL 17 (37°17.32'N, 32°16.52'W, 1648–1700 m), DIVA 1 PL 18 (37°17.36'N, 32°16.65'W, 1685–1730 m), DIVA 1 PL 19 (37°17.50'N, 32°17'W, 1665–1728 m).

Expedition 3. DIVA 2, June 1994, chief scientists D. Desbruyères & A.-M. Alayse.

Samplings. DIVA 2 PL 01 (Isabel site, 37°17.36'N, 32°16.64'W, 1685 m), DIVA 2 PL 02 (Sintra site, 37°17.50'N, 32°16.47'W, 1622 m), DIVA 2 PL 03 (Isabel site), DIVA 2 PL 04 (Tour Eiffel, 37°17.32'N, 32°16.51'W, 1685 m), DIVA 2 PL 05 (Pico site), DIVA 2 PL 06 (Isabel), DIVA 2 PL 07 (Pagode site, 37°17.63'N, 32°16.95'W, 1629 m), DIVA 2 PL 08 (Tour Eiffel), DIVA 2 PL 09 (Tour Eiffel), DIVA 2 PL 10 (Tour Eiffel), DIVA 2 PL 17 (Tour Eiffel), DIVA 2 PL 19 (Pagode, Isabel), DIVA 2 PL 20 (Tour Eiffel, Isabel and Pagode), DIVA 2 PL 21 (Tour Eiffel), DIVA 2 PL 23 (Tour Eiffel and Pagode sites), DIVA 2 PL 24 (Isabel and Tour Eiffel), DIVA 2 PL 25 (Tour Eiffel and Pagode).

Expedition 4. LUSTRE Expedition, July 1996, chief scientists D. Fornari & S. Humphris.

Samplings. JASON lowerings 176, 177, 181, 183; Sintra and Tour Eiffel, as above (gastropods from C. L. Van Dover).

Expedition 5. MARVEL, August 1997, chief scientists D. Desbruyères & A.-M. Alayse.

Samplings. NAUTILE dives 1191 (Bairro Alto = Pagodes), 1192 (Bairro Alto, 1630 m), 1193 (Bairro Alto, 1585 m), 1194 (Tour Eiffel, 1685 m), 1195 (Tour Eiffel, 1685 m), 1200 (Bairro Alto, 1700 m), 1205 (Bairro Alto, 1700 m), 1206 (PP 24 site, 1643 m).

Type of locality. Hydrothermal vents around the periphery of a lave lake, dominated by *Bathymodiolus* sp. Shrimps (Alvinocarididae) common. Non-vent fishes and other fauna penetrate the area.

Gastropod fauna. Valdés & Bouchet (1998), Warén & Bouchet herein: *Alvania stenolopha, Dendronotus comteti, Laeviphitus*

desbruyeresi, *Lepetodrilus* ***atlanticus,*** *Lirapex* ***costellata, Lurifax vitreus,*** *Paralepetopsis* ***ferrugivora,*** *Peltospira* ***smaragdina,*** *Phymorhynchus* ***ovatus,*** *Protolira thorvaldssoni, P. valvatoides, Pseudorimula midatlantica, Shinkailepas* ***briandi,*** *Sutilizona* ***pterodon,*** *Xylodiscula* ***analoga.***

References. Desbruyères et al. (1994a), Fouquet et al. (1994), Van Dover (1995), Murton et al. (1995), Saldanha et al. (1996), Van Dover et al. (1996, 1997), Valdés & Bouchet (1998).

Mid-Atlantic Ridge: Rainbow vent field

Position. 36°13.45′N, 33°54.10′W, 2260 m.

Expedition. MARVEL, chief scientists D. Desbruyères & A.-M. Alayse, August 1997.

Samplings. NAUTILE dives 1196, 1206; particle traps (pièges à particules) PP1-10 at the base of a smoker, 36°13.81′N, 33°54.07′W, 2260 m depth.

Type of locality. Hydrothermal vents

Gastropod fauna. Warén & Bouchet herein: Conidae sp., *Lepetodrilus* ***atlanticus,*** *Protolira thorvaldssoni, Shinkailepas* ***briandi,*** *Xylodiscula* ***analoga*** [*Mitrella nitidulina* (Locard, 1897)]. Species within brackets are not vent fauna.

Mid-Atlantic Ridge: Broken Spur vent field

Position. Broken Spur vent field, Bogdanov site, MAR at 29°10′N, 43°10′W, 3110 m.

Expedition. BRAVEX, British-Russian Atlantic Vents Expedition 1994, chief scientist P. Tyler.

Samplings. Dive at the Bogdanov site (gastropods from P. Tyler).

Type of locality. A series of actively venting platforms and shelves on the western wall of the Eastern Valley region.

Gastropod fauna. Warén & Bouchet herein: Neritid egg capsules.

References. Murton et al. (1995), Van Dover (1995).

Mid-Atlantic Ridge: TAG vent field

Position. Kremlin site, southeastern sector of TAG hydrothermal mount, 26°08′N, 44°49′W, 3660 m.

Expedition. BRAVEX, British-Russian Atlantic Vents Expedition 1994, chief scientist P. Tyler.

Samplings. AMK 3394, Kremlin site (gastropods from P. Tyler).

Type of locality. Hydrothermal vents with *Bathymodiolus* and shrimps (Alvinocarididae).

Gastropod fauna. Sysoev & Kantor (1995), Warén & Bouchet herein: *Phymorhynchus moskalevi.*

References. Grassle (1986a), Rona et al. (1986), Galkin (1990), Fujioka & von Herzen (1994), Van Dover (1995), Humphris et al. (1995).

Mid-Atlantic Ridge: Snake Pit vent field

Position. 23°22.13′N, 44°57.13′W, 3470–3520 m.

Expedition 1. GRAVINAUT, chief scientist J. Dubois, September 1993.

Samplings. GRAVINAUT 02, Just east of "Snake Pit"; GRAVINAUT 16, "Snake Pit" site.

Expedition 2. MAR 93, Chief scientist C. L. Van Dover & A. Fiala.

Samplings. ALVIN dives 2613, 2614, 2615, 2616, 2617 (Elan site, 23°23′N, 44°56′W, 3520 m); dive 2618 (Ruches site, same position, 3490 m); dives 2619, 2620 (Elan and Ruches sites, same position); dives 2621, 2622 (Elan site, same position).

Expedition 3. MICROSMOKE, chief scientist D. Prieur, November 1995.

Samplings. PL 07, Elan site; PL 08, Ruches site; PL 12, Ruches site, 3480 m; PL 14, Elan site, suction sample; PL 16, Ruches site, in a trap; PL 17, Elan site, 3510 m.

Type of locality. Hydrothermal vents with rich populations of mobile fauna, especially shrimps; actinians, *Bathymodiolus* and *Vesicomya.*

Gastropod fauna. McLean (1992), Warén & Bouchet (1993) and herein: *Gymnobela* sp. B, *Lepetodrilus* ***atlanticus,*** *Lirapex* n. sp., *Peltospira* ***smaragdina,*** *Protolira valvatoides, P. thorvaldssoni, Pseudorimula midatlantica, Phymorhynchus* ***carinatus,*** *Phymorhynchus moskalevi, Phymorhynchus* ***ovatus,*** *Shinkailepas* ***briandi,*** *Sutilizona* ***pterodon.***

References. Mevel et al. (1989), Segonzac (1992), Van Dover (1995).

Mid-Atlantic Ridge: Logatchev vent field

Position. 14°45′N, 44°59′W, 3040 m.

Expedition. MICROSMOKE, November/December 1995, chief scientist D. Prieur.

Samplings. PL 20, Irina site, 14°45.10′N, 44°48.60′W, 3005 m; PL 21, Irina site.

Type of locality. Hydrothermal vents with *Bathymodiolus* and shrimps (Alvinocarididae).

Gastropod fauna. Warén & Bouchet herein: *Peltospira* ***smaragdina,*** *Phymorhynchus* ***carinatus,*** *Phymorhynchus* ***ovatus,*** *Pseudorimula midatlantica, Shinkailepas* ***briandi.***

References. Van Dover (1995), Gebruk et al. (1997).

