

NEW ARCHAEOGASTROPOD LIMPETS
FROM HYDROTHERMAL VENTS;
SUPERFAMILY LEPETODRILACEA
I. SYSTEMATIC DESCRIPTIONS

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Nine new species, six in the new genus *Lepetodrilus* and three in the new genus *Gorgoleptis*, are proposed in two new families, which together compose the new archaeogastropod superfamily Lepetodrilacea, as yet known only from the deep-sea hydrothermal-vent habitat in the eastern Pacific.

Shells are limpet-shaped, of non-nacreous aragonite, with tough periostracum enveloping the shell edge. The apex is posterior, in some species projecting posteriorly, and deflected to the right. Sculpture is lacking or of beads or imbricate radial ribs. The muscle scar is horseshoe-shaped and narrowed posteriorly. The radula is rhipidoglossate and unique in forming a V-alignment of lateral teeth descending toward the rachidian. The families differ in morphology of the first lateral tooth, morphology of the ctenidium, and in placement of the penis: on the right ventral side of the neck in Lepetodrilidae and an outgrowth of the left oral region in Gorgoleptidae. Gorgoleptidae further differ in retaining the operculum and in having a posterior periostracal band shielding the posterior viscera and extending adjacent to the operculum. Anatomy is treated in part II by Fretter (*Phil. Trans. R. Soc. Lond. B* 318, 33 (1988)).

Three species (*L. pustulosus*, the type species of *Lepetodrilus*, *L. elevatus* and *L. cristatus*) are known from the Galapagos Rift and two sites on the East Pacific Rise, near 21° N and 13° N. One species, *L. ovalis*, is known from the two sites along the East Pacific Rise. The remaining species are as yet known only from single sites: *L. guaymasensis* from the Guaymas Basin, *L. fucensis* from the Juan de Fuca and Explorer Ridges, *G. emarginatus* from 21° N, *G. spiralis* from 13° N, and *G. patulus* from the Galapagos Rift. Only one of the broadly distributed species, *L. elevatus*, exhibits sufficient geographical variation to warrant the recognition of a subspecies, *L. elevatus galriftensis*, n. subsp., at the Galapagos Rift. These species are known only from sites exposed to warm hydrothermal effluent, not from the hotter environments of the black smokers or from cold sulphide seeps.

Shell characters are most similar to the 'tapersnout' superfamily, yet to be described, from which these species differ in having pitted sculpture on the protoconch. The Jurassic to early Cretaceous Symmetrocipulidae had similar shell proportions but were much larger; the Symmetrocipulidae are best considered an archaeogastropod sister group.

The hydrothermal-vent habitat has been available throughout geological time; hydrogen sulphide toxicity should prevent invasions of new kinds of predators, thus promoting stability and longevity of species established in this community. Differences from other archaeogastropods at the superfamily level suggest that the origin of the Lepetodrilacea took place in the late Palaeozoic to early Mesozoic, the time at which other living archaeogastropod superfamilies appeared. The rift-vent habitat was most likely entered via shallow to successively deeper sites along ridge crests. Unique anatomies and radular characters are considered remnants of early archaeogastropod diversity from the period in which archaeogastropods were the dominant gastropods in shallow seas.

INTRODUCTION

The recently discovered deep-sea hydrothermal-vent communities have yielded a remarkable number of new higher taxa of invertebrates endemic to these communities (Newman 1985). Molluscs are well represented in the rift-vent habitat and the gastropods are dominated in numbers of species by those of limpet form, all of which are members of new groups endemic to this environment. The first of the new limpets to be described was the unique *Neomphalus fretterae* from the Galapagos Rift (McLean 1981; Fretter *et al.* 1981). *Neomphalus* has by now been found at other hydrothermal sites on the East Pacific Rise (at 13° N and 21° N), but the family Neomphalidae remains monotypic. Unlike *Neomphalus*, the additional new limpet

families have radiated in the rift-vent habitat, having members that are known from the Galapagos Rift and two broadly separated sites on the East Pacific Rise at 13° N and 21° N, as well as species apparently endemic to other, more isolated sites.

The presence in the hydrothermal-vent community of three more archaeogastropod limpet groups that cannot be assigned to currently recognised superfamilies has been noted by Hickman (1983), who illustrated radulae typical of each group. A preliminary account of these new superfamilies (McLean 1985) summarized the findings from the anatomical work then under way by Fretter, and gave a table showing the occurrence of 21 additional new species to be described, with vernacular names for the families and species.

This paper gives the systematic descriptions for two families in the new superfamily Lepetodrilacea. The familial and superfamilial diagnoses of the new taxa include basic information about the anatomy, summarized from Fretter (1988) (hereafter referred to as part II), which treats the anatomy of this group, its probable mode of life inferred from anatomy, and the affinity to other living gastropods. Relationships based on shell characters, and potential affinity to fossil groups are discussed in this part.

Members of this superfamily have earlier been mentioned by Hickman (1983) as the 'Group-B' limpets and by McLean (1985) as the 'dimorphic' hydrothermal-vent limpets. Unlike two new superfamilies remaining to be described (the Group-A ('tapersnout') and Group-C ('symmetrical') limpets), the Lepetodrilacea are characterized by sexual dimorphism in the external anatomy, hence the vernacular name. Protoconchs and immature shells of unidentified lepetodrilacean limpets and other hydrothermal-vent limpets and coiled gastropods were illustrated by Turner & Lutz (1984), Turner *et al.* (1985), and Lutz *et al.* (1986); these authors also addressed the potential for larval dispersal in hydrothermal-vent gastropods.

MATERIAL

Material of the nine species here described was collected from five, broadly separated, hydrothermal-vent fields in the eastern Pacific between the years 1977 and 1984. Material from four of the sites (Galapagos Rift, East Pacific Rise at 21° N, Guaymas Basin and Juan de Fuca Ridge) was collected during dives of the deep submersible *Alvin*, operated by the Woods Hole Oceanographic Institution under National Science Foundation sponsorship. I am also privileged to include material from the French expeditions to the East Pacific Rise at 13° N, collected with the submersible *Cyana*, and material from the joint expeditions of the University of British Columbia and the University of Washington to the Juan de Fuca and Explorer Ridges off British Columbia, Washington and Oregon, collected with the submersible *Pisces IV*. Jones *et al.* (1985) gave station data for all relevant dives made by these submersibles. The voluminous literature to date treating the geology and biology of hydrothermal vents has been compiled in a bibliography by Jones & Bright (1985).

The earliest discovered vent field, the Galapagos Rift, was first visited in February 1977 (*Alvin* dives 723–733), and subsequently in January–February 1979 (*Alvin* dives 877–896), and November–December 1979 (*Alvin* dives 983–993). The initial account of the biota at the Galapagos Rift was given by Corliss *et al.* (1979). Hessler & Smithey (1983) discussed ecological relationships at the Galapagos Rift. Limpets were noted by these authors but could not be distinguished by species from their photographs of bottom features. A total of seven limpet species were reported from the Galapagos Rift by McLean (1985). Four of these are

lepetodrilacean limpets described herein. Three of these also occur at both sites on the East Pacific Rise and one, *Gorgolettis patulus*, is known only from the Galapagos Rift.

The next discovered site, near 21° N on the East Pacific Rise, was first visited in November 1979 (Rise Expedition, *Alvin* dives 976–981); this site was again visited in April–May 1982 (Oasis Expedition, *Alvin* dives 1209–1230). The initial account of the biological community was that of Spiess *et al.* (1980); Hessler *et al.* (1985) discussed ecological relationships. Again, the limpet species could not be identified from bottom photographs. This is one of the two richest sites for limpet species. Fourteen limpet species were reported by McLean (1985); five of these are lepetodrilacean species described herein; three of these also occur at the Galapagos Rift and four occur also at 13° N on the East Pacific Rise. One, *Gorgolettis emarginatus*, is known only from 21° N.

The site near 13° N on the East Pacific Rise was first visited in March 1982 (Biocyatherm Expedition, *Cyana* dives 82–33 to 82–36), and again in March 1984 (Biocyarise Expedition, *Cyana* dives 84–32 to 84–38). General accounts are given by Desbruyères *et al.* (1982) and Desbruyères & Laubier (1983). This site on the East Pacific Rise also has 14 limpet species (McLean 1985), of which five are lepetodrilaceans, three of these also occurring at the Galapagos Rift and four at 21° N. One, *Gorgolettis spiralis*, is known only from this site.

The Guaymas Basin site was visited in January 1982 (*Alvin* dives 1168–1177). Lonsdale (1984) reported upon the biological community at this site. Two limpets are known (McLean 1985); the new lepetodrilacean species, *Lepetodrilus guaymasensis*, has not been found elsewhere.

The Juan de Fuca Ridge off Washington was explored at Axial Seamount in August 1983 (*Pisces IV* dives 1320–1327), and the Explorer Ridge off British Columbia was visited in June–August 1984 (*Pisces IV* dives 1488–1506). Further exploration of the Juan de Fuca Ridge was done by the *Alvin* in July–September 1984 (dives 1409–1454). General accounts of these expeditions are those of Chase *et al.* (1985) and Tunnicliffe *et al.* (1985). Two limpets are known; the one new lepetodrilacean species, *Lepetodrilus fucensis*, has not been found elsewhere.

Except at the sites on the Juan de Fuca and Explorer Ridges, many of the limpets and other small invertebrates were collected with specimens of the large vestimentiferan tube worm *Riftia pachyptila* Jones, 1981, which had been removed from the hydrothermal-vent habitat with the mechanical arms of the submersibles. Additional specimens were collected from rubble samples or were attached to the vesicomid clam *Calyptogena magnifica* Boss & Turner, 1980 or the mytilid *Bathymodiolus thermophilus* Kenk & Wilson, 1985.

Specimens were dead on reaching the surface and were originally fixed for 24 h in seawater formalin (10% by volume) buffered with sodium borate, washed in freshwater and transferred to ethanol (70% by volume). Preserved specimens collected by the *Alvin* were sorted and counted at Woods Hole Oceanographic Institution, after which the limpets were sent to me.

Transverse and sagittal histological sections were prepared at the Los Angeles County Museum of Natural History and loaned to V. Fretter for her work on the anatomy. Radulae were examined by scanning electron microscopy (SEM), for which they were prepared by air drying and coating with gold palladium. Juvenile shells and protoconchs were examined by SEM, without removal of organic and inorganic encrustations. Protoconch lengths were taken directly from the SEM micrographs.

Photographs of dorsal and ventral surfaces of limpet bodies are included in this paper to make the photographic record complete. Although the external structures and organs are not

identified in captions herein, fully labelled drawings of anatomy are given in part II, making it possible to identify all illustrated features.

Shell microstructure is not treated here, as this is being studied by Marie-Pierre Triclot at the Université Paris-Sud Orsay, France, who will report separately on it.

Principal repositories of the major series of type material are the Los Angeles County Museum of Natural History (LACM), the United States National Museum of Natural History (USNM) and the Muséum National d'Histoire Naturelle, Paris (MNHN). Specimens of four of the species are sufficiently numerous to enable the distribution of one or more paratypes of each to the following museums: Academy of Natural Sciences, Philadelphia; American Museum of Natural History, New York; Museum of Comparative Zoology, Harvard University, Cambridge; Field Museum of Natural History, Chicago; California Academy of Sciences, San Francisco; Department of Paleontology, University of California, Berkeley; Scripps Institution of Oceanography, La Jolla; National Museum of Canada, Ottawa; British Museum (Natural History), London; National Museum of Wales, Cardiff; Royal Museum of Scotland, Edinburgh; Zoological Museum, Copenhagen; Swedish Museum of Natural History, Stockholm; Zoological Museum, Amsterdam; Rijksmuseum van Natuurlijke Historie, Leiden; Forschungs-Institut Senckenberg, Frankfurt; Zoological Institute, Academy of Sciences, Leningrad; P. P. Shirshov Institute of Oceanology, Moscow; National Science Museum, Tokyo; Museu Oceanografico, Rio Grande; Museo Argentino de Ciencias Naturales, Buenos Aires; Museo Nacional de Historia Natural, Santiago; South African Museum, Cape Town; Natal Museum, Pietermaritzburg; Australian Museum, Sydney; National Museum of Victoria, Melbourne; Western Australian Museum, Perth; National Museum of New Zealand, Wellington; Auckland Institute and Museum, Auckland.

SYSTEMATIC DESCRIPTIONS: LEPETODRILACEA, NEW SUPERFAMILY

Description

Shell of limpet form, bilaterally symmetrical except for early stage; anterior slope long, convex; apex posterior, below highest elevation, slightly to strongly projecting, slightly to strongly offset toward right. Protoconch small, maximum length 130 μm , surface with sculpture of fine pitting; protoconch II lacking, mature sculpture of teleoconch arising directly; teleoconch with brief coiled phase. Shell structure of lamellar aragonite; nacreous interior lacking. Periostracum thick, enveloping shell edge. Sculpture of imbricate radial ribs, diverging rows of beads, or lacking. Muscle scar paired, either connected or interrupted posteriorly.

Radula rhipidoglossate, lateral teeth 5 pairs, alignment of inner lateral teeth in descending V. Rachidian tooth with broad shaft, the main cusp relatively small and sharp pointed. First lateral large with broad shaft and numerous denticles; four remaining laterals with long, tapered cusps, interlocked by lateral extensions on shafts and having bend at mid-height to accommodate cusps of laterals in row behind. Lateromarginal plates lacking. Marginals numerous.

Epipodial appendages and placement of penis varied. Cephalic tentacles long, eyes lacking. Outer fold of mantle thin (to extend under inturned periostracum), inner fold with fine tentacles. Oral disc circular; mouth a Y-shaped vertical slit with short branches; jaws with

protruding chitinous rods. Foot oval, with prominent opening of pedal gland; small operculum present or absent.

Mantle cavity extending to $\frac{3}{4}$ of length enclosed by shell muscle, narrowed posteriorly on left side. Ctenidium bipectinate at anterior free tip, monopectinate and fused to mantle skirt posteriorly.

Nervous system hypoathroid–dystenoid. Heart with two auricles; intestine with anterior loop, rectum passing through ventricle. Left kidney within mantle skirt. Sexes separate, gonad ventralmost in body cavity, discharging through right kidney. Gonoducts varied; fertilization in mantle cavity.

Two families, the Lepetodrilidae and the Gorgoleptidae, each with a single genus, are recognized in the Lepetodrilacea. Six species of *Lepetodrilus* and three of *Gorgoleptis* are known.

The two families differ in configuration of the shell muscles, presence or absence of the operculum, elaboration of the epipodial appendages, detail of gill structure, and structure and position of the penis, as detailed in part II. Such anatomical differences are generally recognized at the family level in other prosobranch gastropods. The affinity of the two families on the basis of shell and radular characters, as well as most features of the internal anatomy, is recognized by uniting the two families within the same superfamily. The Gorgoleptidae, in which juvenile shells are most like those of coiled gastropods, the muscles not continuous posteriorly and the operculum retained, are considered the more primitive family in having more features suggestive of the coiled predecessor (part II).

For comparisons between the shells of these limpets and those of other living and fossil limpet families, see Discussion.

KEY TO THE FAMILIES OF LEPETODRILACEA

- Muscle scar forming horseshoe; penis near base of right cephalic tentacle; operculum lacking . . . Lepetodrilidae
 Muscle scar not forming horseshoe pattern; penis formed by expansion of snout on left side;
 operculum present Gorgoleptidae

LEPETODRILIDAE, NEW FAMILY

With characters of genus.