Gulf of Mexico, Louisiana slope

Position. Bush Hill seep, 27°46.91′N, 91°30.34′W, 540–580 m.

Expedition. Chief scientist R.S. Carney.

Samplings. Johnson Sealink dive 3129, 15 Sept. 1991 (gastropods from R.S. Carney).

Type of locality. Methane seep.

Gastropod fauna. Listed by Warén & Bouchet (1993): *Bathynerita naticoidea, Cancellaria rosewateri, Cantrainea macleani, Cataegis meroglypta, Provanna sculpta,* [*Eosipho canetae, Gaza fischeri, Gymnobela extensa, Hyalorisia galea*]. Species within brackets may not be strictly seep fauna.

References. Carney (1994).

Florida Escarpment

Position. West of southern Florida, 26°02′N, 84°55′W, 3270 m.

Type of locality. Sulfide rich seeps.

Gastropod fauna. Fucaria sp., *Paralepetopsis floridensis, Provanna admetoides,* neogastropods 2 spp.

Barbados Prism

Position. North Barbados, ca. 13°49′N, 57°39′W, 4940 m.

Expedition 1. BARESNAUT, chief scientists X. Le Pichon and J.P. Foucher.

Samplings. PL 94, 13°49′N, 57°39′W, 4935 m.

Expedition 2. MANON, February/March 1992, chief scientists X. Le Pichon and S. Lallemant.

Samplings. MANON 06, 13°47.05′N, 57°32.40′W, 4940 m.

Type of locality. Cold seeps; mud volcanoes surrounded by chemosynthetically active fauna.

Gastropod fauna. Warén & Bouchet herein. *Phymorhynchus* aff. *alberti.*

References. Le Pichon et al. (1990), Olu et al. (1997).

End of Barbados Prism

Position. West of Tobago, ca. 10°20'N, 1700–2000 m (Orenoque) - 11°14'N, 1135–1236 m (El Pilar Sector).

Expedition. DIAPISUB, December 1992/January 1993, chief scientist J.C. Faugères.

Samplings. DIAPISUB 05-2, 10°20.09'N, 58°53.97'W, 1754 m; DIAPISUB 10, 1969 m; DIAPISUB 10-4, 10°19.97'N, 58°37.30'W, 1947 m, in mud; DIAPISUB 15-2, 15/8, 11°13.97'N, 59°29.92'W, 1135 m; DIAPISUB 15-4, 1135 m; DIAPISUB 16-3, 11°13.82'N, 59°21.82'W, 1236 m.

Type of locality. Cold seeps in a subduction zone (domes, mud volcanoes, and diapiric ridges), with mussels, vesicomyids and Vestimentifera.

Gastropod fauna. Warén & Bouchet herein: *Bathynerita naticoidea, Cataegis meroglypta, Phymorhynchus* aff. *alberti, Trophon* spp.

References. Jollivet et al. (1990), Olu et al. (1996b).

Aleutian Trench Seeps

Position. Shumagin site: 54°18'N, 157°12'W, 4800 m; Edge site: 57°27'N, 147°59'W, 4960 m.

Expedition 1. Sonne Cruise 110/1b, chief scientist E. Suess.

Samplings. Sta. 23, ROPOS (Remote Operated Platform for Ocean Science) #344, Edge site, 57°26.9'N, 147°00'W, 4947–4919 m; TVG (TV monitored grab) 24, Edge site, 57°27.631'N, 148°00.013'W, 4890 m; TVGKG (TV monitored 0.25 m² corer) 40, Shumagin site, 54°18.17'N, 157°11.82'W, 4808 m; TVG 43, Shumagin site, 54°18.196'N, 157°11.936'W, 4810 m (gastropods from H. Sahling).

Expedition 2. Sonne Cruise 110/2, chief scientist E. Suess.

Samplings. TVG 48, Shumagin site, 54°18.064'N, 157°11.895'W, 4877 m; TVGKG 49, Shumagin site, 54°18.056'N, 157°12.107'W, 4809 m; TVG 63, Edge site, 57°27.326'N, 148°00.275'W, 4774 m (gastropods from H. Sahling).

Type of locality. Sulfide/methane seeps at a subduction zone with *Calyptogena phaseoliformis, Acharax* cf. *johnsoni,* Vestimentifera and Pogonophora. Fauna (and seepage ?) more concentrated at Edge site; diffuse at Shumagin site.

Gastropod fauna. Sahling (1997) and Warén & Bouchet herein: *Bayerius arnoldi, Bruceiella* ***athlia,*** *Hyalogyrina* ***umbellifera,*** *Provanna* sp. 2, ***Retiskenea diploura, Sahlingia xandaros.*** In addition, the following species were identified by McLean (unpublished) from material collected by Sahling: *Admete* sp., *Microglyphis* sp. nov., Naticidae sp., *Oenopota* sp.

References. Suess (1994, 1997); Lutz et al. (1996); Orange et al. (1996); Suess & Bohrmann (1997), Sahling (1997).

Juan de Fuca Ridge: Explorer Ridge

Position. Magic Mountain, Steve 4 Vent (14b), 49°45.53'N, 130°15.50'W, 1762 m.

Expedition. CANRIDGE III Expedition, July 1997, chief scientist S. Scott.

Samplings. ROPOS #284, Steve 4 Vent, 27 June 1994 (from V. Tunnicliffe).

Type of locality. Hydrothermal vents with vestimentifera, gastropods, alvinellids, and ampharetids.

Gastropod fauna. Listed by Warén & Bouchet (1993) and herein: *Clypeosectus curvus, Depressigyra globulus, Lepetodrilus fucensis, Provanna variabilis,* ***Speculator cariosus,*** *Temnocinclis euripes.*

References. Johnson (1993), Tunnicliffe et al. (1986), Tunnicliffe (1988).

Juan de Fuca Ridge: Middle Valley

Position. Off Vancouver Island, Canada, 48°25.8'N, 128°40.9'W, 2423 m.

Expedition.

Samplings. ROPOS 149, HHFA, Club Clam, 2416 m, 1992-04-07 (gastropods from V. Tunnicliffe). ALVIN dive 3146, 48°27.34'N, 128°42.57'W, 2410 m, 1997-10-06 (gastropods from J. Voight).

Type of locality. Hydrothermal vents.

Gastropod fauna. Listed by Warén & Bouchet (1993) and herein: *Clypeosectus curvus, Depressigyra globulus, Fucaria striata, Hyalogyrina* ***globularis,*** *Lepetodrilus corrugatus, L. fucensis, Provanna variabilis, Buccinum* (*viridum*?).

References. Tunnicliffe (1991).

Juan de Fuca Ridge: Endeavour Segment

Position. Off Vancouver Island, Canada, ca. 47°57'N, 129°06'W, 2200–2400 m.

Expedition 1. High Rise Expedition 1995, chief scientist C.L. Van Dover.

Samplings. Advanced Tehtered Vehicle 50-1, sample 270, High Rise Vent Field, Fairy Castle edifice, 47°58.13'N, 129°05.26'W, 2200 m.

Expedition 2. BIOROPOS Expedition, chief scientist S.K. Juniper.

Samplings. ROPOS #278, Fissure at Main Field, 47°56.9'N, 129°06.9'W, 2202 m, 12 June 1994 (gastropods from V. Tunnicliffe).

Expedition 3. REVEL-ROPOS Cruise, August 1996, chief scientists S.K. Juniper, C.R. Fisher & J. Delaney.

Samplings. ROPOS HYS 351, ROPOS HYS 364, Clam Bed Vent Field, 47°57.780'N, 129°05.493'W, 2200–2250 m (gastropods from J. Voight).

Expedition 4. Not named, chief scientist J. Delaney.

Samplings. ALVIN dive 2409, 47°57'N, 129°06'W, 2192 m, Main Field, Grotto vent (gastropods from V. Tunnicliffe).

Type of locality. Hydrothermal vents.

Gastropod fauna. Listed by Warén & Bouchet (1993) and herein: *Buccinum* (*viridum*?), *Clypeosectus curvus, Depressigyra globulus, Hyalogyrina* ***globularis,*** *Lepetodrilus fucensis, Melanodrymia brightae, Phymorhynchus* sp., *Provanna variabilis, Sutilizona* ***tunnicliffae,*** *Temnocinclis eurypes.*

References. Delaney et al. (1992), Johnson (1993), Juniper et al. (1996).