LEPETODRILUS, NEW GENUS

Type species: *Lepetodrilus pustulosus*, new species.

Description

Shell of limpet form with long, convex anterior slope; apex posterior, below highest elevation, slightly to strongly projecting, slightly to strongly offset toward right; early coiled phase less than one whorl. Protoconch small, maximum length 130 μm ; right side remaining visible; surface with sculpture of fine pitting. Periostracum thick, with broad margin reflected over shell edge. Sculpture of imbricate radial ribs, diverging rows of beads, or lacking. Posterior slope of some species with thickened radial ridge below apex; other species lacking it. Shell

interior with strong transverse ridge in some species; others lacking it. Muscle scar horseshoe-shaped; anterior extremities of scar rounded, left arm slightly longer than right; scar narrow posteriorly, where connected only by narrow band.

Radula rhipidoglossate, rachidian well formed, lateral teeth 5 pairs, marginals numerous. Rachidian broad, shorter than laterals, with long tapered central cusp, edges with 3–5 sharply pointed denticles; rachidian with flat appendage projecting anteriorly above cusp to attach to basal ribbon; shaft with strong lateral projections to articulate with first lateral. First lateral tooth relatively large and oblique, attached below and extending above rachidian, inner edge of cusp aligned with cusp of rachidian, but outer edge rising anteriorly to height of rachidian in row above; entire edge of cusp strongly and sharply denticulate, but having one particularly strong cusp above lateral extension of rachidian. Second, third and fourth laterals similar to each other, with tapered cusps; edges simple or finely denticulate; shafts long, with bend at mid-height to accommodate cusps of laterals in row below; cusp of third lateral the highest and most anteriorly projecting tooth in row. Fifth lateral broader, with larger cusp and stronger denticulation. Marginal teeth numerous, about 18 pairs, shafts flattened, broader at tips; cusps finely denticulate; cusp alignment descending away from rachidian.

Epipodium three pairs of broad, short appendages, pointed at tips, one pair near anterior end of foot, two pairs posteriorly, the anterior and posterior group connected by epipodial fold. Cephalic tentacles long, encircled laterally and ventrally by epipodial folds; eyes lacking. Outer fold of mantle thin (to extend under inturned periostracum); inner fold with fine tentacles. Oral disc broad, mouth a Y-shaped vertical slit with short branches; jaws with protruding chitinous rods. Penis with origin near base of right cephalic tentacle, with deep seminal groove on dorsal side. Foot oval, with prominent opening of pedal gland. Operculum lacking.

Mantle cavity extending $\frac{3}{4}$ of length enclosed by shell muscle, narrowed posteriorly on left side. Ctenidium bipectinate at anterior free tip; lamellae of right side long and slender; lamellae of left side of axis (dorsal side) present only on free tip, short (about $\frac{1}{8}$ length of those on right); ctenidium monopectinate posterior to free tip, fused to mantle skirt. Lamellae of right side aid in food collecting and overlie ciliated tract.

Nervous system hypoathroid–dystenoid. Heart with two auricles; intestine with anterior loop; rectum passing through ventricle; left kidney within mantle skirt. Sexes separate, gonad ventralmost in body cavity, discharging through right kidney. Gonoduct of female with receptaculum seminis, that of male with vesicula seminalis and prostate. Fertilization in mantle cavity.

Remarks

The rachidian and inner lateral tooth elements of the lepetodrilid radula are characterized by the relatively short rachidian and large, oblique inner lateral. Alignment of the cusp rows is unusual: there is major dip in the row at the rachidian, rising to a peak at the third lateral and descending again so that the marginals commence at nearly the same level as the rachidian. Most other rhipidoglossate radulae have the rachidian the highest element in the row. The lepetodrilacean radula is unique, not suggesting comparison with that of other rhipidoglossate groups.

Specific characters in the genus are those of shell sculpture, shell proportions, whether the ends or sides are raised, the presence or absence of a thickened, triangular ridge on the posterior

slope that subtends the protoconch, presence or absence of a transverse posterior ridge on the interior, prominence of the projecting gill lamellae, and the size and morphology of the penis. Radular differences are chiefly those of the enlarged first lateral: the relative breadth of the overhanging cusp and prominence of the major cusps of this tooth. These differences are comparable to those within genera in other families of prosobranchs.

Three species are broadly distributed, known from the three major sites, the Galapagos Rift and the two sites on the East Pacific Rise at 13° N and 21° N; another is known from the two sites on the East Pacific Rise. Collection data for dive stations and numbers of specimens of the four broadly distributed species of *Lepetodrilus* at these three sites are given in table 1. The remaining two species are known only from their more isolated sites, one from the Guaymas Basin and one from the Juan de Fuca Ridge and Explorer Ridges. Dive stations and counts of these two species are given in table 2.

At sites on the East Pacific Rise and the Galapagos Rift, each of the lepetodrilid limpets has been recovered from washings of collections of the large vestimentiferan tube worm *Riftia pachyptila* Jones, 1981. Most species have been taken in such large numbers that there is no doubt that a primary habitat of these limpets is directly on *Riftia*. However, other sampling methods, including washes of the clam *Calyptogena magnifica* Boss & Turner, 1980, and the mussel *Bathymodiolus thermophilus* Kenk & Wilson, 1985, have produced specimens.

Unlike the Galapagos rift limpet *Neomphalus fretterae*, which is sedentary and has the shell margin irregular, the *Lepetodrilus* species, with the possible exception of *L. fucensis*, do not have irregular shell margins and are not inferred to be sedentary. Unfortunately, there are no observations of living animals. Close-up video footage taken at the Galapagos Rift in 1979 shows that the type species *L. pustulosus* is capable of rapid movement along the *Riftia* tubes, although this may have been a response to the bright lighting that was necessary for observation and photography. Some members of this group have shells with raised ends; others have raised sides. Differences of this kind suggest that there are microhabitat differences for each species; however, no observations are available to indicate what these distinctions may be.

Etymology: the name combines the Greek noun *lepas*, limpet, and the Greek noun *drilos*, penis, recognizing the most apparent distinction of the group, which is lacking in other new superfamilies of rift-vent limpets.

KEY TO THE SPECIES OF *LEPETODRILUS*

- | | |
|--|---------------------------------|
| 1. Sculpture of radial ribs, beaded or imbricate | 2 |
| Sculpture lacking | 3 |
| 2. Sculpture of beaded radial ribs | <i>L. pustulosus</i> |
| Sculpture of imbricate radial ribs | <i>L. cristatus</i> |
| 3. Apex $\frac{1}{3}$ shell length from posterior end | <i>L. ovalis</i> |
| Apex near to or extending beyond posterior end | 4 |
| 4. Apex approximately $\frac{1}{10}$ shell length from posterior end | 5 |
| Apex extending beyond posterior end of shell | 6 |
| 5. Shell height approximately $\frac{1}{2}$ shell length | <i>L. elevatus elevatus</i> |
| Shell height approximately $\frac{1}{3}$ shell length | <i>L. elevatus galriftensis</i> |
| 6. Apex medial or nearly so | <i>L. guaymasensis</i> |
| Apex markedly displaced to the right | <i>L. fucensis</i> |

Lepetodrilus pustulosus, new species

(Figures 1–4, plate 1, and figures 25–35, plates 5 and 6; part II, figures 1–6)

LIMPETS FROM HYDROTHERMAL VENTS

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TABLE 1. STATION DATA AND NUMBER OF SPECIMENS FROM DIVES YIELDING THE FOUR BROADLY DISTRIBUTED *LEPETODRILUS* SPECIES

dive	depth/m	position	date	<i>pustulosus</i>	<i>elevatus</i>	<i>ovalis</i>	<i>cristatu</i>
<i>Alvin</i> dives, Galapagos Rift							
733	2496	00° 47.3' N, 86° 07.8' W	16 Mar. 1977	8	—	—	—
879	2495	00° 48.2' N, 86° 04.1' W	20 Jan. 1979	—	2	—	—
880	2493	00° 47.6' N, 86° 06.4' W	21 Jan. 1979	209	—	—	—
883	2493	00° 47.0' N, 86° 08.0' W	24 Jan. 1979	—	1	—	—
884	2482	00° 48.1' N, 86° 07.0' W	25 Jan. 1979	125	955	—	—
887	2488	00° 48.5' N, 86° 09.1' W	12 Feb. 1979	11	6	—	—
888	2483	00° 47.1' N, 86° 08.5' W	13 Feb. 1979	46	7	—	1
890	2447	00° 48.9' N, 86° 13.3' W	15 Feb. 1979	67	2	—	—
891	2488	00° 48.3' N, 86° 13.4' W	16 Feb. 1979	2	—	—	—
892	2454	00° 48.3' N, 86° 13.8' W	17 Feb. 1979	1	—	—	—
894	2457	00° 48.2' N, 86° 14.9' W	19 Feb. 1979	2	4	—	—
896	2460	00° 48.2' N, 86° 13.6' W	21 Feb. 1979	10	2	—	—
983	2457	00° 48.0' N, 86° 13.0' W	30 Nov. 1979	11	2	—	—
984	2451	00° 48.0' N, 86° 13.0' W	01 Dec. 1979	97	7	—	—
989	2482	00° 48.0' N, 86° 09.0' W	06 Dec. 1979	7	13	—	—
990	2451	00° 48.0' N, 86° 13.0' W	07 Dec. 1979	20	17	—	—
991	2490	00° 48.0' N, 86° 09.0' W	08 Dec. 1979	68	8	—	1
993	2518	00° 47.0' N, 86° 08.0' W	10 Dec. 1979	12	112	—	1
			total	696	1138	—	3
<i>Cyana</i> dives, East Pacific Rise at 13° N							
82-33	2633	12° 48.6' N, 103° 56.7' W	08 Mar. 1982	6	190	2	1
82-34	2633	12° 48.6' N, 103° 56.7' W	11 Mar. 1982	7	2400	—	5
82-35	2633	12° 48.6' N, 103° 56.7' W	12 Mar. 1982	60	640	13	11
82-36	2633	12° 48.6' N, 103° 56.7' W	13 Mar. 1982	11	400	—	3
84-32	2635	12° 48.1' N, 103° 56.9' W	09 Mar. 1984	—	3	—	1
84-34	2630	12° 49.1' N, 103° 56.9' W	11 Mar. 1984	—	240	1	—
84-37	2630	12° 46.6' N, 103° 56.7' W	14 Mar. 1984	—	200	1	—
84-38	2630	12° 48.8' N, 103° 56.8' W	15 Mar. 1984	—	110	—	8
84-39	2635	12° 48.6' N, 103° 56.7' W	16 Mar. 1984	1	3020	13	—
84-40	2635	12° 48.6' N, 103° 56.7' W	17 Mar. 1984	—	55	3	—
84-41	2635	12° 48.6' N, 103° 56.7' W	23 Mar. 1984	10	500	—	—
84-42	2635	12° 48.6' N, 103° 56.7' W	24 Mar. 1984	152	8200	13	—
84-43	2635	12° 48.6' N, 103° 56.7' W	25 Mar. 1984	29	145	6	4
84-44	2635	12° 48.8' N, 103° 56.8' W	26 Mar. 1984	—	320	1	2
84-45	2635	12° 48.8' N, 103° 56.8' W	27 Mar. 1984	42	577	4	2
84-46	2635	12° 48.6' N, 103° 56.7' W	28 Mar. 1984	18	2200	2	3
			total	336	19200	59	40
<i>Alvin</i> dives, East Pacific Rise at 21° N							
978	2622	20° 50.0' N, 109° 06.0' W	02 Nov. 1979	—	1	—	—
1211	2615	20° 50.0' N, 109° 06.0' W	17 Apl 1982	199	5397	2	13
1213	2617	20° 50.0' N, 109° 06.0' W	19 Apl 1982	—	3	—	1
1214	2633	20° 50.0' N, 109° 06.0' W	20 Apl 1982	1853	14574	202	1
1215	2616	20° 50.0' N, 109° 06.0' W	21 Apl 1982	3	29	6	—
1218	2618	20° 50.0' N, 109° 06.0' W	24 Apl 1982	—	20	7	—
1219	2612	20° 50.0' N, 109° 06.0' W	25 Apl 1982	512	2569	57	—
1221	2618	20° 50.0' N, 109° 06.0' W	04 May 1982	198	4697	179	1
1222	2614	20° 50.0' N, 109° 06.0' W	06 May 1982	27	446	3	2
1223	2616	20° 50.0' N, 109° 06.0' W	07 May 1982	9	2393	30	5
1225	2618	20° 50.0' N, 109° 06.0' W	09 May 1982	145	20410	29	10
1226	2616	20° 50.0' N, 109° 06.0' W	10 May 1982	50	751	16	16
1229	2615	20° 50.0' N, 109° 06.0' W	14 May 1982	—	4	—	—
			total	2996	51294	531	49
			grand total	4028	71632	590	92

TABLE 2. STATION DATA AND NUMBER OF SPECIMENS FROM DIVES YIELDING SHORT RANGING
LEPETODRILUS SPECIES

dive	depth/m	position	date	number
<i>Lepetodrilus guaymasensis</i>				
<i>Alvin</i> dives, Guaymas Basin				
1170	2019	27° 01.0' N, 111° 25.0' W	12 Jan. 1982	4
1177	2014	27° 02.0' N, 111° 24.0' W	20 Jan. 1982	1
			total	5
<i>Lepetodrilus fucensis</i>				
<i>Pisces IV</i> dives, Explorer Ridge				
1494	1818	49° 45.6' N, 130° 16.1' W	01 Jly 1984	11
1495	1808	49° 45.6' N, 130° 16.1' W	02 Jly 1984	7
1497	1812	49° 45.5' N, 130° 16.1' W	04 Jly 1984	13
<i>Alvin</i> dives, Endeavor Segment, Juan de Fuca Ridge				
1419	2208	47° 57.0' N, 129° 04.0' W	25 Jly 1984	878
1451	2199	47° 57.0' N, 129° 06.0' W	06 Sep. 1984	15
<i>Pisces IV</i> dives, Axial Seamount, mid-Juan de Fuca Ridge				
1322	1599	45° 59.5' N, 130° 03.5' W	10 Aug. 1983	15
1323	1587	45° 59.5' N, 130° 03.5' W	12 Aug. 1983	13
1327	1592	45° 59.5' N, 130° 03.5' W	12 Aug. 1983	2
<i>Alvin</i> dives, Southern Juan de Fuca Ridge				
1410	2380	45° 13.0' N, 130° 09.0' W	15 Jly 1984	592
			total	1546

Diagnosis

Sculpture of beaded ribs in curved rows; apex medial, $\frac{9}{10}$ shell length from anterior; penis large, recurved; thickest at midlength.