Juan de Fuca Ridge: CoAxial Segment

Position. Beard Chimney Source site, 46°09.3'N, 129°48.4'W, 2060 m.

Expedition. CoAxial Response, chief scientist J. Delaney.

Samplings. Grab sample from Beard Chimney Source site (gastropods from V. Tunnicliffe and C. Van Dover).

Type of locality. Hydrothermal vent.

Gastropod fauna. Warén & Bouchet herein: *Adeuomphalus* ***trochanter.***

References. Johnson (1993), Embley et al. (1995).

Juan de Fuca Ridge: Axial Seamount

Position. Off Oregon, 45°56′N, 130°01′W, 1500–1600 m.

Samplings. ROPOS station R406, Ashes vent field, worm grab, 45°56.01′N, 130°00.87′W, 1543 m (gastropods from J. Voight).

Type of locality. Hydrothermal vents.

Gastropod fauna. Listed by Warén & Bouchet (1993), McLean & Geiger (1998) and herein: *Clypeosectus curvus, Cornisepta verenae, Depressigyra globulus, Lacunoides* ***vitreus,*** *Lepetodrilus fucensis, Provanna laevis, P. variabilis, Pyropelta musaica, Temnocinclis euripes.*

References. Tunnicliffe et al. (1985), Canadian American Seamount Expedition (1985), ASHES Expedition (1986), Tunnicliffe (1988).

Oregon Margin: 45°N

Position. 250 km west of Oregon, 44°40′N, 125°06′W, 500–800 m.

Expedition 1. Sonne Cruise 109/1, chief scientist E. Suess.

Samplings. TVG 36/1, 44°40.494′N, 125°07.268′W, 681 m; TVG 43/1, 44°40.195′N, 125°06.538′W, 609 m (gastropods from H. Sahling).

Expedition 2. Sonne Cruise 109/2-3, chief scientist E. Suess.

Samplings. TVG 109, 44°40.170′N, 125°05.796′W, 598 m, gray-green sediment with H_2S; TVG 110, 44°40.1′N, 125°05.8′W, 602 m, carbonate blocks; TVG 115, 44°40.293′N, 125°06.296′W, 616 m, from calcareous blocks; TVG 115, 44°40.293′N, 125°06.296′W, 618 m, gray-green sediment with H_2S; TVG 121, 44°40.2′N, 125°06.6′W, 622 m, gray green sediment with *Calyptogena* (gastropods from H. Sahling).

Expedition 3. Sonne Cruise 110/1a, chief scientist E. Suess.

Samplings. ROPOS #339, 44°40.3′N, 125°06.5′W, 635–632 m, sample tray 4/5; ROPOS #339, 44°40.3′N, 125°06.5′W, 635–632 m, Pete Vent Field; ROPOS #341, 44°40.14′N, 125°05.8′W, 600 m, suction sample 1; TVG 11, 44°40.134′N, 125°06.503′N, 524 m; TVG 18, 44°34.235′N, 125°08.191′W, 785 m (gastropods from H. Sahling).

Expedition 4. Juan de Fuca Cruise, July 1994, chief scientist R. Lutz.

Samplings. ALVIN dive 2796, 44°40.53′N, 125°07.10′W, 675 m, 16 July 1994 (gastropods from V. Tunnicliffe).

Type of locality. Sulfide and methane seeps at a subduction zone, with *Calyptogena* spp. and *Solemya* sp.

Gastropod fauna. Warén & Bouchet herein: (*Hyalogyrina* sp., too poor to be identified SMF 311989), *Provanna laevis, P. lomana, P. variabilis, Pyropelta corymba,* ***Retiskenea*** cf. ***diploura.*** In addition, the following species were identified by McLean (unpublished) from material collected by Sahling: *Boreotrophon* n. sp. (Muricidae), *Colus aphelus* (Dall, 1890), *C. halidonus* Dall, 1919, *Fusitriton oregonensis* (Redfield, 1846), *Margarites* n. sp., *Neptunea amianta* (Dall, 1890), *N. lyrata* (Gmelin, 1791), and Pyramidellidae gen. sp. indet.

References. Suess et al. (1985, 1996), Herzig et al. (1997), Suess & Bohrmann (1997).

Juan de Fuca Ridge, Southern Part

Position. 44°39′–44°57′N, 130°13′–130°22′W, 2200–2280 m.

Samplings. ALVIN dive 2078, Megaplume South, 1988-08-06 (gastropods from V. Tunnicliffe).

Type of locality. Hydrothermal vent.

Gastropod fauna. Listed by Warén & Bouchet (1993): *Depressigyra globulus, Lepetodrilus fucensis, Temnocinclis euripes.*

Gorda Ridge

Position. Off northern California, 41°00′N, 127°29′W, 3271 m.

Type of locality. Hydrothermal vents.

Gastropod fauna. Listed by Warén & Bouchet (1993): *Amphiplica gordensis, Depressigyra globulus, Lepetodrilus fucensis, Melanodrymia* sp., *Neolepetopsis gordensis, Provanna variabilis.*

Guaymas Basin

Position. Central Gulf of California, ca. 27°01′N, 111°24′W. 2020–2033 m.

Expedition. GUAYNAUT, November 1991, chief scientist A.-M. Alayse.

Samplings. PL 07 (27°00.53′N, 111°24.49′W); PL 08 (27°00.47′N, 111°24.55′W); PL 13 (27°00′N, 111°24′W); PL 15 (27°00.94′N, 111°24.50′W); PL 16 (27°00.95′N, 111°24.54′W); PL 17 (27°00.93′N, 111°24.63′W); PL 18 (27°00.93′N, 111°24.65′W).

Type of locality. Warm seeps with methane and hydrocarbons, penetrating thick layers of sediment and hydrothermal vents; vestimentifera, vesicomyids, alvinellids.

Gastropod fauna. Listed by Warén & Bouchet (1993): *Eulimella lomana, Hyalogyrina grasslei, Lepetodrilus guaymasensis, Provanna goniata, P. laevis, Pyropelta corymba.*

References. Unpublished report of GUAYNAUT, Grassle 1986b.

East Pacific Rise (EPR), 21°N

Position. Off southern tip of Baja California, 20°51′N, 109°04′W, 2600 m.

Type of locality. Hydrothermal vents.

Gastropod fauna. Listed by Warén & Bouchet (1993): *Bathymargarites symplector, Clypeosectus delectus, Cyathermia naticoides, Echinopelta fistulosa, Eulepetopsis vitrea, Gorgoleptis emarginatus, Lepetodrilus cristatus, L. elevatus, L. ovalis, L. pustulosus, Lirapex granularis, L. humata, Melanodrymia aurantiaca, Neolepetopsis verruca, Neomphalus fretterae, Nodopelta heminoda, Pachydermia laevis, Peltospira operculata, Phymorhynchus* sp., *Planorbidella planispira, Provanna ios, P. muricata, Rhynchopelta concentrica, Sinezona* sp., *Solutigyra reticulata, Temnozaga parilis.*

References. Desbruyères (1998).

Remarks: A nearby locality is Green Seemount, 20°49′N, 109°17′W, 1990 m, from where *Neolepetopsis occulta* has been reported from an inactive sulfide chimney (Warén & Bouchet 1993).

Mid America Trench, Jalisco Block Seeps, at 20°N

Position. 20°N, 106°W, 3800 m.

Expedition. NAUTIMATE, chief scientists B. Mercier de Lépinay & F. Michaud, February 1994.

Samplings. NAUTIMATE PL 10, 18°22′N, 104°23′W, 3000–3300 m; NAUTIMATE PL 16, 20°01.79′N, 106°17.33′W, 3795 m; NAUTIMATE PL 18, 20°05′N, 106°18′W, 3662 m.

Type of locality. Cold seeps at the accretion zone off the Jalisco Block.

Gastropod fauna. Warén & Bouchet herein: *Bathybela* ***papyracea,*** *Bayerius* sp., *Neolepetopsis* sp., *Pleurotomella* sp., *Provanna* sp. 3, *Pyropelta* cf. *musaica.*

References. Unpublished expedition report.

East Pacific Rise (EPR), 13°N

Position. Ca. 12°49'N, 103°56.5'W, 2630 m.

Expedition 1. HERO 91, chief scientist D. Desbruyères, October 1991.

Samplings. PL 02 (Parigo, Genesis, Totem sites); PL 04 (La Chainette, 12°50.5N, 103°57.03'W, 2600 m); PL 05 (Genesis, Totem); PL 10 (Totem, Genesis); PL 11 (Genesis); PL 12 (Genesis, Julie); PL 13 (Elsa); PL 14 (Elsa); PL 16 (Elsa, Julie); PL 17 (Elsa); PL 18 (Elsa); PL 19 (Elsa); PL 20 (Elsa); PL 21 (Elsa); PL 22 (Elsa); PL 23 (Elsa); PL 24 (Elsa); PL 25 (Caldera, 10 km south of main locality, 12°42.65'N, 103°54.65'W, 2563 m); PL 26 (Elsa); PL 27 (Totem, Genesis, Pogosud). For detailed positions of sites not given here, see Warén & Bouchet (1993).

Expedition 2. HERO 92, April 1992, chief scientist J. Childress.

Samplings. ALVIN dives 2512 (Julie, Genesis, Parigo); 2514 (Genesis, Elsa); 2516 (Elsa, Genesis); 2517 (Elsa, Genesis); 2519 (Totem & Julie); 2520 (Parigo, Elsa, Genesis, Pogosud); 2521 (Parigo, Elsa); 2522 (Parigo, Pogosud & Genesis); 2523 (Elsa, Genesis); 2524 (Parigo, Gensis, Elsa); 2525 (Julie, Parigo, Genesis); 2526 (Julie, Parigo, Genesis); 2527 (Genesis, Elsa); 2528 (Totem, Genesis, Elsa); 2531 (Genesis); 2532 (Genesis). For detailed positions of sites not given here, see Warén & Bouchet (1993).

Type of locality. Hydrothermal vents with Vestimentifera, *Bathymodiolus,* vesicomyids, alvinellids.

Gastropod fauna. Listed by Warén & Bouchet (1993) and herein: *Bathymargarites symplector, Clypeosectus delectus, Ctenopelta porifera, Cyathermia naticoides, Echinopelta fistulosa, Eulepetopsis vitrea, Gorgoleptis emarginatus, G. spiralis, Gymnobela* sp. A., *Hirtopelta hirta, Lepetodrilus cristatus, L. elevatus, L. ovalis, L. pustulosus, Melanodrymia aurantiaca, M. "rustcovered," M.* ***galeronae,*** *Moelleriopsis* sp., *Neolepetopsis densata, Neomphalus fretterae, Nodopelta heminoda, N.* ***rigneae,*** *N. subnoda, Pachydermia laevis, Peltospira delicata, P. lamellifera, P. operculata, Phymorhynchus major, Planorbidella planispira, Provanna ios, Rhynchopelta concentrica, Solutigyra reticulata, Sutilizona theca.*

References. Fustec et al. (1987), Desbruyères (1995, 1998), Jollivet (1993).

Remarks: Other, nearby localities are "Volcano 5", 12°58.0'N, 103°26.0'W, 1160 m and "Volcano 6," 12°44.0'N, 103°33.0'W, 1775 m, from where *Clathrosepta depressa* and *Cornisepta levinae,* respectively have been described (McLean & Geiger, 1998).

East Pacific Rise (EPR), 12°N

Position. Southwest off Mexico, 11°46'N, 103°47'W, 2725 m.

Type of locality. Inactive sulfide chimney without megafaunal vent species.

Gastropod fauna. Listed by Warén & Bouchet (1993): *Neolepetopsis densata, Sutilizona theca.*

East Pacific Rise (EPR), 11°N

Position. Southwest off Mexico, 11°26'N, 103°47'W, 2600 m.

Gastropod fauna. Listed by Warén & Bouchet (1993): *Eulepetopsis vitrea, Lepetodrilus tevnianus.*

East Pacific Rise (EPR), 09°50'N

Position. 09°50'N, 104°17'W, 2505 m.

Expedition. HERO 91, October 1991, chief scientist D. Desbruyères.

Samplings. PL 06 (Worm Barbecue site, 09°50.20'N, 104°17.40'W, 2505 m); PL 07 (Brasoucade site, just south of PL 06, 09°50.09'N, 104°17.43'W, 2517 m); PL 08 (Hole to Hell site, 09°50.30'N, 104°17.50'W, 2520 m); PL 09 (Worm Barbecue site).

Type of locality. Hydrothermal vents with Vestimentifera, *Bathymodiolus,* vesicomyids, alvinellids.

Gastropod fauna. Mullineaux et al. (1996), Warén & Bouchet herein: *Bathymargarites symplector, Clypeosectus delectus, Cyathermia naticoides, Eulepetopsis vitrea, Gorgoleptis* sp., *Laeviphitus* sp., *Lepetodrilus elevatus, Lepetodrilus ovalis, Lirapex granularis, Melanodrymia* spp., *Neomphalus fretterae, Pachydermia laevis, Peltospira delicata, Peltospira operculata, Phymorhynchus* ***major,*** *Rhynchopelta concentrica.*

References. Chevaldonné et al. (1995), Desbruyères (1998).

Galapagos Rift

Position. 00°48'N, 86°08'W, 2500–2700 m.

Type of locality. Hydrothermal vents.

Gastropod fauna. Listed by Warén & Bouchet (1993): *Clypeosectus delectus, Eulepetopsis vitrea, Gorgoleptis patulus, Lacunoides exquisitus, Lepetodrilus cristatus, L. elevatus, L. pustulosus, Melanodrymia* sp., *Neomphalus fretterae, Nepotilla* sp., *Phymorhynchus* sp., *Provanna ios, P. muricata.*

East Pacific Rise: Northeast of Easter Island

Position. ca. 17°S, 113°W, ca. 2600 m.

Expedition. NAUDUR, J.-M. Auzende, November/December 1995.

Samplings. NAUDUR PL 03 (Nadir site, 17°25.79'S, 113°12.33'W, 2572 m); NAUDUR PL 04 (Rehu site, 1993-12-09, 17°24.85'S, 113°12.15'W, 2578 m); NAUDUR PL 06 (Rehu site); NAUDUR PL 08 (18°25.82'S, 113°12.15'W, 2623 m); NAUDUR PL 09 (Fromveur site, 18°25.96'S, 113°23.35'W, 2622 m), NAUDUR PL 18 (Le Chat, 17°24.86'S, 113°12.07'W, 2582 m; Gwen Meur, same position; Rehu), NAUDUR PL 19, site Rehu.

Type of locality. Hydrothermal vents with Vestimentifera, *Bathymodiolus,* vesicomyids, cirripeds, actinians, alvinellids.

Gastropod fauna. Warén & Bouchet herein: *Bathymargarites symplector, Clypeosectus delectus, Eosipho* ***auzendei,*** *Eulepetopsis vitrea, Falsimargarita* ***nauduri,*** *Lepetodrilus elevatus, Lepetodrilus ovalis, Lepetodrilus pustulosus, Melanodrymia aurantiaca, Nodopelta subnoda, Pachydermia laevis, Planorbidella planispira, Peltospira delicata, Peltospira operculata, Provanna ios, Rhynchopelta concentrica.*

References. Geistdoerfer et al. (1994), Guinot & Segonzac (1997).

Comments. Fauna very similar to the northern parts of EPR at 09–21°N.

Peru, Off Paita

Position. 05–10°S, 81–82°W, 3000–3500 m.

Expedition. NAUTIPERC, chief scientist J. Bourgois, March–April 1991.

Samplings. NAUTIPERC PL 01-4-13 (05°36.38'S, 81°42.19'W, 3542 m); NAUTIPERC PL 1-15-8 (05°42.27'S, 81°38.25'W, 2988 m); NAUTIPERC PL 02 (05°36'S, 81°41'W, 4240–3370 m); NAUTIPERC PL 18 (10°01'S, 80°07'W, 5996–5385 m).