Description

Outline of aperture oval, anterior end slightly narrower than posterior; margin of aperture in same plane; highest elevation posterior to midpoint; early growth with convex slopes, that of later stages flat to concave. Apex on midline, $\frac{3}{4}$ shell length from anterior. Protoconch dark-coloured, right side remaining visible. Protoconch length 120 μm ; juvenile shell of 1 mm length, coiled, with large, inflated aperture. Postprotoconch coil of $\frac{3}{4}$ whorl before full expansion of aperture (figure 33). Periostracum yellow-brown, inturned at shell edge. Early shell of 1–3 mm devoid of sculpture (figure 32); subsequent growth with numerous, finely beaded ribs emerging on anterior mid-dorsum in posteriorly curved rows; concentric sculpture lacking, although beads are aligned with growth increments. Beads produced until shell attains about half its maximum size; later growth may lack beading and tends to show concentric growth irregularities. Posterior slope with stronger, more broadly spaced ribs and thick, short ridges on either side of apical whorl (figures 34 and 35). Muscle scar horseshoe-shaped, midway between margin and midline, relatively broad; anterior extremities of muscle scar broader by expansion on outer side; left arm of scar extending slightly more anterior than right; posterior extent of scar evenly curved along outer edge; posterior region of scar narrow by reduction on inner side. Juvenile shell with posterior ridge on interior (figure 33). Apical pit at $\frac{2}{3}$ depth of scar; surface near margin showing coalescing lamellae and metallic lustre. Dimensions of holotype: 10.0 mm \times 7.5 mm \times 2.9 mm.

Radula (figures 1–4) typical for genus, first lateral with moderately broad overhanging cusp and strong, irregular denticulation. Penis (figure 29; part II, figure 5) large, recurved, thickest at midlength.

Type material

Holotype (figures 25–27) (female), LACM 2126, Mussel Bed vent field, Galapagos Rift (0° 47.6' N, 86° 06.4' W), *Alvin* dive 880, 2493 m, 21 January 1979. Paratypes: LACM, USNM, MNHN and other designated museums. The holotype was selected for the prominence of the beaded sculpture. The 209 specimens from dive 880 were labelled 'from mussel washings'.

Material

Galapagos Rift: 696 paratype specimens from 16 *Alvin* dives in 1977 and 1979 (table 1).
East Pacific Rise at 13° N: 336 specimens from 10 *Cyana* dives in 1982 and 1984 (table 1).
East Pacific Rise at 21° N: 2996 specimens from 9 *Alvin* dives in 1982 (table 1).

Remarks

This is the only species having the characteristic sculpture of beads in curved rows. Except for the strongly ribbed *L. cristatus*, shell surfaces of the other *Lepetodrilus* species are smooth. It is the largest of the four broadly distributed species and second to *L. elevatus* in abundance. The penis is larger, broader and more recurved than that of other species of the genus.

Lepetodrilus pustulosus is variable in strength of the beading; the Galapagos specimens are more strongly beaded than those from 21° N, on some of which the beads may be barely detectable (figure 28). Specimens from 13° N are also strongly beaded; the beading tends to extend to the shell margin, more so than in specimens from the other two localities. There are no apparent differences between radulae of a specimen from the Galapagos Rift (figures 1 and 2) and a specimen from the East Pacific Rise at 21° N (figures 3 and 4).

Shell surfaces are prone to heavy infestations of an unknown sedentary organism, which forms globular irregularities on the shell (see holotype, figure 25). Reddish-brown metallic deposits are also seen on some of the specimens.

The name is a Latin adjective meaning full of blisters, with reference to the beaded sculpture. The vernacular name for this species used earlier (McLean 1985) was 'beaded'. Berg (1985) gave data on egg size for specimens from dive 1214 at 21° N.

Lepetodrilus elevatus, new species

Two subspecies of this new species are recognized: *L. elevatus elevatus* from the two sites on the East Pacific Rise and *L. elevatus galriftensis* from the Galapagos Rift.

Lepetodrilus elevatus elevatus, new subspecies

(Figures 5 and 6, plate 1, and figures 36–44, plates 6 and 7; part II, figures 7 and 8)

Diagnosis

Shell relatively small and high, with apex nearly overhanging posterior, anterior end narrow; ends raised relative to sides; surface smooth; interior with thickened ridge posteriorly; penis short, broad, triangular in shape; gill filaments projecting over head.

Description

Outline of aperture oval, but with anterior and posterior ends unusually acute; margin of aperture not in one plane, ends raised relative to sides; profile high, highest point at $\frac{2}{3}$ shell length from anterior. Apex on midline, $\frac{9}{10}$ shell length from anterior. Protoconch length 120 μm ; exposed on right side; first postprotoconch whorl in juvenile shells of 1 mm length overhanging posterior margin of shell (figure 44). Periostracum light greenish-brown, tightly adhering, enveloping shell edge. Sculpture lacking except for broadly spaced growth irregularities. Posterior slope with a slight thickening below apex. Shell interior with thickened transverse ridge subtending apical pit at posterior. Area within muscle scar glossy; surface near inturned periostracum showing fine coalescing lamellae. Muscle scar horseshoe-shaped, broad, rounded anteriorly, narrowed posteriorly (thinner on inside), where placed on inner side of thickened ridge. Left arm of scar extending slightly more anteriorly than right (figure 37). Dimensions of holotype: 6.6 mm \times 4.8 mm \times 2.9 mm.

Radula (figures 5 and 6) typical for genus; first lateral with long and narrow overhanging cusp and relatively even, sharp denticulation. Ctenidial filaments of free tip prominently projecting over head (figure 39; part II, figure 7A). Penis broad at base, flattened, triangular in outline, with tapered tip (figure 39; part II, figure 7A). Neck with short sensory process on left-ventral side.

Type material

Holotype (figures 36–38, 40–42) (female), LACM 2127, East Pacific Rise at 21° N (20° 50.0' N, 109° 06.0' W), *Alvin* dive 1214, 2633 m, 20 April 1982. Paratypes: LACM, USNM, MNHN and other designated museums.

Material

East Pacific Rise at 21° N: 51 294 paratype specimens from 13 *Alvin* dives in 1979 and 1982 (table 1).

East Pacific Rise at 13° N: 19 200 specimens from 16 *Cyana* dives in 1982 and 1984 (table 1).

Remarks

This is the smallest and most abundant of the *Lepetodrilus* species. Washings from large samples of *Riftia* have produced specimens in the tens of thousands. This species has the most posterior apex of the four broadly distributed species and is the only species with strongly raised ends. It shares with *L. guaymasensis* an interior having the transverse, thickened ridge posteriorly. The tapered anterior and posterior ends produce a diamond-shaped outline that is unique among limpets. The broad but not recurved penis is also distinctive. The ctenidium has fewer lamellae than that of *L. pustulosus*. The sensory process on the left side of the neck is not present in the other species of *Lepetodrilus*.

The raised ends suggest that this species lives in a microhabitat differing from that of *L. pustulosus*, perhaps in a more depressed area on the surface of *Riftia*. The narrow first lateral tooth is characteristic and cannot be confused with that of other members of the genus.

The same organism that attaches to the shell of *L. pustulosus* is present on *L. elevatus*.

The name is a Latin adjective meaning raised, with reference to the high profile of this species. The vernacular name for this species used earlier (McLean 1985) was 'high-smooth'.

Turner *et al.* (1985, figures 7a–7c) illustrated the protoconch and early juvenile, identified only as ‘unnamed limpet’. Berg (1985) reported egg diameters for this species at the East Pacific Rise at 21° N.

Lepetodrilus elevatus galriftensis, new subspecies

(Figures 7 and 8, plate 2, and figures 45–50, plate 7)

Diagnosis

Shell differing from *L. elevatus elevatus* in generally smaller size, lower elevation; body with longer neck, but shorter gill filaments that do not project over head.

Description

Outline of aperture oval with tapered anterior and posterior ends as in *L. elevatus elevatus*, ends raised relative to sides; highest point at $\frac{2}{3}$ shell length from anterior. Apex on midline, $\frac{9}{10}$ shell length from anterior. Protoconch length 120 μm ; exposed on right side. Periostracum light greenish-brown, tightly adhering, enveloping shell edge. Sculpture lacking except for broadly spaced growth irregularities. Posterior slope with slight thickening below apex. Shell interior with thickened, transverse ridge subtending apical pit at posterior. Area within muscle scar glossy; surface near inturned periostracum showing fine coalescing lamellae. Muscle scar horseshoe-shaped, broad, rounded anteriorly, narrowed posteriorly (thinner on inside), where it is placed on inner side of thickened ridge. Left arm of muscle scar slightly longer than right. Dimensions of holotype: 6.3 mm \times 4.6 mm \times 2.1 mm.

Radula (figures 7 and 8) like that of *L. elevatus elevatus*; first lateral with same long, narrow overhanging cusp and relatively even, sharp denticulation. Neck relatively long; sensory process of left side prominent (figure 48). Penis broad at base, flattened, triangular in outline, with tapered tip (figure 48).

Type material

Holotype (figures 45–48) (male), LACM 2128, Rose Garden vent field, Galapagos Rift (0° 48.0' N, 86° 13.0' W), *Alvin* dive 990, 2451 m, 7 December 1979. Paratypes: LACM, USNM, MNHN and designated museums. The type specimen was selected for its large size.

Material

Galapagos Rift: 1138 paratype specimens from 14 *Alvin* dives in 1979 (table 1). This was not collected on the first expedition to the Galapagos Rift in 1977.

Remarks

Although there are no apparent radular differences, shells of the entire sample from the Galapagos Rift are about $\frac{2}{3}$ the height of those from the East Pacific Rise. This difference in shell proportions is striking. No explanation can be offered. Unlike the preserved specimens of the typical subspecies, the ctenidial lamellae of the free tip do not project over the head and the neck is longer. These differences may be consequences of the reduced shell volume in *L. elevatus galriftensis*. No other limpets in this or other families in the rift-vent habitat have geographical differences of any significance.

The globular organism that occurs on many shells of the typical subspecies is also present on *L. elevatus galriftensis*, although it may have a different appearance, seeming to form a series of short ridges, usually aligned as if it represented shell sculpture produced at the growing edge. This has been scraped off the holotype, but can be seen in figure 49.

The name is based on the type, and only known, locality: the Galapagos Rift. The existence of this subspecies has not been previously noted. Turner *et al.* (1985, figures 8a–8c) illustrated the protoconch and early juvenile, identified only as 'unnamed limpet'.

Lepetodrilus ovalis, new species

(Figures 9–12, plate 2, and figures 51–56, plate 8; part II, figures 9 and 10)

Diagnosis

Sculpture lacking; shell relatively small, height moderate, apex at posterior $\frac{2}{3}$, differing from *L. pustulosus* in lacking sculpture, having a more oval basal outline, and a more slender penis.

Description

Outline of aperture broadly and evenly elliptical; margin of aperture nearly in one plane; ends slightly raised relative to sides; highest elevation just slightly anterior to apex. Apex on midline, $\frac{2}{3}$ shell length from anterior margin. Protoconch length 130 μ m, exposed on right side; triangular ridge subtends protoconch (figure 56). Periostracum greenish-brown, thin, enveloping margin. Sculpture lacking except for faint growth increments. Shell interior glossy, apical pit very small, transverse posterior ridge lacking. Muscle scar horseshoe-shaped, tips rounded, relatively close to centre of shell, only slightly narrowed posteriorly; left arm of muscle scar extending slightly more anteriorly than right. Dimensions of holotype: 5.7 mm \times 4.9 mm \times 1.7 mm.

Radula (figures 9–12) typical for genus, first lateral with unusually broad overhanging area and even, sharp denticulation in addition to primary cusp; second to fifth lateral having longer overhang than that of other species.

Ctenidium much reduced compared with *L. pustulosus* and *L. elevatus*; lamellae short, monopectinate. Penis broad at base but very slender at tip (figure 55).

Type material

Holotype (figures 51–55) (male), LACM 2129, East Pacific Rise at 21° N (20° 50.0' N, 109° 06.0' W), *Alvin* dive 1214, 2633 m, 20 April 1982. Paratypes: LACM, USNM, MNHN and other designated museums.

Material

East Pacific Rise at 21° N: 531 paratype specimens from 10 *Alvin* dives in 1982 (table 1).

East Pacific Rise at 13° N: 59 specimens from 11 *Cyana* dives in 1982 and 1984 (table 1).

Remarks

Lepetodrilus ovalis is relatively low with an elliptical outline, has a very tapered penis, and a fully monopectinate ctenidium. Compared with *L. pustulosus* the outline is more oval and the beaded sculpture of that species is lacking.

Many specimens have a partial or sometimes complete coating of black inorganic material (remaining residue shown on holotype, figure 51); none seem to have the globular organism that frequents the shells of *L. pustulosus* and *L. elevatus*. The slightly raised ends suggest that this species may occur in rounded depressions.

No apparent differences were noted between radulae of specimens from the East Pacific Rise at 21° N (figures 9 and 10) and from 13° N (figures 11 and 12). This is the only broadly distributed species along the East Pacific Rise that is not as yet known from the Galapagos Rift.

The name is a Latin adjective meaning oval, with reference to the characteristic outline of the shell. The vernacular name for this species used earlier (McLean 1985) was 'oval-smooth'. Turner *et al.* (1985, figures 6a–6c) illustrated the protoconch and early juvenile, identified only as 'unnamed limpet'.

Lepetodrilus cristatus, new species

(Figures 13 and 14, plates 3, and figures 57–65, plate 9; part II, figures 11 and 12)

Diagnosis

Sculpture of strong, scabrous primary and secondary ribs; tertiary ribs extremely fine; apex at posterior $\frac{3}{4}$, moderately projecting, ventral margin of sides raised relative to ends; penis long and very slender.

Description

Outline of aperture oval, anterior broader than posterior; ventral margin of sides markedly raised relative to ends; highest elevation of shell at midpoint; posterior slope concave, lateral slopes concave. Apex on midline, $\frac{3}{4}$ shell length from anterior end, moderately projecting. Protoconch length 130 μ m, right side exposed, although shell apex not deflected from midline; early growth stage immersed in posterior slope; thickened ridge below apex lacking. Periostracum thin, grey-brown, enveloping shell edge. Sculpture of about 20 strong primary ribs, emerging after shell attains 1 mm in length; secondary ribs arise at shell length of 1–2 mm, not attaining same strength as primary ribs. Rib interspaces filled by up to six very fine but distinct tertiary ribs. Ribs and interspaces finely and evenly imbricated by sharp, raised ridges corresponding to growth increments, about 10 per millimetre (figure 65). Shell interior glossy, muscle scar indistinct, horseshoe-shaped, narrowed posteriorly. Dimensions of holotype: 8.1 mm \times 6.0 mm \times 2.6 mm.

Radula (figures 13 and 14) typical for genus; overhanging surface of first lateral deeply indented at midlength, cusp surface lateral to this indentation broader than inner portion; cusp edge with fine but weak denticulation.

Ctenidium relatively small; lamellae of free tip not projecting over head in ventral view. Penis long and slender, of same diameter and taper as cephalic tentacles, but slightly shorter.

Type material

Holotype (figures 57–59) (sex unknown, body lost) LACM 2130, East Pacific Rise at 21° N (20° 50.0' N, 109° 06.0' W), *Alvin* dive 1211, 2615 m, 17 April 1982. The holotype is the largest known specimen. Paratypes: LACM, USNM and MNHM.

Material

East Pacific Rise at 21° N: 49 paratype specimens from 8 *Alvin* dives in 1982 (table 1).

East Pacific Rise at 13° N: 40 specimens from 10 *Cyana* dives in 1982 and 1984 (table 1).

Galapagos Rift: 3 specimens from 3 *Alvin* dives in 1979 (table 1).

Remarks

Lepetodrilus cristatus is the only species in this genus with strong ribs, imbricate sculpture, raised sides, the anterior broader than the posterior, and an extremely slender penis. Although the apex projects like that of *L. elevatus*, the interior ridge of *L. elevatus* is lacking. The triangular ridge below the apex, which characterizes *L. pustulosus*, *L. elevatus* and *L. ovalis*, is lacking in *L. cristatus*.