Type of locality. Cold sulfide seeps with rich *Calyptogena* beds.

Gastropod fauna. Listed by Warén & Bouchet (1993) and herein: *Bayerius* ***peruvianus,*** *Neolepetopsis* cf. *gordensis, Tractolira sparta.*

References. Warén & Bouchet (1993), Olu et al. (1996a).

Sagami Bay

Position. 34°58′N, 139°31′E, 1130–1180 m (Okinoyama Bank); 35°00′N, 139°13′E, 1170 m (Off Hatsushima).

Type of locality. Cold seeps.

Gastropod fauna. Okutani & Fujikura (1992), Okutani et al. (1992), Okutani et al. (1993): *Bathyacmaea nipponica, Gymnobela sagamiana, Margarites shinkai, Phymorhynchus buccinoides, Provanna glabra, Serradonta vestimentifericola.* [Not strictly seep fauna: *Buccinum soyomaruae, Neptunea acutispiralis*].

References. Hashimoto et al. (1989).

Nankai Trough

Position. 33°37′N, 137°32′E, 3800–4020 m (Tenryu Canyon); 33°50′N, 137°50′E, 1900–2200 m.

Expedition. KAIKO-NANKAI, August–September 1995, leader X. Le Pichon.

Samplings. KAIKO-NANKAI PL 14, 33°49.40′N, 137°55.20′E, 2140 m.

Type of locality. Cold seeps with Vestimentifera, *Calyptogena* spp., *Solemya* sp.

Gastropod fauna. Warén & Bouchet (1993 and herein): *Bathybela* sp., *Costaria* sp. [Tenryu Canyon]; *Paralepetopsis* ***lepichoni.***

References. Lallemant et al. (1992), Kojima & Ohta (1997).

Okinawa Back-Arc Basin: Minami-Ensei Knoll

Position. 28°24′N, 127°38′E, 700 m.

Type of locality. Hydrothermal vents with Vestimentifera, *Bathymodiolus,* and *Calyptogena.*

Gastropod fauna. Okutani & Fujikura (1990) and Okutani et al. (1993): *Bathyacmaea secunda, Cantrainea jamsteci, Lepetodrilus japonicus, Provanna glabra, Puncturella parvinobilis.* [Not strictly vent fauna: *Neptunea insularis*].

References. Hashimoto et al. (1995).

Okinawa Back-Arc Basin: Iheya Ridge

Position. 27°32.9′N, 126°58.2′E, 1350 m.

Type of locality. Hydrothermal vents.

Gastropod fauna. Okutani et al. (1993): *Bathyacmaea secunda, Provanna glabra, Lepetodrilus nux.*

Okinawa Back-Arc Basin: Izena Hole

Position. 27°16′N, 127°04.9′E, 1340 m.

Type of locality. Hydrothermal vents.

Gastropod fauna. Okutani et al. (1993): *Margarites shinkai, Provanna glabra, Puncturella rimaizenaensis, Lepetodrilus nux.*

Kaikata Seamount

Position. North of Iwo Jima, 26°43′N, 141°05′E, 470 m.

Type of locality. Hydrothermal vents with bythograeid crabs.

Gastropod fauna. Okutani et al. (1989), Okutani et al. (1993): *Laeviphitus japonicus, Oenopota ogasawarana, Shinkailepas kaikatensis.*

Mariana Back-Arc Basin, Alice Springs Field

Position. North of Guam, 18°12′N, 144°43′E, 3650 m.

Type of locality. Hydrothermal vents.

Gastropod fauna. Listed by Okutani (1990), Warén & Bouchet (1993) and Hasegawa et al. (1997): Acmaeidae n. gen. et sp., *Alviniconcha hessleri,* Buccinidae sp., *Desbruyeresia marianaensis, Lepetodrilus* n. sp. aff. *elevatus* [= *L. schrolli*?], *Phymorhynchus* aff. *starmeri, Provanna nassariaeformis, Pseudorimula marianae, Shinkailepas* aff. *kaikatensis, Symmetromphalus regularis, Ventsia* aff. *tricarinata.*

Mariana Back-Arc Basin, Forecast Vent Field

Position. 13°24′N, 143°55′E, 1450 m.

Type of locality. Hydrothermal vents.

Gastropod fauna. Listed by Hasegawa et al. (1997): *Alviniconcha hessleri, Desbruyeresia marianaensis, D.* aff. *spinosa, Lepetodrilus* n. sp. aff. *elevatus* [=*L. schrolli*?], *Pachydermia* aff. *sculpta, Phymorhynchus* aff. *starmeri, Pseudorimula marianae, Shinkailepas* aff. *kaikatensis, Symmetromphalus regularis, Ventsia* aff. *tricarinata.*

Edison Seamount

Position. Off east coast of New Ireland, 3 miles south of Lihir Island, Edison Seamount, 03°01.185′S, 152°03.492′E, 1483 m.

Expedition. SONNE 94 Edison Expedition, chief scientist P. Herzig, on German ship *Sonne,* April 1994.

Samplings. 30-GTVA; 66-GTVA (gastropods from V. Tunnicliffe & I. Jonasson). Samplings made with a TV-monitored dredge and Russian submersible Mir-2.

Type of locality. Submarine volcano with hydrothermal vents; vesicomyids, gastropods, shrimps and actinians.

Gastropod fauna. Sysoev & Kantor (1995), Beck (1996a) and Warén & Bouchet herein: *Bathyacmaea jonassoni, Fucaria* ***mystax,*** *Paralepetopsis rosemariae, Phymorhynchus wareni, Provanna* sp. 1, *Puncturella solis, Pyropelta bohlei.*

References. Herzig et al. (1994), Beck (1996a), McInnes (1998).

Manus Back-Arc Basin: Vienna Woods

Position. Bismarck Sea, north of New Britain. Wienerwald [Vienna Woods] site: 03°09.8′S, 150°16.7′E, 2500 m.

Expedition. OLGA II, chief scientist W. Tufar, on German ship *Sonne,* May–June 1990. Samplings made with a TV-monitored dredge.

Type of locality. Hydrothermal vents.

Gastropod fauna. Beck (1991, 1992a, b, 1993), McLean & Geiger (1998): *Alviniconcha hessleri, Clathrosepta becki, Ifremeria nautilei, Lepetodrilus schrolli, Olgasolaris tollmanni, Shinkailepas tufari, Symmetromphalus hageni.*

References. Tufar (1990).

Manus Back-Arc Basin: PACMANUS fields

Position. Bismarck Sea, north of New Britain, ca. 03°43.6′S, 151°40.3′E.

Expedition. BIOACCESS '96 and '98 with submersible *Shinkai 2000.*

Type of locality. Hydrothermal vents.

Gastropod fauna. Hashimoto et al. (1999): *Alviniconcha* cf. *hessleri, Bathyacmaea jonassoni, Desbruyeresia melanioides, Eosipho desbruyeresi, Ifremeria nautilei, Lepetodrilus schrolli,*

Lepetodrilus sp., "*Margarites*" sp., *Olgasolaris tollmanni, Phymorhynchus starmeri, Provanna buccinoides, P. nassariaeformis, Provanna* sp., *Shinkailepas tufari, Shinkailepas* sp., *Symmetromphalus hageni.*

References. Hashimoto et al. (1999).

Manus Back-Arc Basin: DESMOS Cauldron

Position. Bismarck Sea, north of New Britain, 03°41.75'S, 151°52.30'E, 2000 m.

Expedition. BIOACCESS '96 and '98 with submersible *Shinkai 2000.*

Type of locality. Hydrothermal vents.

Gastropod fauna. Hashimoto et al. (1999): *Bathyacmaea jonassoni, Lepetodrilus schrolli, Lepetodrilus* sp., "*Margarites*" sp., *Phymorhynchus starmeri, Provanna* sp., "unidentified limpet."

References. Hashimoto et al. (1999).

North Fiji Basin

Position. West of Fiji, 17–18.8°S, 173.5-174°W, 1955–2000 m.

Expedition 1. STARMER 2, chief scientists D. Desbruyères & S. Ohta.