The microhabitat must differ from that of other *Lepetodrilus* species, as raised sides are not known in the other species. This shell form would be most effective for an animal that is attached to rounded objects, such as pebbles. Another clue that the habitat differs is the fact that shells of all specimens are nearly free of organic encrustations, which suggests that the shell is not exposed directly to the environment. However, the specimens from the Galapagos Rift and the East Pacific Rise at 13° N have a reddish-orange inorganic coating.

This is the least common of the broadly distributed species of *Lepetodrilus*. Most of the specimens are juvenile or extremely small. One sample, from dive *Alvin* 1211, East Pacific Rise at 21° N, contained nine specimens over 5 mm in length, but this sample had been poorly preserved and all but two of the bodies had separated from the shells and were lost. The largest specimen from the Galapagos Rift is 6.6 mm in length.

The name is a Latin adjective meaning crested or ridged, with reference to the characteristic shell sculpture. The vernacular name for this species used earlier (McLean 1985) was 'scabrous'. Turner *et al.* (1985, figures 2a–2c) and Lutz *et al.* (1986, figures 2a–c) illustrated the protoconch and early juvenile, identified only as 'unnamed limpet'.

Lepetodrilus guaymasensis, new species

(Figures 15 and 16, plate 3, and figures 66–74, plate 10; part II, figures 13 and 14)

Diagnosis

Shell relatively large, apical whorl projecting and recurved over posterior margin of shell; sculpture of growth increments only.

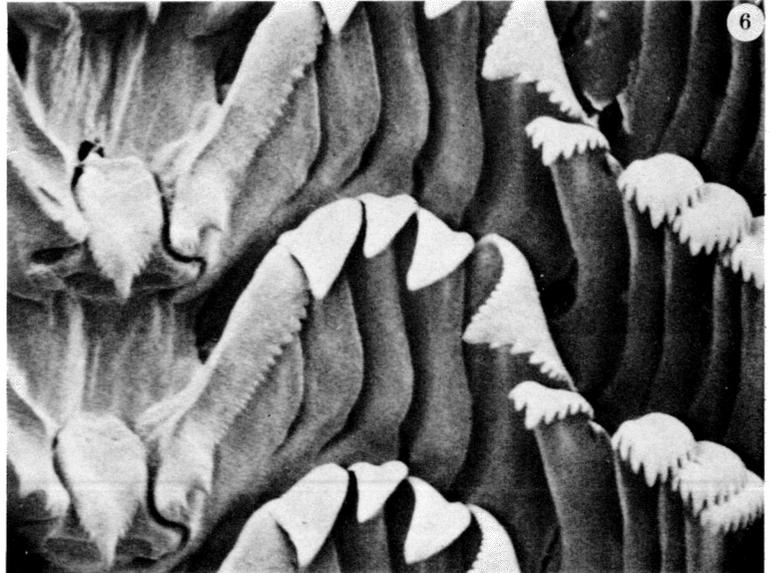
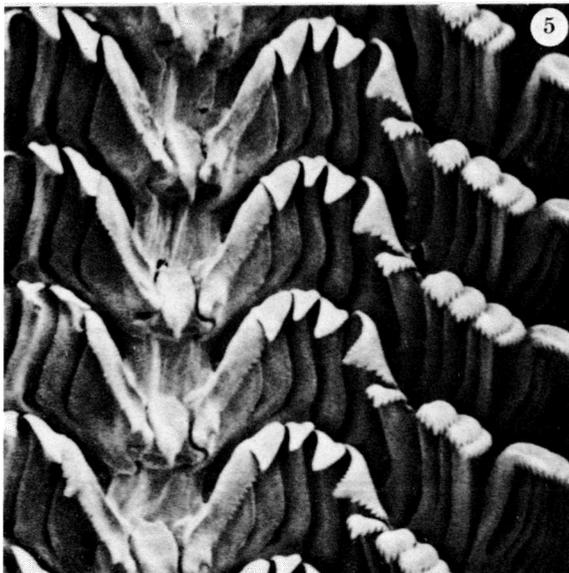
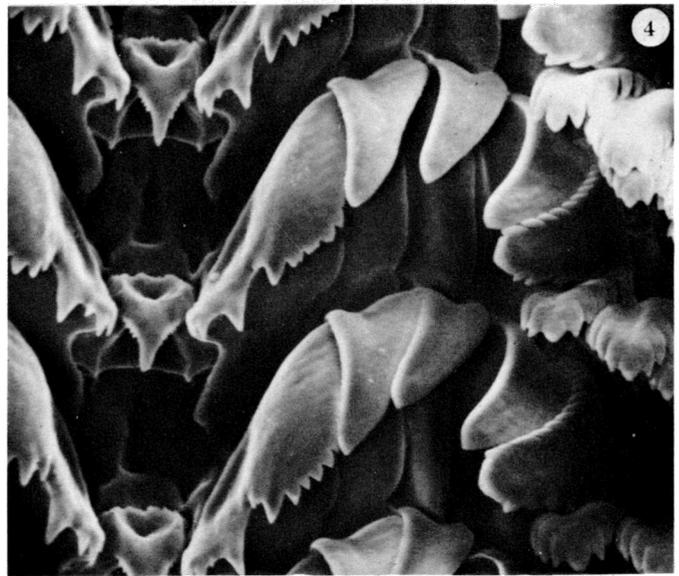
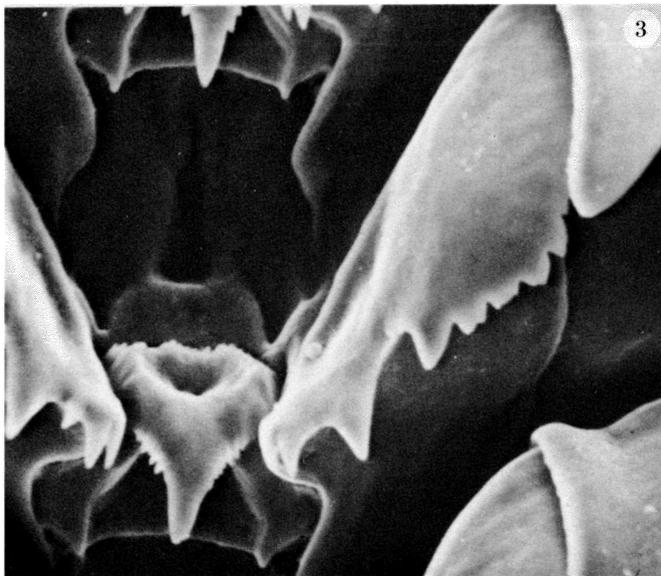
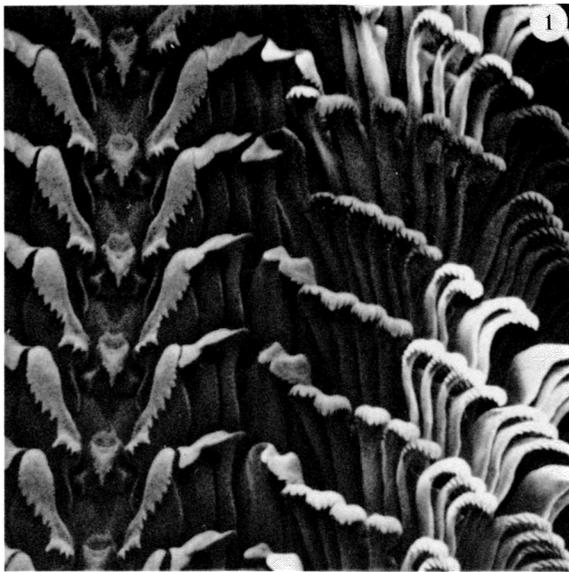
Description

Shell relatively thin. Outline of aperture elongate oval, anterior end slightly narrower than posterior; ends raised relative to sides. Profile high, apex projecting and overhanging posterior

DESCRIPTION OF PLATE 1

FIGURES 1–4. Radula of *Lepetodrilus pustulosus*, new species. Figures 1 and 2: Galapagos Rift, *Alvin* dive 880 (magns × 500 and × 1000 respectively). Figures 3 and 4: East Pacific Rise at 21° N, *Alvin* dive 1214 (magns × 2000 and × 1000 respectively). For orientation see text under generic description.

FIGURES 5 AND 6. Radula of *Lepetodrilus elevatus*, new species. East Pacific Rise at 21° N, *Alvin* dive 1214 (magn. × 500 and × 1000 respectively).



FIGURES 1-6. For description see opposite.

(Facing p. 16)

DESCRIPTION OF PLATE 2

FIGURES 7 AND 8. Radula of *Lepetodrilus elevatus galriftensis*, new subspecies. Galapagos Rift, *Alvin* dive 884 (magns $\times 500$ and $\times 2000$ respectively).

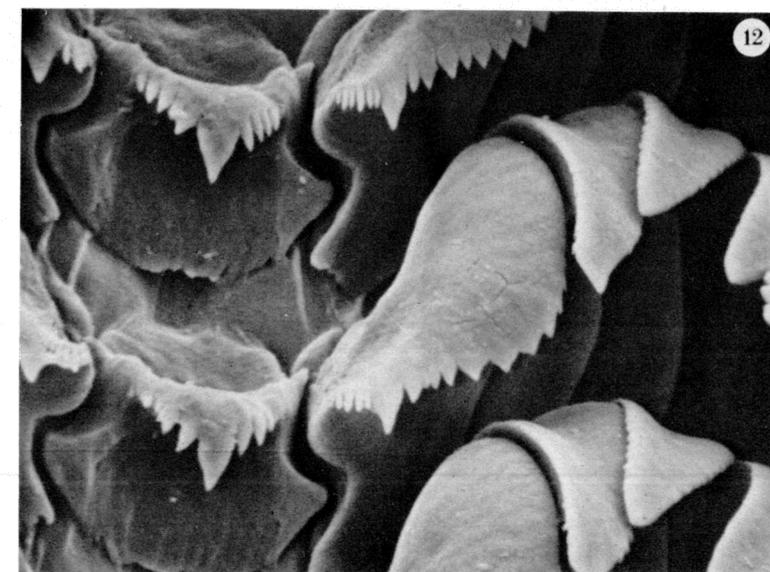
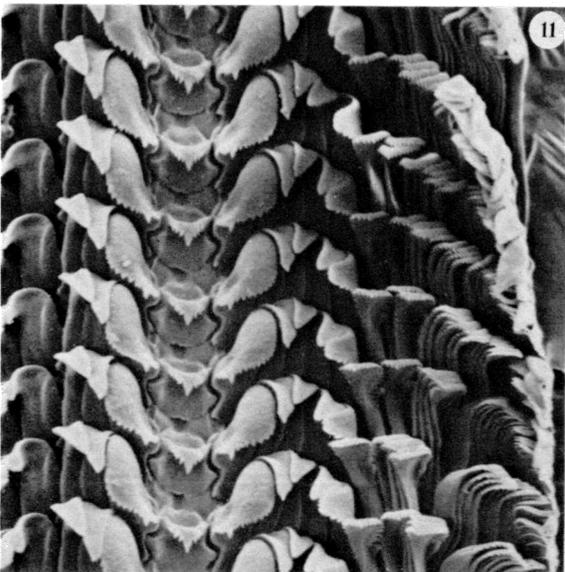
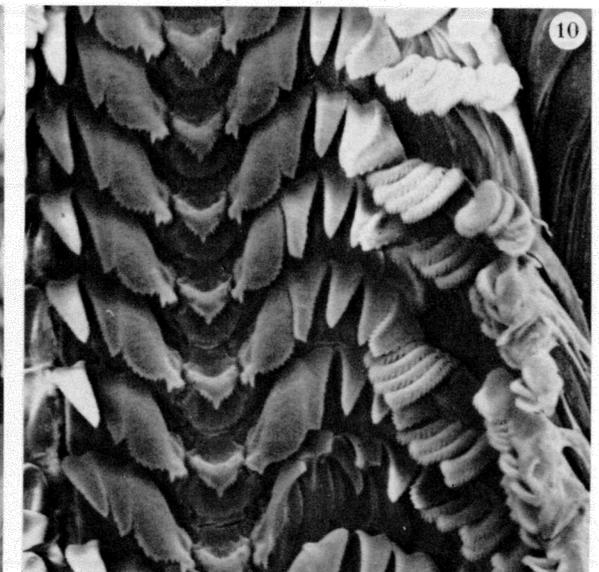
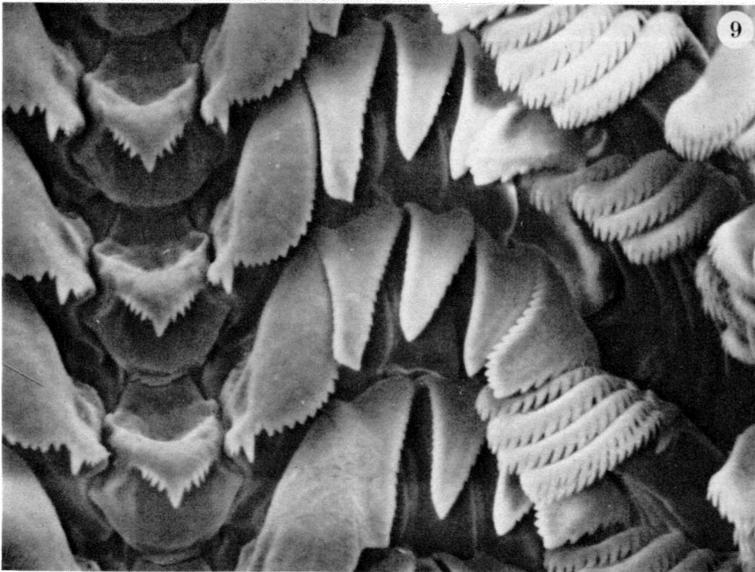
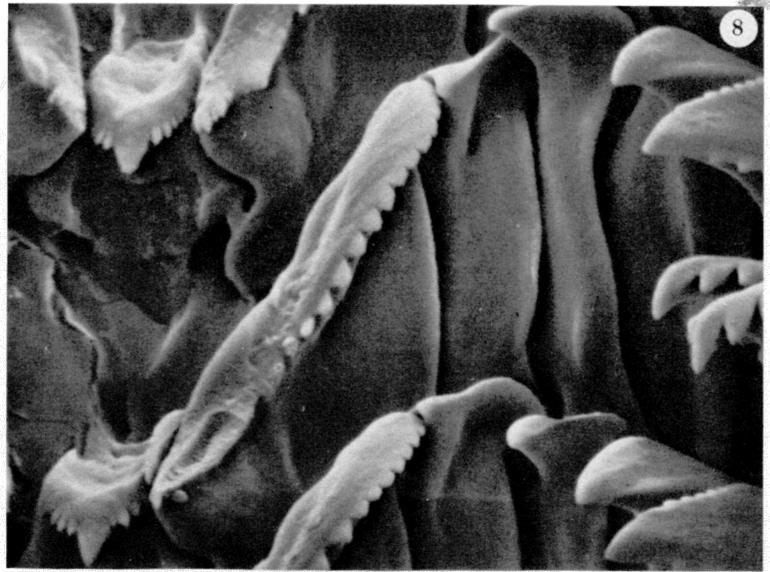
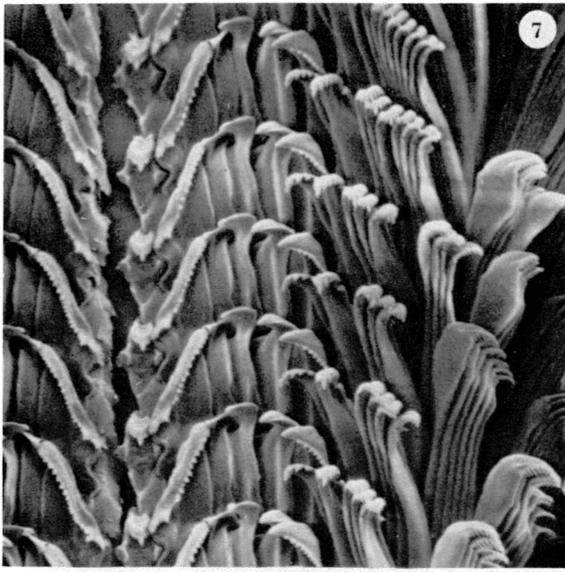
FIGURES 9–12. Radula of *Lepetodrilus ovalis*, new species. Figures 9 and 10: East Pacific Rise at 21° N, *Alvin* dive 1219 (magns $\times 1000$ and $\times 500$ respectively). Figures 11 and 12: East Pacific Rise at 13° N, *Cyana* dive 82–35 (magns $\times 500$ and $\times 2000$ respectively).

DESCRIPTION OF PLATE 3

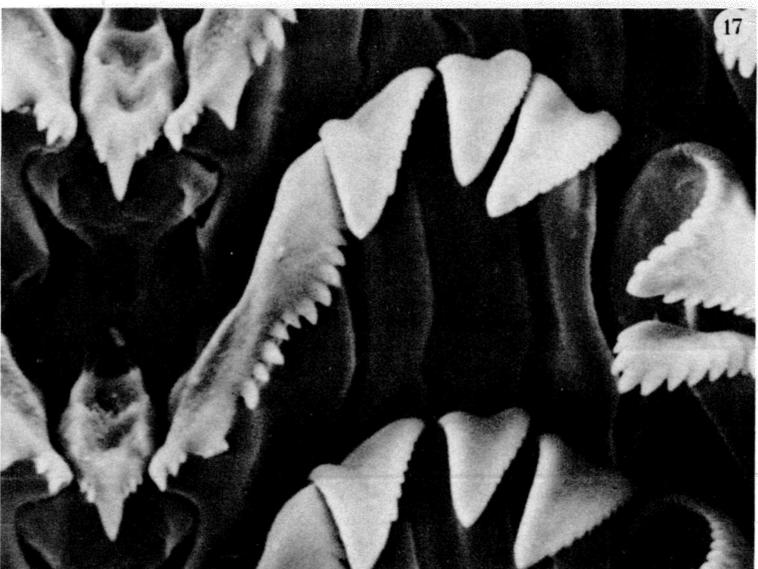
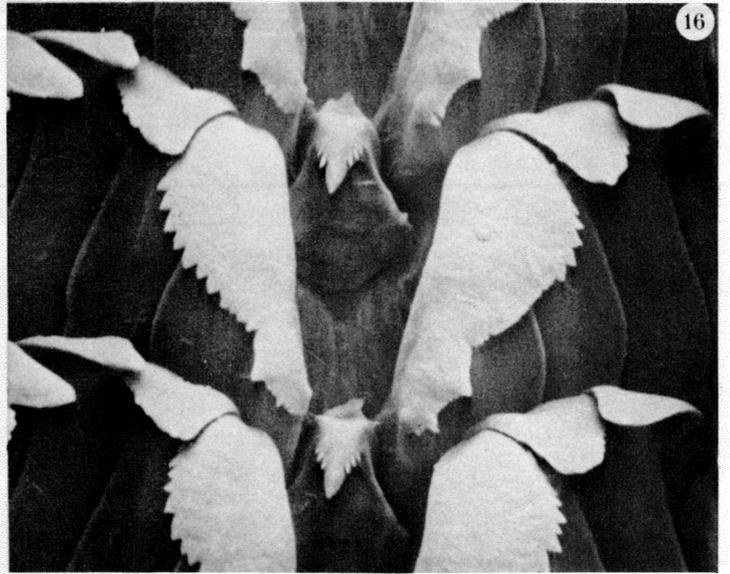
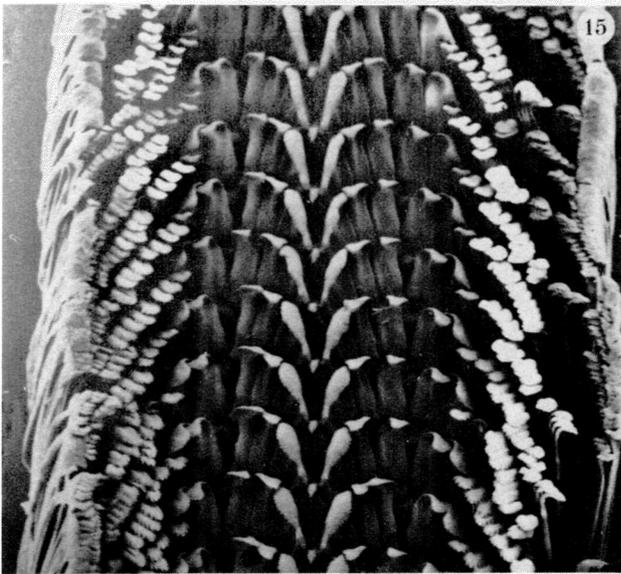
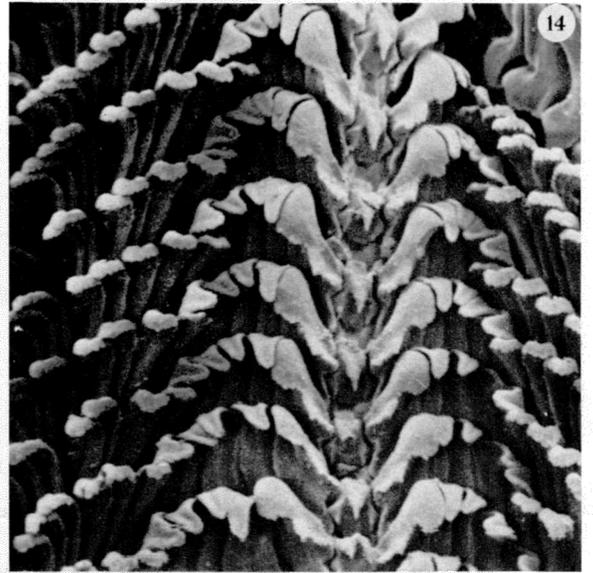
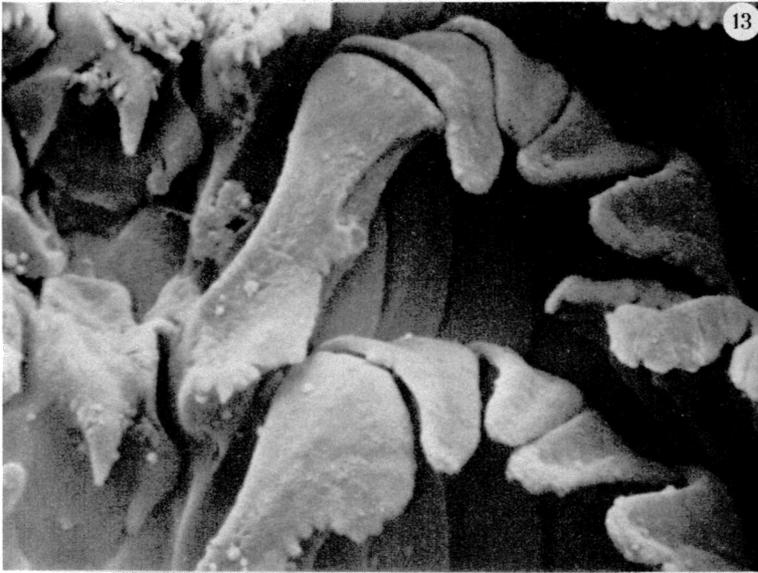
FIGURES 13 AND 14. Radula of *Lepetodrilus cristatus*, new species. East Pacific Rise at 21° N, *Alvin* dive 1211 (magns $\times 2000$ and $\times 500$ respectively).

FIGURES 15 AND 16. Radula of *Lepetodrilus guaymasensis*, new species. Guaymas Basin, *Alvin* dive 1170 (magns $\times 200$ and $\times 1000$ respectively).

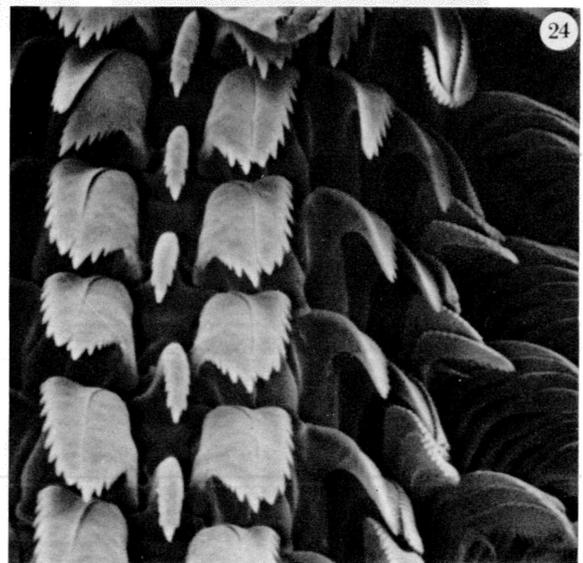
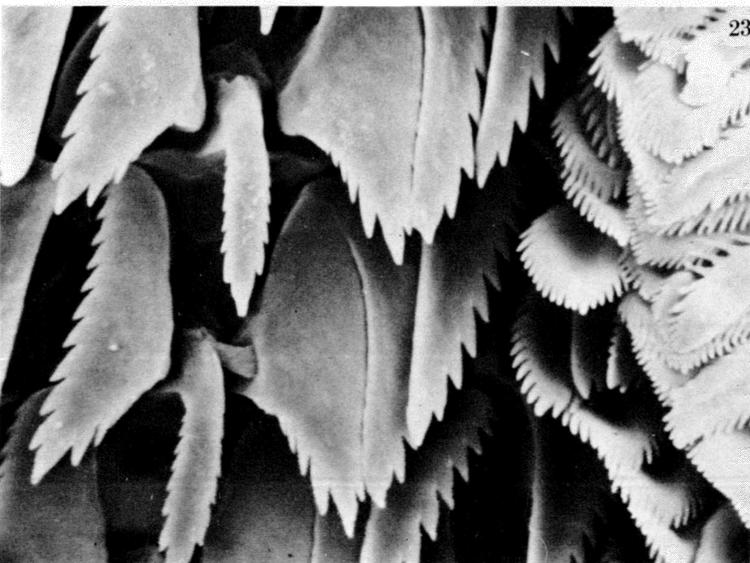
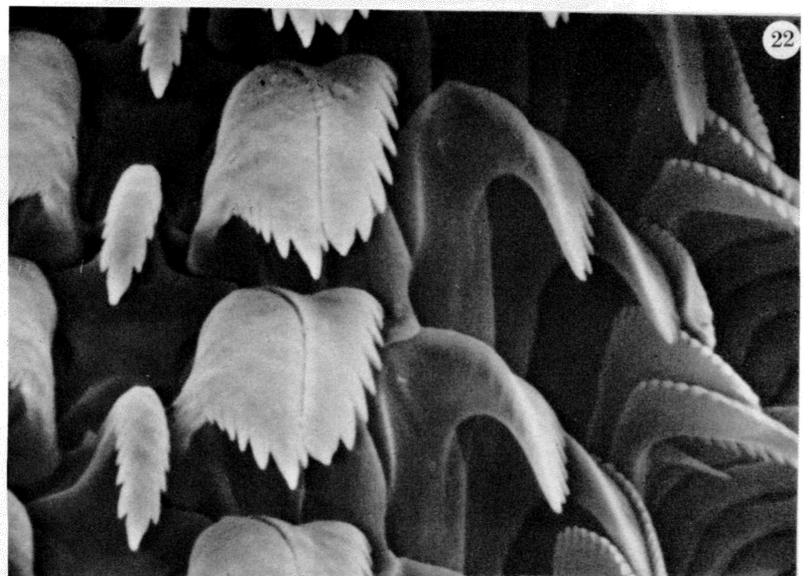
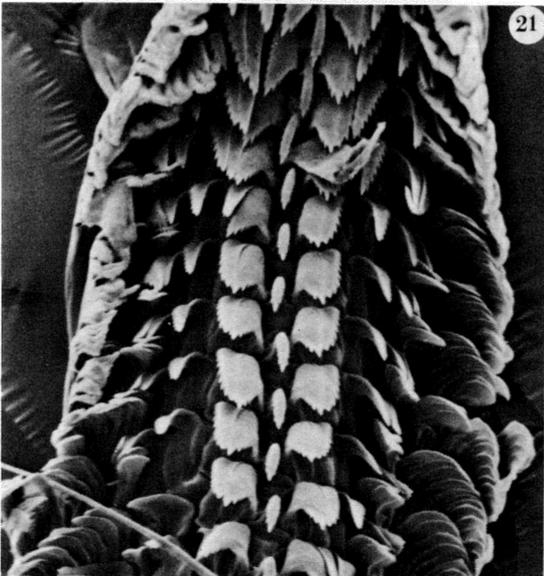
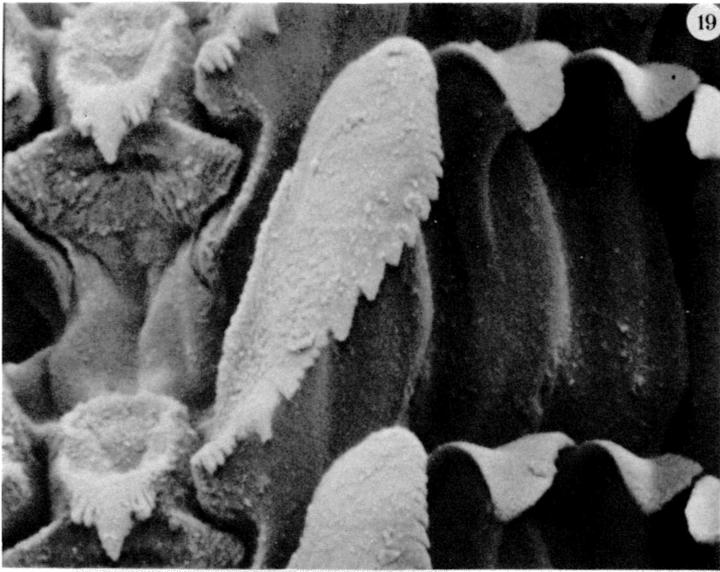
FIGURES 17 AND 18. Radula of *Lepetodrilus fucensis*, new species. Juan de Fuca Ridge, *Alvin* dive 1419 (magns $\times 2000$ and $\times 500$ respectively).



FIGURES 7-12. For description see opposite.



FIGURES 13-18. For description see facing plate 2.



FIGURES 19–24. For description see facing plate 5.



FIGURES 25-33. For description see opposite.

DESCRIPTION OF PLATE 4

FIGURES 19 AND 20. Radula of *Lepetodrilus fucensis*, new species. Explorer Ridge, *Pisces IV* dive 1494 (magns $\times 2000$ and $\times 500$ respectively).