Samplings. PL 10–16, PL 20–21, La Dame Blanche, 16°59.50'S, 173°55.47'W, 2000 m; PL 18–19, La Vallée des Moules, 18°50'S, 173°29'W, 2765 m.

Expedition 2. YOKOSUKA, chief scientists T. Urabe and E. Ruellan; dives with Shinkai 6500 September and October 1991.

Samplings. West of Fiji; PL 05, PL 07, PL 92, 16°59.4S, 173°54.9'E, 1966 m, (La Dame Blanche); PL 12, 18°50.59'S, 173°29.89'E, 2750 m (Sunset site).

Expedition 3. SONNE 99. Samplings made with a TV-monitored dredge, 1995.

Type of locality. White Lady and Sunset sites are hydrothermal vents with gastropods, cirripeds, Vestimentifera, *Bathymodiolus.*

Gastropod fauna. Listed by Warén & Bouchet (1993), Okutani & Ohta (1993), and Beck (1996b): 1 species of limpet, *Alviniconcha hessleri, Bruceiella globulus,* Buccinidae sp., *Desbruyeresia cancellata, D. spinosa, Eosipho desbruyeresi, Gymnobela* sp., *Ifremeria nautilei, Lepetodrilus schrolli* [originally as *L. elevatus*], *Olgasolaris* sp., *Pachydermia sculpta, Phymorhynchus hyfifluxi, P. starmeri, Provanna buccinoides, Symmetromphalus* cf. *regularis, Vetulonia phalcata, Xylodiscula major.*

Comments. Additional species will be reported by Beck (in press).

References. Auzende et al. (1992), Jollivet et al. (1989), Desbruyères et al. (1994b).

Lau Basin

Position. Northwest of Tongatapu, Ride de Valufa, ca. 22°S, 177°W, 1900–1750 m.

Expedition. BIOLAU 89, chief scientist A.-M. Alayse, 1989.

Samplings. PL 01–3, PL 05, PL 07 (Hine Hina, a site with no smokers, 22°32'S, 176°43'W, 1900 m), PL 04, PL 06, 09–12 (Vai Lili, a site with smokers, 22°13'S, 176°36.5'W, 1750 m).

Type of locality. Hydrothermal vents with gastropods, cirripeds, Vestimentifera, *Bathymodiolus.*

Gastropod fauna. Listed by Warén & Bouchet (1993) and Okutani & Ohta (1993): *Alviniconcha hessleri, Anatoma* sp., *Bruceiella globulus,* Cocculiniformia sp., Columbellidae sp., *Desbruyeresia cancellata, D. melanioides, Eosipho desbruyeresi, Helicrenion reticulatum, Hyalogyra vitrinelloides, Ifremeria nautilei, Lepetodrilus schrolli* [originally as *L. elevatus*], *Leptogyra inflata, Olgasolaris* sp., *Pachydermia sculpta,* Patellogastropoda sp., Peltospirid sp. A, *Planorbidella depressa, Provanna buccinoides, P. segonzaci, Pseudorimula* cf. *marianae, Shinkailepas* aff. *kaikatensis, Symmetromphalus* cf. *regularis,* Turrid sp., unidentified Cephalaspid, *Ventsia tricarinata.*

Comments. Additional species will be reported by Beck (in press).

References. Desbruyères et al. (1994b).

New Zealand

Several cold seeps fields have been infered from mollusk faunas (including *Calyptogena* and *Bathymodiolus*) collected by dredging and trawling, but so far these have not been surveyed by manned submersibles.

References. Lewis & Marshall (1996), Marshall (personal communication).

Position. Ritchie Ridge, 39°26'S, 178°24'E, 1100–1200 m.

Gastropod fauna. Limpet sp., ?*Tentaoculus* sp., *Provanna* sp. A. *Provanna* sp. B, ?*Hyalogyrina* sp., *Xylodiscula* sp., *Lurifax* sp., *Laeviphitus* sp. [as *Odostomia* sp.].

Position. Puysegur Bank, 46°58'S, 165°25'E, 960 m.

Gastropod fauna. ?*Provanna* sp. C, *Laeviphitus* sp. B.

Appendix 2

List of gastropods from hydrothermal vents and seeps, arranged alphabetically by genus name.

Species	Family/higher taxon	Type of locality	Locality
Adeuomphalus ***trochanter,*** sp. nov.	Vetigastropoda	vent	JdF
Alvania stenolopha Bouchet & Warén, 1993	Rissoidae	vent?	MAR: 37–38°N
Alviniconcha hessleri Okutani, 1988	Provannidae	vent	WP: Marianas, Manus, Fiji, Lau
Amphiplica gordensis McLean, 1991	Cocculiniformia	vent	Gorda Ridge
Bathyacmea jonassoni Beck, 1996	Pectinodontinae	vent	WP: Edison Seamount, Manus
Bathyacmaea nadinae Beck, in press	Pectinodontinae	vent	WP: Fiji
Bathyacmea nipponica Okutani, Tsuchida & Fujikura, 1992	Pectinodontinae	seep	Sagami Bay
Bathyacmea secunda Okutani, Fujikura & Sasaki, 1993	Pectinodontinae	vent	WP: Okinawa Basin
Bathybela ***papyracea,*** sp. nov.	Conidae	seep	Jalisco Block
Bathymargarites symplector Warén & Bouchet 1989	Trochidae	vent	EPR: 13°N–17°S
Bathynerita naticoidea Clarke, 1989	Neritoidea	seep	Louisiana Slope, Barbados Prism
Bayerius arnoldi (Lus, 1985)	Buccinidae	seep	Aleutian Trench
Bayerius ***peruvianus,*** sp. nov.	Buccinidae	seep	Off Peru
Bayerius sp.	Buccinidae	seep	Jalisco Block Seeps
Bruceiella globulus Warén & Bouchet, 1993	Skeneidae	vent	Fiji, WP
Bruceiella ***athlia,*** sp. nov.	Skeneidae	seep	Aleutian Trench
Buccinum soyomaruae Okutani, 1977	Buccinidae	seep?	Sagami Bay
Buccinum sp. (*viridis* Dall, 1890?)	Buccinidae	vent?	JdF
Cancellaria rosewateri Petit, 1983	Cancellariidae	seep	Louisiana Slope
Cantrainea jamsteci (Okutani & Fujikura, 1990)	Turbinidae	vent	WP: Okinawa Basin
Cantrainea macleani Warén & Bouchet, 1993	Turbinidae	seep	Louisiana Slope
Cataegis meroglypta McLean & Quinn, 1987	Trochidae	seep	Louisiana Slope, Barbados Prism
Clathrosepta becki McLean & Geiger, 1998	Fissurellidae	vent	WP: Manus
Clathrosepta depressa McLean & Geiger, 1998	Fissurellidae	vent	EPR: 13°N
Clypeosectus curvus McLean, 1989	Lepetodrilidae	vent	JdF
Clypeosectus delectus McLean, 1989	Lepetodrilidae	vent	EPR: 21°N–17°S, Galapagos Rift
Cornisepta levinae McLean & Geiger, 1998	Fissurellidae	vent	EPR: 13°N
Cornisepta verenae McLean & Geiger, 1998	Fissurellidae	vent	JdF
Ctenopelta porifera Warén & Bouchet, 1993	Peltospiridae	vent	EPR: 13°N
Cyathermia naticoides Warén & Bouchet, 1989	Neomphalidae	vent	EPR: 21°–10°N
Dendronotus comteti Valdes & Bouchet, 1998	Dendronotidae	vent	MAR: 37°N
Depressigyra globulus Warén & Bouchet, 1989	Peltospiridae	vent	JdF
Desbruyeresia cancellata Warén & Bouchet, 1993	Provannidae	vent	WP: Fiji, Lau
Desbruyeresia marianaensis (Okutani, 1990)	Provannidae	vent	WP: Marianas
Desbruyeresia melanioides Warén & Bouchet, 1993	Provannidae	vent	WP: Lau, Manus
Desbruyeresia spinosa Warén & Bouchet, 1993	Provannidae	vent	WP: Fiji
Desbruyeresia sp. aff. *spinosa*	Provannidae	vent	WP: Marianas
Echinopelta fistulosa McLean, 1989	Peltospiridae	vent	EPR: 21°–13°N
Eosipho ***auzendei,*** sp. nov.	Buccinidae	vent	EPR: 17°S
Eosipho canetae (Clench & Aguayo, 1944)	Buccinidae	seep	Louisiana Slope
Eosipho desbruyeresi Okutani & Ohta, 1993	Buccinidae	vent	WP: Fiji, Lau, Manus
Eulepetopsis vitrea McLean, 1990	Neolepetopsidae	vent	EPR: 21°N–17°S, Galapagos Rift
Falsimargarita ***nauduri,*** sp. nov.	Trochidae	vent	EPR: 17°S
Fucaria ***mystax,*** sp. nov.	Trochidae	vent	WP: Edison Seamount
Fucaria striata Warén & Bouchet, 1993	Trochidae	vent	JdF
Fucaria sp.	Trochidae	seep	Florida Escarpment
Fumocapulus alaysae Beck, in press	Peltospiridae	vent	WP: Fiji
Gaza fischeri Dall, 1889	Trochidae	seep	Louisiana Slope
Gorgoleptis emarginatus McLean, 1988	Lepetodrilidae	vent	EPR: 21°–13°N
Gorgoleptis patulus McLean, 1988	Lepetodrilidae	vent	Galapagos Rift
Gorgoleptis spiralis McLean, 1988	Lepetodrilidae	vent	EPR: 13°N
Gymnobela extensa (Dall, 1881)	Conidae	seep	Louisiana Slope
Gymnobela sagamiana (Okutani & Fujikura, 1992)	Conidae	seep	Sagami Bay