FIGURES 21-24. Radula of *Gorgolettis marginatus*, new species. East Pacific Rise at 21° N, *Alvin* dive 1221 (magns $\times 500$, $\times 2000$, $\times 2000$ and $\times 1000$ respectively).

DESCRIPTION OF PLATE 5

FIGURES 25-33. *Lepetodrilus pustulosus*, new species. Figures 25-27: exterior, interior and left lateral views of holotype shell (female). Galapagos Rift, *Alvin* dive 880 (magn. $\times 6.5$). Figure 28: exterior view of female shell. East Pacific Rise at 21° N, *Alvin* dive 1214 (magn. $\times 7.3$). Figures 29 and 30: ventral and dorsal views of male body. Galapagos Rift, *Alvin* dive 733 (magn. $\times 7.4$). Figure 31: ventral view of female body. East Pacific Rise at 21° N, *Alvin* dive 1214 (magn. $\times 8.4$). Figure 32: oblique lateral view of juvenile shell. Galapagos Rift, *Alvin* dive 890 (magn. $\times 95$). Figure 33: interior view of apex of juvenile shell. East Pacific Rise at 21° N, *Alvin* dive 1214 (magn. $\times 100$).

DESCRIPTION OF PLATE 6

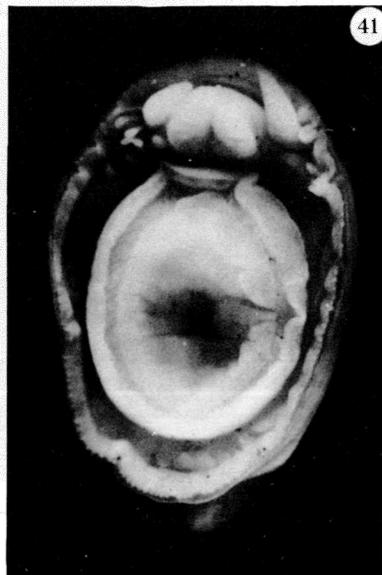
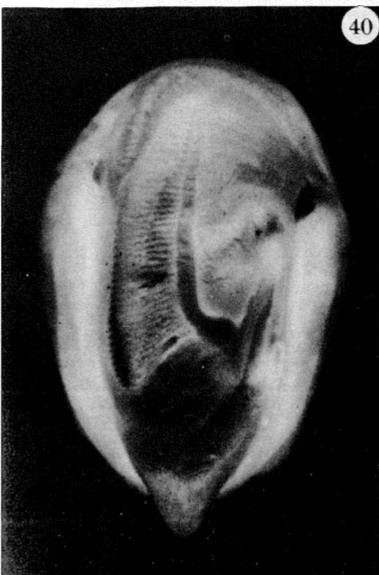
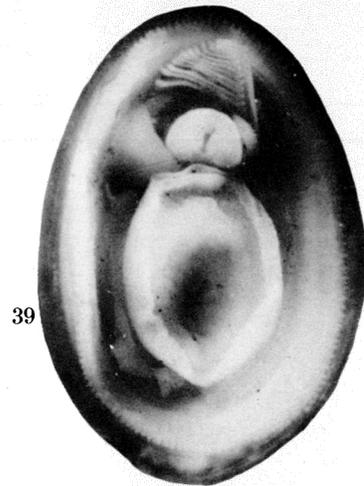
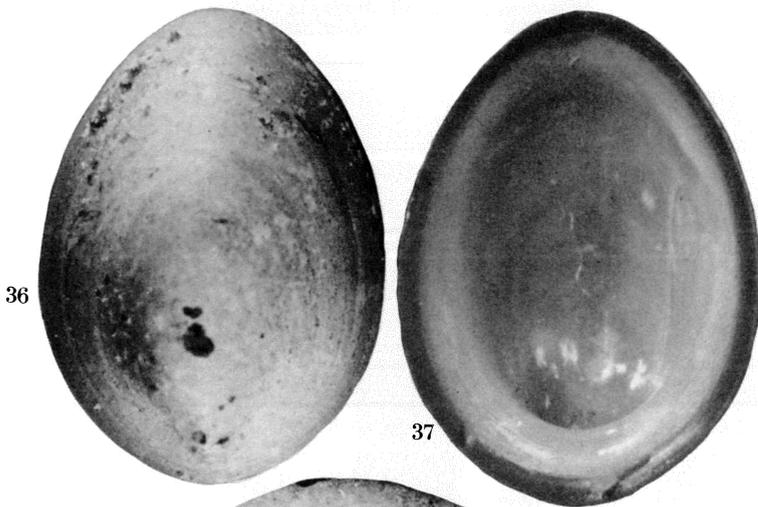
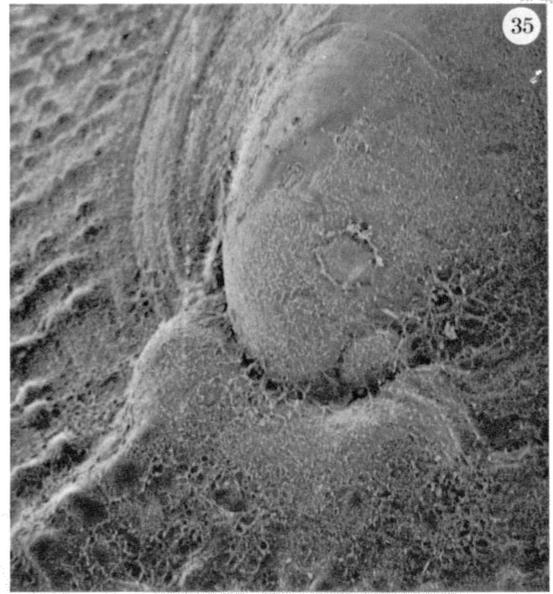
FIGURES 34 AND 35. *Lepetodrilus pustulosus*, new species. Figure 34: oblique view of right side of immature shell. Galapagos Rift, *Alvin* dive 884 (magn. $\times 20$). Figure 35: oblique posterior view of protoconch. Same specimen as figure 34 (magn. $\times 100$).

FIGURES 36–42. *Lepetodrilus elevatus elevatus* new species. Figures 36–38: exterior, interior and right lateral views of holotype shell (female). East Pacific Rise at 21° N, *Alvin* dive 1214 (magn. $\times 9.5$). Figure 39: ventral view of male body in shell. Same dive number (magn. $\times 11.1$). Figures 40–42: dorsal, ventral and right lateral view of holotype body (magn. $\times 13.2$).

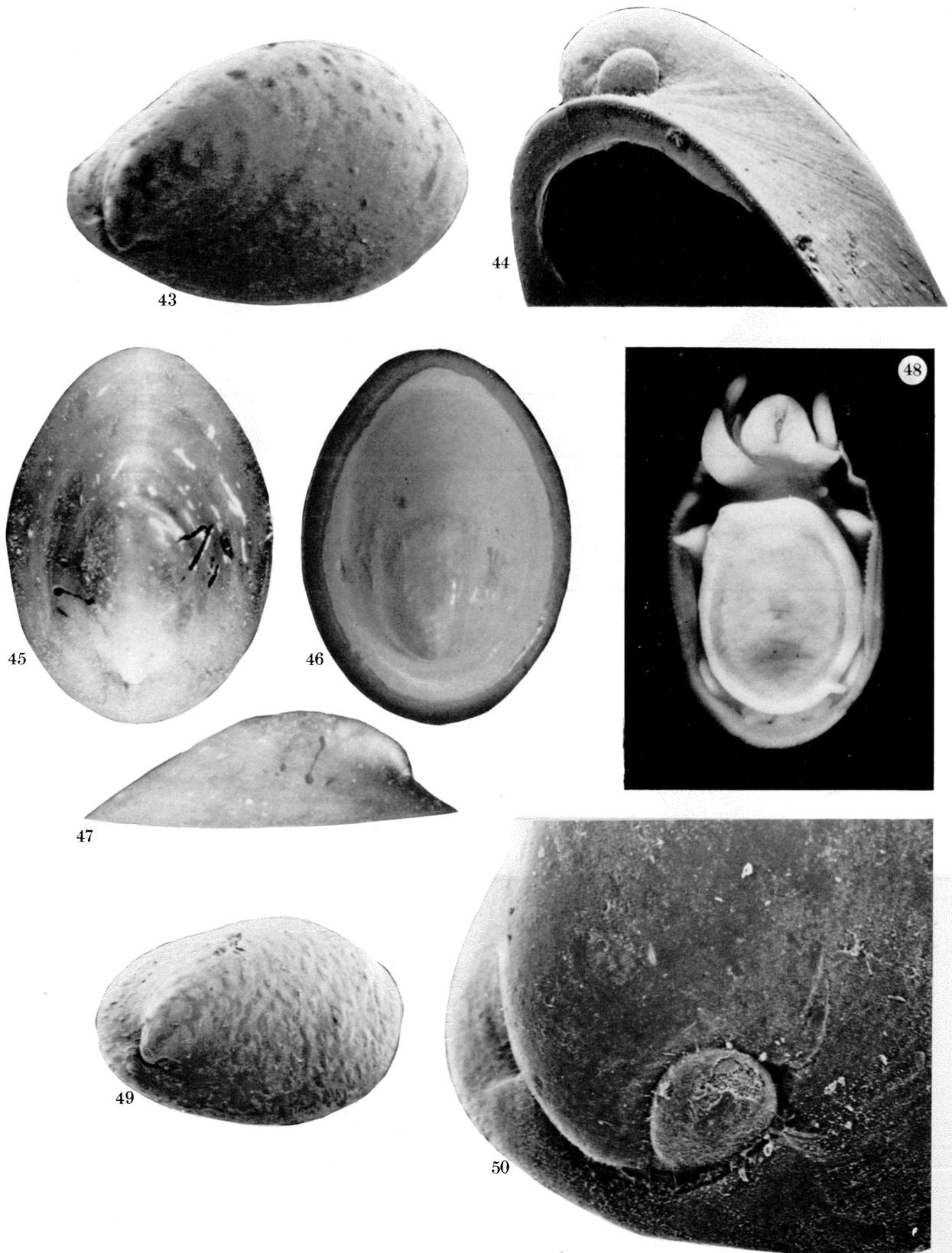
DESCRIPTION OF PLATE 7

FIGURES 43 AND 44. *Lepetodrilus elevatus elevatus* new species. Figure 43: oblique lateral view of right side of immature specimen. East Pacific Rise at 21° N, *Alvin* dive 1214 (magn. $\times 40$). Figure 44: oblique view of protoconch of juvenile specimen. Same dive number. (Magn. $\times 100$.)

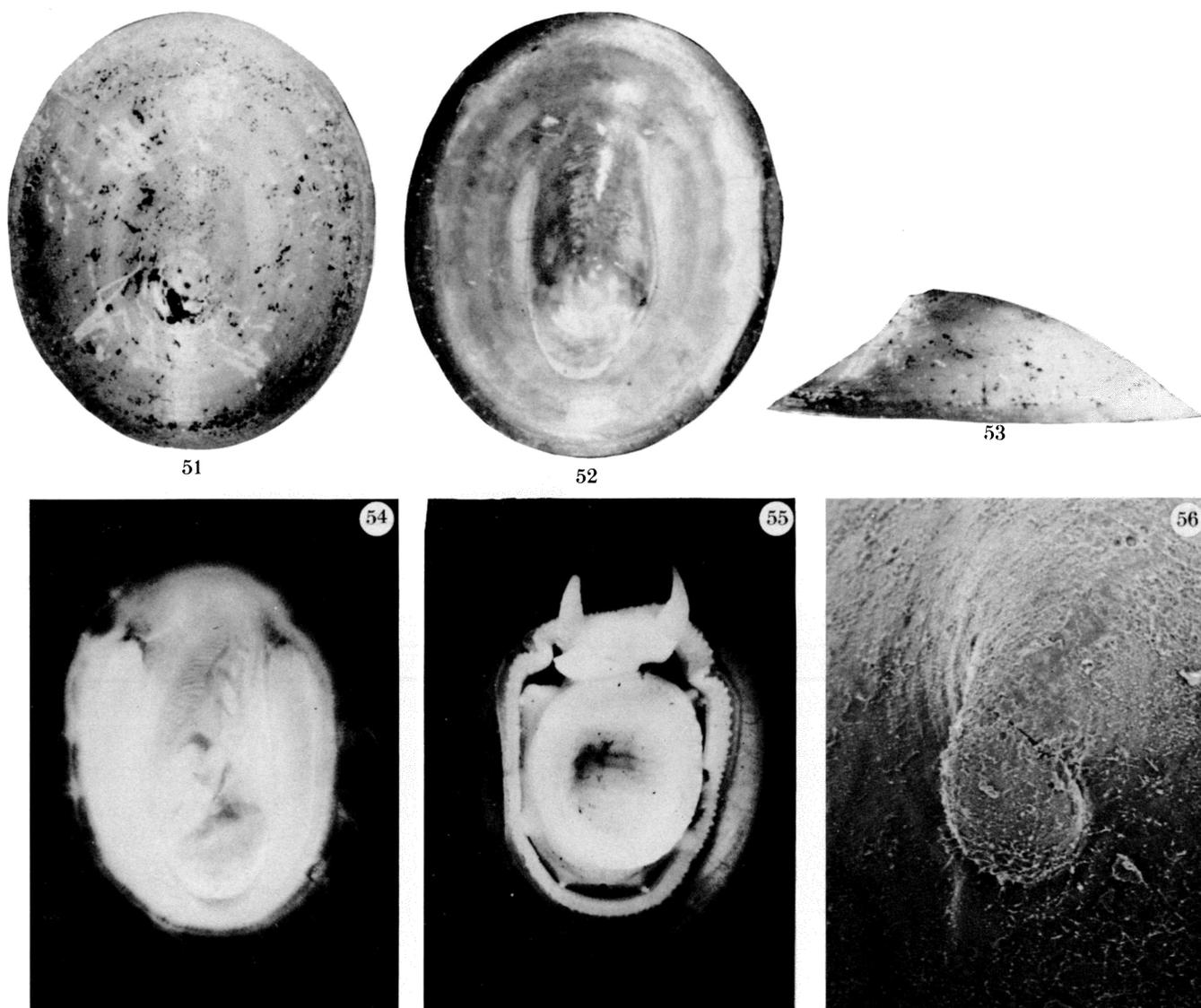
FIGURES 45–50. *Lepetodrilus elevatus galriftensis*, new subspecies. Figures 45–47: exterior, interior and left lateral views of holotype shell (male). Galapagos Rift, *Alvin* dive 990 (magn. $\times 10.3$). Figure 48: same specimen, ventral view of body (magn. $\times 14.4$). Figure 49: oblique lateral view of immature shell. Same dive number (magn. $\times 20$). Figure 50: protoconch of immature shell. Same dive number (magn. $\times 220$).



FIGURES 34-42. For description see opposite.



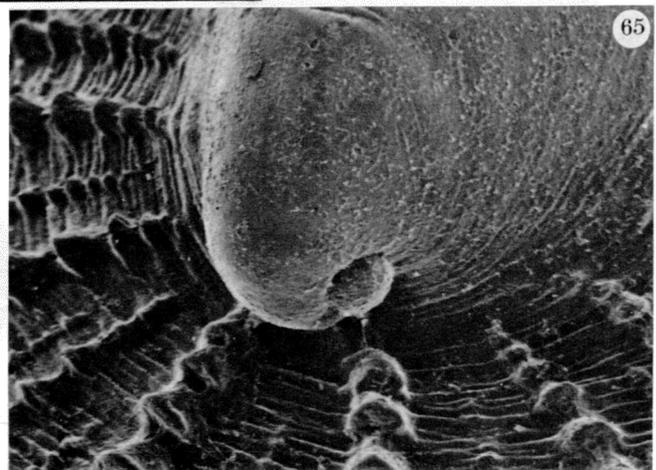
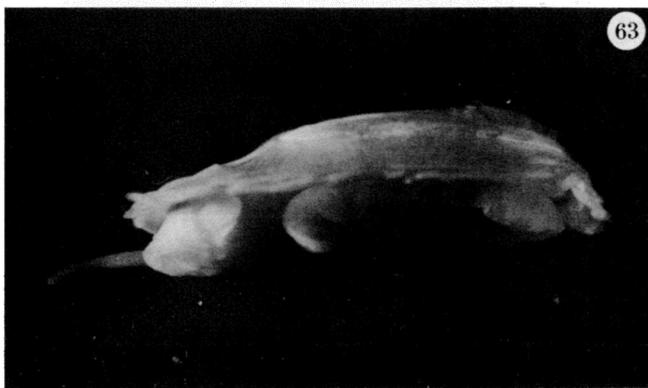
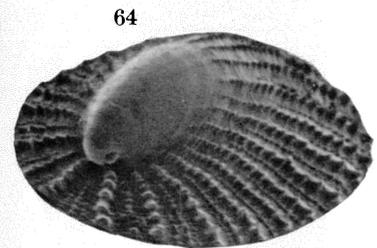
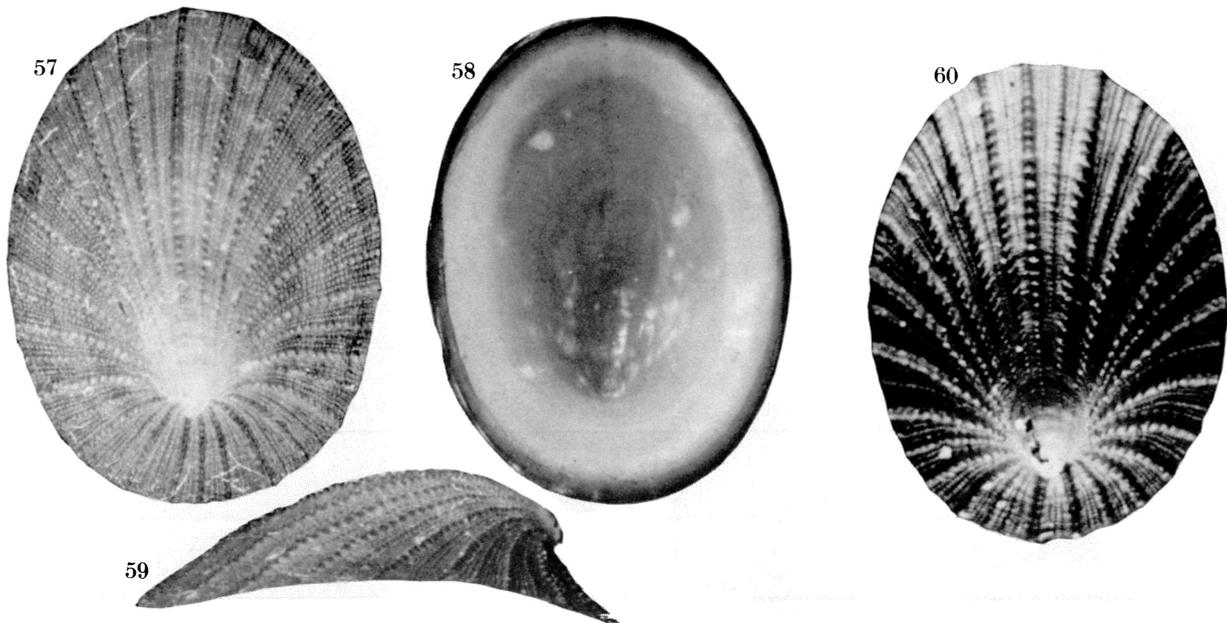
FIGURES 43-50. For description see facing plate 6.



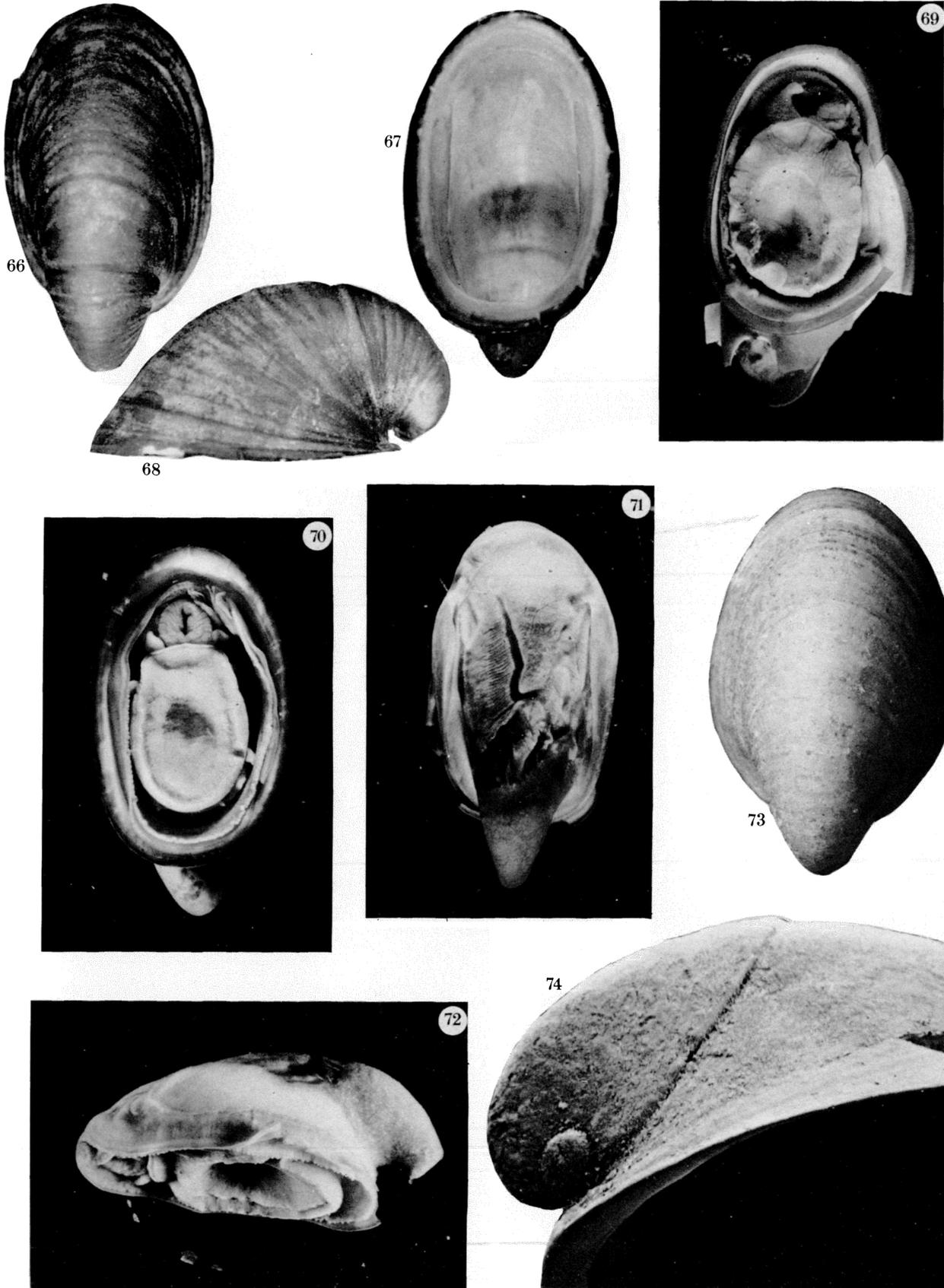
FIGURES 51-56. *Lepetodrilus ovalis*, new species. Figures 51-53: exterior, interior and right lateral views of holotype (male). East Pacific Rise at 21° N, *Alvin* dive 1214 (magn. $\times 11.2$). Figure 54: dorsal view of holotype body (magn. $\times 13.5$). Figure 55: ventral view of male body in shell. Same dive number (magn. $\times 10.2$). Figure 56: protoconch of immature specimen. Same dive number (magn. $\times 200$).

DESCRIPTION OF PLATE 9

FIGURES 57–65. *Lepetodrilus cristatus*, new species. Figures 57–59: exterior, interior and left lateral views of holotype (sex unknown). East Pacific Rise at 21° N, *Alvin* dive 1211 (magn. × 8.0). Figure 60: exterior view of female shell. Same dive number (magn. × 9.4). Figures 61–63: ventral, dorsal and left lateral view of female body (before sectioning). Galapagos Rift, *Alvin* dive 989 (magn. × 15.2). Figure 64: immature shell, East Pacific Rise at 21° N, *Alvin* dive 1211 (magn. × 30). Figure 65: protoconch of specimen in figure 64 (magn. × 100).



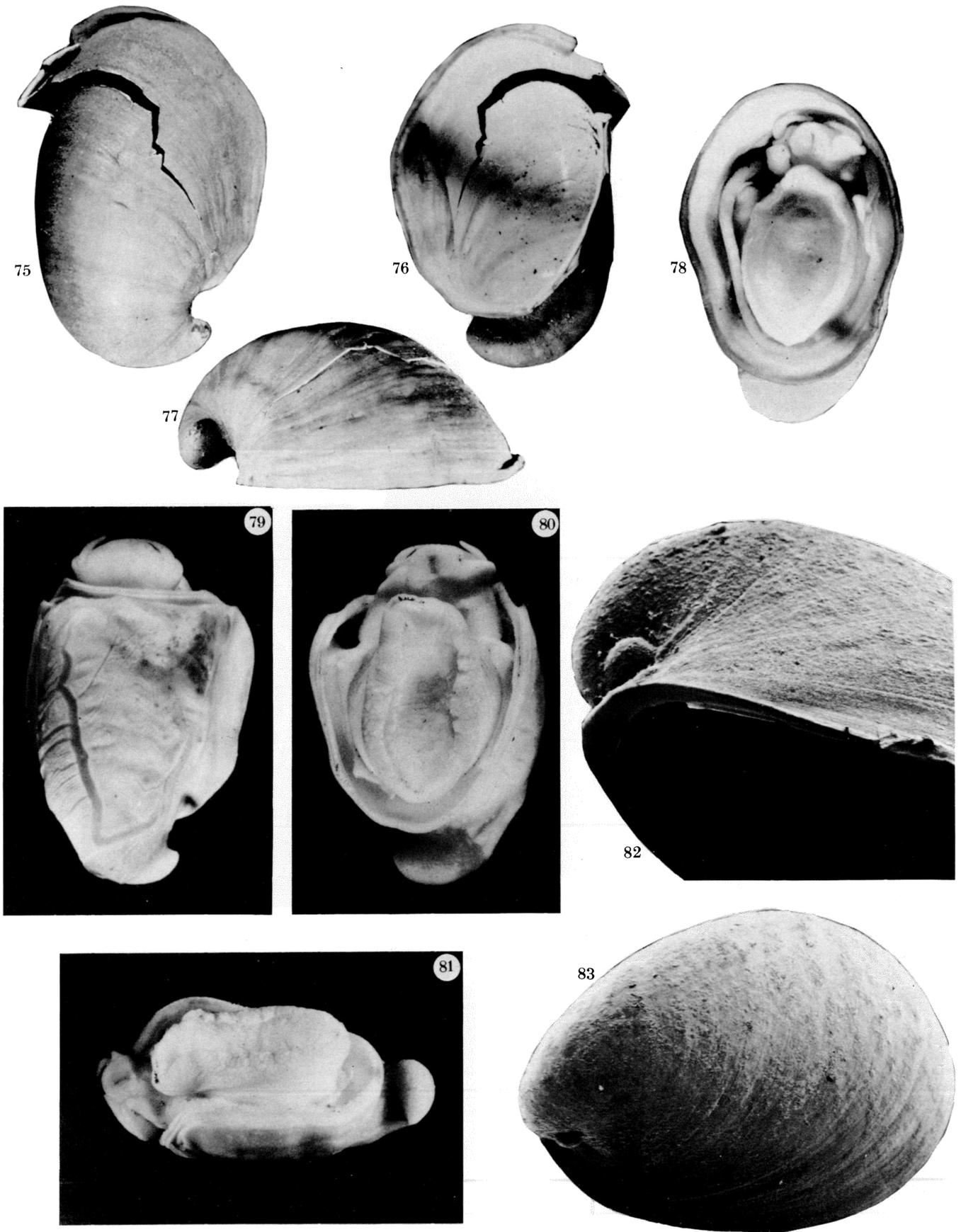
FIGURES 57-65. For description see opposite.



FIGURES 66-74. For description see opposite.