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Continued.

Species	Family/higher taxon	Type of locality	Locality
Gymnobela sp. A	Conidae	vent	EPR: 13°N
Gymnobela (?) sp. B	Conidae	vent	MAR: 23°N
Helicrenion reticulatum Warén & Bouchet, 1993	Trochidae	vent	WP: Lau
Hirtopelta hirta McLean, 1989	Peltospiridae	vent	EPR: 21°–13°N
Hyalogyra vitrinelloides Warén & Bouchet, 1993	Hyalogyrinidae	vent	WP: Lau
Hyalogyrina ***globularis,*** sp. nov.	Hyalogyrinidae	vent	JdF
Hyalogyrina grasslei Warén & Bouchet, 1993	Hyalogyrinidae	seep	Guaymas
Hyalogyrina ***umbellifera,*** sp. nov.	Hyalogyrinidae	seep	Aleutian Trench
Hyalogyrina? sp.	Hyalogyrinidae	seep	New Zealand
Hyalorisia galea (Dall, 1889)	Capulidae	seep	Louisiana Slope
Ifremeria nautilei Bouchet & Warén, 1991	Provannidae	vent	WP: Manus, Fiji, Lau
Lacunoides exquisitus Warén & Bouchet, 1989	Neomphalidae	vent	Galapagos Rift
Lacunoides ***vitreus,*** sp. nov.	Neomphalidae	vent	JdF
Laeviphitus ***desbruyeresi,*** sp. nov.	Elachisinidae	vent	MAR
Laeviphitus japonicus Okutani, Fujikura & Sasaki, 1993	Elachisinidae	vent	WP: Kaikata Seamount
Laeviphitus sp.	Elachisinidae	seep	New Zealand
Laeviphitus sp. (veligers only)	Elachisinidae	vent	EPR: 10°N
Lepetodrilus ***atlanticus,*** sp. nov.	Lepetodrilidae	vent	MAR: 38°–23°N
Lepetodrilus corrugatus McLean, 1993	Lepetodrilidae	vent	JdF
Lepetodrilus cristatus McLean, 1988	Lepetodrilidae	vent	EPR: 21°–13°N, Galapagos Rift
Lepetodrilus elevatus McLean, 1988	Lepetodrilidae	vent	EPR: 21°N–17°S, Galapagos Rift WP: Fiji, Lau
Lepetodrilus fucensis McLean, 1988	Lepetodrilidae	vent	JdF
Lepetodrilus guaymasensis McLean, 1988	Lepetodrilidae	seep	Guaymas Basin
Lepetodrilus japonicus Okutani, Fujikura & Sasaki, 1993	Lepetodrilidae	vent	WP: Okinawa Basin
Lepetodrilus nux (Okutani, Fujikura & Sasaki, 1993)	Lepetodrilidae	vent	WP: Okinawa Basin
Lepetodrilus ovalis McLean, 1988	Lepetodrilidae	vent	EPR: 21°N–17°S, Galapagos Rift
Lepetodrilus pustulosus McLean, 1988	Lepetodrilidae	vent	EPR: 21°N–17°S, Galapagos Rift
Lepetodrilus schrolli Beck, 1993	Lepetodrilidae	vent	WP: Manus
Lepetodrilus tevnianus McLean, 1993	Lepetodrilidae	vent	EPR: 11°N
Lepetodrilus sp.	Lepetodrilidae	vent	WP: Manus
Leptogyra inflata Warén & Bouchet, 1993	Skeneidae	vent	WP: Lau
Lirapex ***costellata,*** sp. nov.	Peltospiridae	vent	MAR: 37°N
Lirapex granularis Warén & Bouchet, 1993	Peltospiridae	vent	EPR: 21°–10°N
Lirapex humata Warén & Bouchet, 1989	Peltospiridae	vent	EPR: 21°N
Lirapex sp.	Peltospiridae	vent	MAR: 23°N
Lurifax vitreus, gen. et sp. nov.	Orbitestellidae	vent	MAR: 38°–36°N
Lurifax sp.	Orbitestellidae	seep	New Zealand
Margarites shinkai Okutani, Tsuchida & Fujikura, 1992	Trochidae	seep	Sagami Bay
Margarites sp.	Trochidae	vent	WP: Manus
Melanodrymia aurantiaca Hickman, 1984	Neomphalidae	vent	EPR: 21°N–17°S
Melanodrymia brightae Warén & Bouchet, 1993	Neomphalidae	vent	JdF
Melanodrymia ***galeronae,*** sp. nov.	Neomphalidae	vent	EPR: 13°N
Melanodrymia "rust covered"	Neomphalidae	vent	EPR: 13°N
Melanodrymia sp.	Neomphalidae	vent	Galapagos Rift
Moelleriopsis sp.	Trochidae	vent	EPR: 13°N
Neolepetopsis densata McLean, 1990	Neolepetopsidae	vent	EPR: 13°–12°N, Galapagos Rift
Neolepetopsis gordensis McLean, 1990	Neolepetopsidae	seep, vent	Gorda Ridge, Jaliso Block, Peru
Neolepetopsis occulta McLean, 1990	Neolepetopsidae	vent	EPR: 21°N
Neolepetopsis verruca McLean, 1990	Neolepetopsidae	vent	EPR: 21°N
Neomphalus fretterae McLean, 1981	Neomphalidae	vent	EPR: 21°–10°N, Galapagos Rift
Neptunea acutispiralis Okutani, Fujikura & Sasaki, 1993	Buccinidae	seep?	Sagami Bay
Neptunea insularis (Dall, 1895)	Buccinidae	vent?	WP: Okinawa Basin

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Species	Family/higher taxon	Type of locality	Locality
Neusas gen nov. *marshalli* (Sykes, 1925)	Vitrinellidae	vent?	MAR: 38°N
Nodopelta heminoda McLean, 1989	Peltospiridae	vent	EPR: 21°–13°N
Nodopelta ***rigneae,*** sp. nov.	Peltospiridae	vent	EPR: 13°N
Nodopelta subnoda McLean, 1989	Peltospiridae	vent	EPR: 13°N–17°S
Oenopota ogasawarana Okutani, Fujikura & Sasaki, 1993	Conidae	vent	WP: Kaikata Seamount
Olgasolaris ethmoconcha Beck, in press	Neritoidae	vent	Fiji: VP
Olgasolaris tollmanni Beck, 1992	Neritoidea	vent	WP: Manus
Pachydermis laevis Warén & Bouchet, 1989	Neomphalidae	vent	EPR: 21°N–17°S
Pachydermia sculpta Warén & Bouchet, 1993	Neomphalidae	vent	WP: Fiji, Lau
Pachydermia sp. aff. *sculpta*	Neomphalidae	vent	WP: Marianas
Paralepetopsis ***ferrugivora,*** sp. nov.	Neolepetopsidae	vent	MAR: 37°N
Paralepetopsis floridensis McLean, 1990	Neolepetopsidae	seep	Florida Escarpment
Paralepetopsis ***lepichoni,*** sp. nov.	Neolepetopsidae	seep	Nankai Trough
Paralepetopsis rosemariae Beck, 1996	Neolepetopsidae	vent	WP: Edison Seamount
Peltospira delicata McLean, 1989	Peltospiridae	vent	EPR: 13°–10°N
Peltospira lamellifera Warén & Bouchet, 1989	Peltospiridae	vent	EPR: 13°N
Peltospira operculata McLean, 1989	Peltospiridae	vent	EPR: 21°–10°N
Peltospira ***smaragdina,*** sp. nov.	Peltospiridae	vent	MAR: 38°–15°N
Phymorphynchus aff. *alberti* (Dautzenberg & Fischer, 1906)	Conidae	seep	Barbados Prism
Phymorhynchus buccinoides Okutani, Fujikura & Sasaki, 1993	Conidae	seep	Sagami Bay
Phymorhynchus ***carinatus,*** sp. nov.	Conidae	vent	MAR: 23°–15°N
Phymorphynchus hyfifluxi Beck, 1996	Conidae	vent	WP: Fiji
Phymorphynchus ***major,*** sp. nov.	Conidae	vent	EPR
Phymorhynchus moskalevi Sysoev & Kantor, 1995	Conidae	vent	MAR: 26°–23°N
Phymorhynchus ***ovatus,*** sp. nov.	Conidae	vent	MAR: 37°–15°N
Phymorhynchus starmeri Okutani & Ohta, 1993	Conidae	vent	WP: Fiji, Manus
Phymorhynchus wareni Sysoev & Kantor, 1995	Conidae	vent	WP: Edison Seamount
Planorbidella depressa Warén & Bouchet, 1993	Neomphalidae	vent	WP: Lau
Planorbidella planispira (Warén & Bouchet, 1989)	Neomphalidae	vent	EPR: 21°–13°N
Protolira thorvaldssoni Warén, 1996	Skeneidae	vents, whale bone	MAR: 38°–36°N
Protolira valvatoides Warén & Bouchet, 1993	Skeneidae	vent	MAR: 38°–37°N
Provanna admetoides Warén & Ponder, 1991	Provannidae	seep	Florida Escarpment
Provanna buccinoides Warén & Bouchet, 1993	Provannidae	vent	WP: Fiji, Lau, Manus
Provanna glabra Okutani, Tsuchida & Fujikura, 1992	Provannidae	seep, vent	WP: Sagami Bay, Okinawa Basin
Provanna goniata Warén & Bouchet, 1986	Provannidae	seep	Guaymas Basin
Provanna ios Warén & Bouchet, 1986	Provannidae	vent	EPR: 21°N–17°S, Galapagos Rift
Provanna laevis Warén & Ponder, 1991	Provannidae	vent, seep	JdF, Oregon Margin, Guaymas Basin,
Provanna lomana (Dall, 1918)	Provannidae	seep	Oregon Margin
Provanna macleani Warén & Bouchet, 1989	Provannidae	seep	Oregon Margin
Provanna muricata Warén & Bouchet, 1986	Provannidae	vent	EPR: 21°N, Galapagos Rift
Provanna nassariaeformis Okutani 1990	Provannidae	vent	WP: Marianas, Manus
Provanna sculpta Warén & Ponder, 1991	Provannidae	seep	Louisiana Slope
Provanna segonzaci Warén & Ponder, 1991	Provannidae	vent	WP: Lau
Provanna variabilis Warén & Bouchet, 1986	Provannidae	vent, seep	JdF, Gorda Ridge, Oregon Margin
Provanna sp. 1	Provannidae	vent	WP: Edison Seamount, Manus
Provanna sp. 2	Provannidae	seep	Aleutian Trench
Provanna sp. 3	Provannidae	vent	Jalisco Block
Provanna spp.	Provannidae	seep	New Zealand
Pseudorimula leisei Beck, in press	Lepetodrilidae	vent	WP: Fiji
Pseudorimula marianae McLean, 1989	Lepetodrilidae	vent	WP: Marianas
Pseudorimula midatlantica McLean, 1992	Lepetodrilidae	vent	MAR: 37°–15°N
Puncturella parvinobilis Okutani, Fujikura & Sasaki, 1993	Fissurellidae	vent	WP: Okinawa Basin

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Species	Family/higher taxon	Type of locality	Locality
Puncturella rimaizenaensis Okutani, Fujikura & Sasaki, 1993	Fissurellidae	vent	WP: Okinawa Basin
Puncturella solis Beck, 1996	Fissurellidae	vent	WP: Edison Seamount
Pyropelta bohlei Beck, 1996	Cocculiniformia	vent	WP: Edison Seamount
Pyropelta corymba McLean & Haszprunar, 1987	Cocculiniformia	seep, biogenic substrates	Oregon Margin, Guaymas
Pyropelta musaica McLean & Haszprunar, 1987	Cocculiniformia	seep, vent, biogenic substrates	JdF, Jalisco Block
Retiskenea diploura, gen. et sp. nov.	Neomphalidae	seep	Aleutian Trench
Retiskenea sp.	Neomphalidae	seep	Oregon Margin
Rhynchopelta concentrica McLean, 1989	Peltospiridae	vent	EPR: 21°N–17°S
Sahlingia xandaros, gen. et sp. nov.	Vetigastropoda	seep	Aleutian Trench
Serradonta vestimentifericola Okutani, Tsuchida & Fujikura, 1992	Pectinodontinae	seep	Sagami Bay
Shinkailepas ***briandi,*** sp. nov.	Neritoidea	vent	MAR: 38°–15°N
Shinkailepas conspira Beck, in press	Neritoidea	vent	WP: Fiji
Shinkailepas kaikatensis Okutani, Saito & Hashimoto, 1989	Neritoidea	vent	WP: Kaikata Seamount
Shinkailepas tufari Beck, 1992	Neritoidea	vent	WP: Manus
Shinkailepas sp.	Neritoidea	vent	WP: Manus
Solutigyra reticulata Warén & Bouchet, 1989	Neomphalidae	vent	EPR: 21°–13°N
Speculator cariosus, gen. et sp. nov.	Cerithiopsidae	vent	JdF
Sutilizona ***pterodon,*** sp. nov.	Sutilizonidae	vent	MAR: 37°–23°N
Sutilizona theca McLean, 1989	Sutilizonidae	vent	EPR: 13°N
Sutilizona ***tunnicliffae,*** sp. nov.	Sutilizonidae	vent	JdF
Symmetriapelta wareni Beck, in press	Peltospiridae	vent	WP: Fiji
Symmetromphalus hageni Beck, 1992	Neomphalidae	vent	WP: Manus
Symmetromphalus macleani Beck, in press	Neomphalidae	vent	WP: Fiji
Symmetromphalus regularis McLean, 1990	Neomphalidae	vent	WP: Marianas
Temnocinclis euripes McLean, 1989	Sutilizonidae	vent	JdF
Temnozaga parilis McLean, 1989	Sutilizonidae	vent	EPR: 21°N
Tentaoculus? sp.	Cocculiniformia	seep	New Zealand
Tractolira sparta Dall, 1896	Volutidae	seep	Peru
Trophon sp. 1	Muricidae	seep	Barbados Prism
Trophon sp. 2	Muricidae	seep	Barbados Prism
Ventsia tricarinata Warén & Bouchet, 1993	Trochidae	vent	WP: Lau
Vetulonia phalcata Warén & Bouchet, 1993	Trochidae	vent	WP: Fiji
Ventsia sp. aff. *tricarinata*	Trochidae	vent	WP: Marianas
Xylodiscula ***analoga,*** sp. nov.	Xylodisculidae	vent	MAR: 37°–36°N
Xylodiscula major Warén & Bouchet, 1993	Xylodisculidae	vent	WP: Fiji
Xylodiscula sp.	Xylodisculidae	seep	New Zealand