DESCRIPTION OF PLATE 10

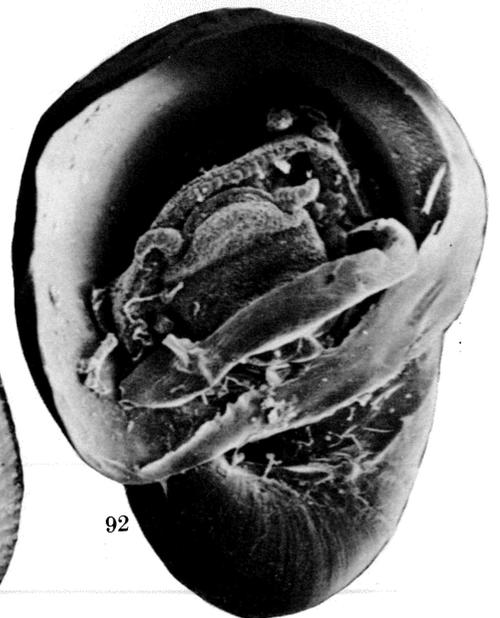
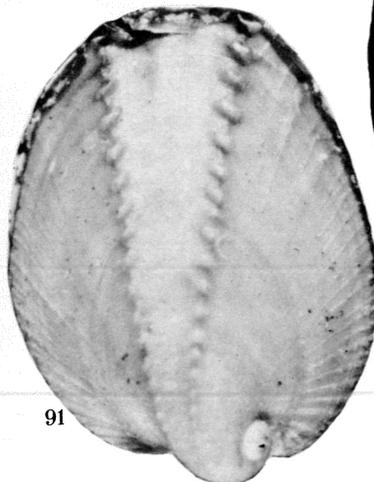
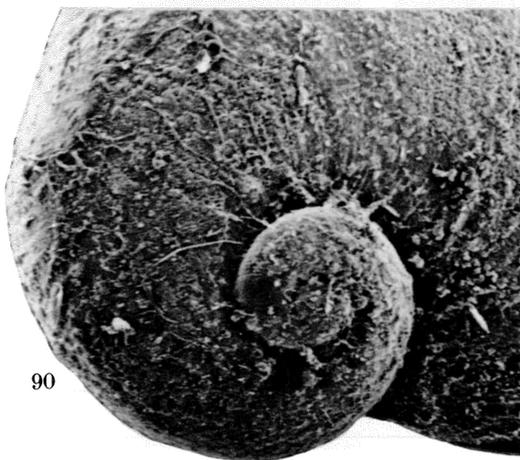
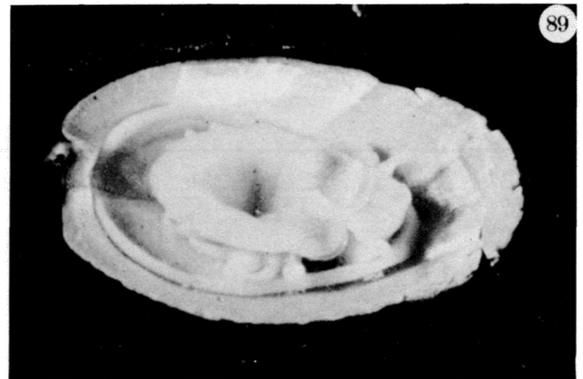
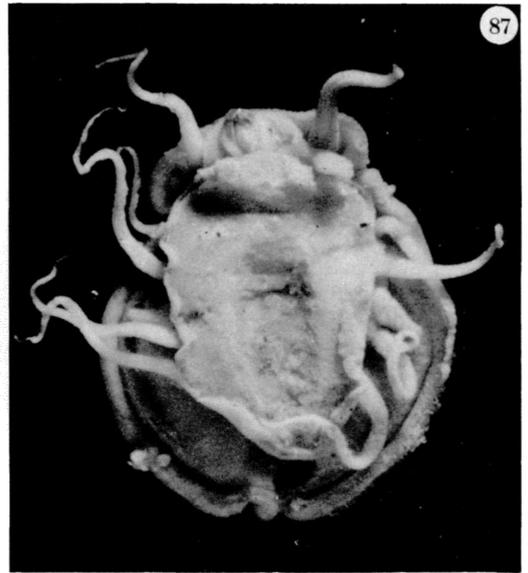
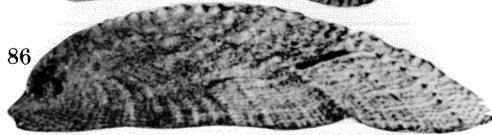
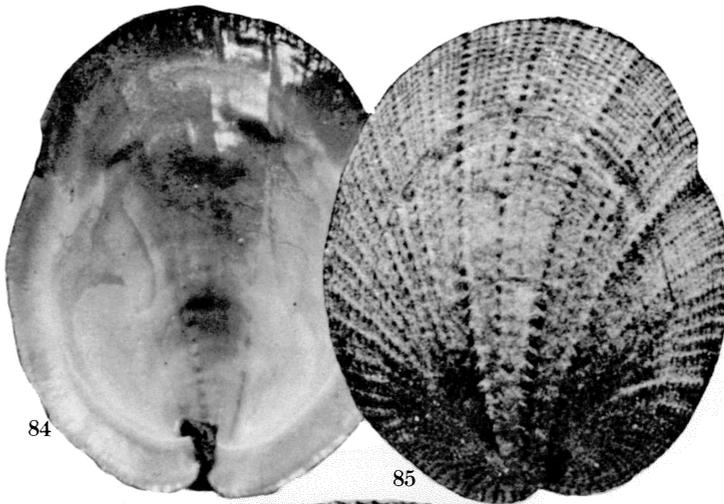
FIGURES 66-74. *Lepetodrilus guaymasensis*, new species. Figures 66-68: exterior, interior and left lateral views of holotype shell (female). Guaymas Basin, *Alvin* dive 1170 (magn. $\times 4.5$). Figure 69: ventral view of male body in partly crushed shell. Same dive number, shell now fragmented, dimensions not taken. Figures 70: ventral view of holotype body in shell (magn. $\times 5.3$). Figures 71 and 72: dorsal and left lateral views of holotype body (magn. $\times 5.3$). Figure 73: exterior view of female shell. Same dive number (magn. $\times 5.8$). Figure 74: protoconch of juvenile shell. Same locality, *Alvin* dive 1177 (magn. $\times 100$).



FIGURES 75-83. For description see opposite.

DESCRIPTION OF PLATE 11

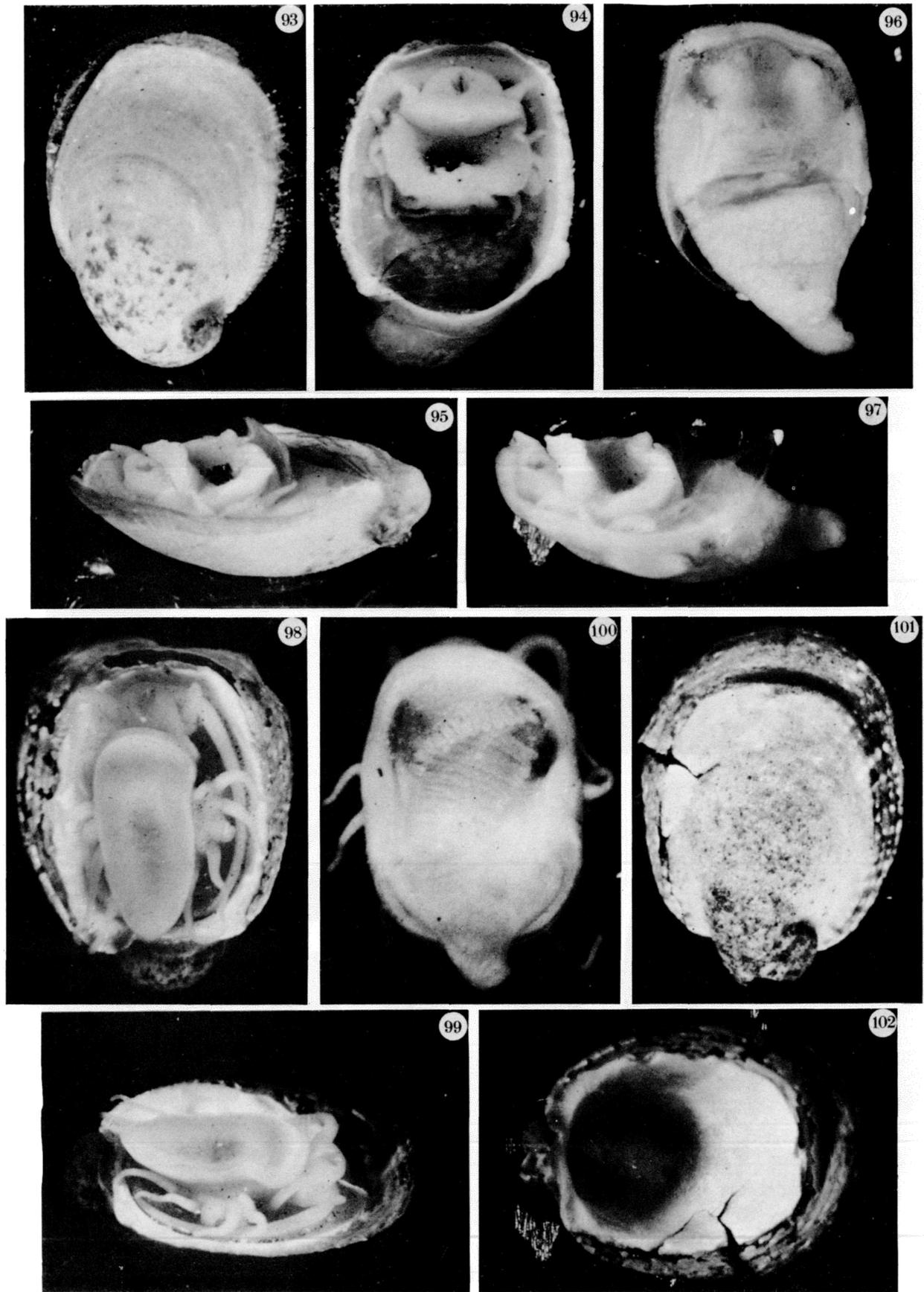
FIGURES 75-83. *Lepetodrilus fucensis*, new species. Figures 75-77: exterior, interior and right lateral views of holotype shell (male). Juan de Fuca Ridge, *Alvin* dive 1419 (magn. $\times 2.9$). Figure 78: ventral view of male body attached to shell. Same dive number (magn. $\times 8.3$). Figures 79-81: dorsal, ventral and right lateral views of holotype body (magn. $\times 5.9$). Figure 82: protoconch of juvenile shell. Same locality, *Alvin* dive 1410 (magn. $\times 100$). Figure 83: oblique lateral view of immature shell. Same locality, *Alvin* dive 1410 (magn. $\times 50$).



FIGURES 84-92. For description see opposite.

DESCRIPTION OF PLATE 12

FIGURES 84–92. *Gorgolettis emarginatus*, new species. Figures 84–86: interior, exterior and right lateral views of holotype shell (male). East Pacific Rise at 21° N, *Alvin* dive 1225 (magn. $\times 7.1$). Figures 87 and 88: ventral and dorsal views of body of holotype (magn. $\times 10.3$). Figure 89: left ventral view of immature male in shell showing periostracal band and penis. Same locality, *Alvin* dive 1221 (magn. $\times 16.2$). Figure 90: apex of immature shell showing protoconch. Same locality, *Alvin* dive 1221 (magn. $\times 95$). Figure 91: exterior view of shell, sex unknown (body lost at preservation). Same locality, *Alvin* dive 1211 (magn. $\times 15.6$). Figure 92: apertural view of juvenile with dried body and operculum. Same locality, *Alvin* dive 1221 (magn. $\times 100$).



FIGURES 93-102. For description see opposite.

margin; highest point at $\frac{1}{2}$ length of shell. Projecting apex a result of minimal growth of aperture at posterior; successive traces of aperture placement show apex to be recurved about $\frac{3}{4}$ of a whorl. Protoconch length 130 μm , right side exposed. Posterior slope lacking thickened structure below apex. Periostracum light to dark greenish-brown, tightly adhering, enveloping shell edge. Sculpture lacking except for coarse, unevenly spaced growth irregularities. Shell interior with thickened transverse ridge at posterior. Muscle scar horseshoe-shaped, narrowed posteriorly where located on inner side of interior ridge; lateral extensions of scar broad, anterior extremities rounded; left arm of muscle scar slightly longer than right. Aperture of mature shell flaring. Dimensions of holotype: 14.1 mm \times 8.8 mm \times 6.6 mm.

Radula (figures 15 and 16) typical for genus, overhanging cusp of rachidian markedly narrow, first lateral with inflated area of cusp in distal region; edge of cusp finely denticulate. Penis triangular, broad at base, not recurved (figure 69).

Type material

Holotype (figures 66–67 and 70–72) (female), LACM 2131, southern trough of Guaymas Basin (27° 01.0' N, 111° 25.0' W), *Alvin* dive 1170, 2019 m, 12 January 1982. Two paratypes (figure 69) (male), LACM, same dive, both specimens badly crushed; the radula (figures 15 and 16) was prepared from the specimen in figure 69. Paratype (figure 73) (female), USNM, same dive number (dimensions: 11.8 mm \times 7.7 mm \times 6.2 mm). One juvenile shell (figure 74), LACM, from *Alvin* dive 1177, southern trough of Guaymas Basin (27° 02.0' N, 111° 24.0' W), 2014 m, 20 January 1982.

Remarks

Lepetodrilus guaymasensis is one of the two largest species of the genus, exceeded in size only by *L. fucensis*. It shares the recurved apex only with *L. fucensis*, another species from a remote site. *Lepetodrilus guaymasensis* has some features (interior transverse ridge, raised ends and a relatively high profile) in common with *L. elevatus*. It may have been derived from *L. elevatus*, although other characters, such as the lack of the thickened area on the posterior slope and the different morphology of the first lateral tooth, do not lend support to that derivation.

There is some uncertainty about the habitat of this species, whether it is primarily associated with sulphide rocks or vestimentiferan tubes, both of which were collected from the Guaymas Basin site (Lonsdale 1984). Specimens were received in two vials, one reading 'on vestimentiferan tubes' and another 'from rock'. The only vestimentiferan reported from this site by Jones (1985) is *Riftia pachyptila* Jones, 1981. It is most likely that the species is associated with *Riftia*, but the question cannot be answered until the species is again collected. Of the species of *Lepetodrilus*, this species is represented by the smallest number of specimens. This may

DESCRIPTION OF PLATE 13

FIGURES 93–97. *Gorgolettis spiralis*, new species. Figures 93–95: dorsal, ventral and left lateral views of holotype (female) with attached body. East Pacific Rise at 13° N, *Cyana* dive 84–46 (magn. \times 18.5). Figures 96 and 97: dorsal and left lateral views of holotype specimen removed from shell (magn. \times 21.4).

FIGURES 98–102. *Gorgolettis patulus*, new species. Figures 98 and 99: ventral and right lateral views of holotype (male) with attached body, showing penis as outgrowth of oral disc on left side. Galapagos Rift, *Alvin* dive 989 (magn. \times 22.5). Figure 100: dorsal view of holotype body (magn. \times 27.2). Figures 101 and 102: exterior and interior views of holotype shell preserved in alcohol, damaged after removal of body (magn. \times 22.5).

be a reflection of inadequate sampling, though it is clear that *L. guaymasensis* is not an abundant species in its habitat.

The holotype (figure 66) and the figured male specimen (figure 69) have a basal outline that is elongate oval. However, this is subject to variation, as the female paratype (figure 73) has an outline with the anterior markedly narrow and a broader shell overall than the holotype.

The name is based on the type, and only known, locality: the Guaymas Basin. The vernacular name for this species used earlier (McLean 1985) was 'Guaymas'.

Lepetodrilus fucensis, new species

(Figures 17–20, plates 3 and 4, and figures 75–83, plate 11; part II, figure 15)

Diagnosis

Shell very thin, apical region projecting over posterior margin and strongly deflected to right; sculpture of growth increments only; penis triangular, broad at base.

Description

Shell extremely thin. Outline of aperture oval, anterior broader than posterior; margin of aperture not in one plane, randomly uneven. Profile high, apex projecting and overhanging posterior margin; highest point at $\frac{1}{2}$ length of shell. Projecting apex resulting from minimal growth of aperture at posterior; successive traces of aperture placement show apex to be recurved one full whorl. Protoconch length 120 μm , right side exposed (figure 82). Posterior slope lacking thickened structure below apex. Periostracum light to dark greenish-brown, tightly adhering, enveloping shell edge. Sculpture lacking except for coarse, unevenly spaced growth irregularities and irregular, broad, undulating ridges apparent as irregularities in shell margin. Shell interior lacking thickened transverse ridge at posterior. Muscle scar horseshoe-shaped, narrowed posteriorly; lateral extensions of scar broad, anterior extremities rounded. Aperture of large shell only slightly flaring. Dimensions of holotype: 23.1 mm \times 9.0 mm \times 5.5 mm.

Radula (figures 17 and 18) typical for genus; overhanging cusp of rachidian narrow, first lateral with broadly inflated overhanging area, broadest distally, edge evenly denticulate. Penis triangular, broad at base, not recurved (figures 78 and 80). Tip of gill not projecting over head.

Type material

Holotype (figures 75–77, 79–81) (male), LACM 2132, unnamed vent field, Endeavor Segment, Juan de Fuca Ridge (47° 57.0' N, 129° 04.0' W), *Alvin* dive 1419, 2208 m, 25 July 1984. Holotype the largest specimen from this dive. Paratypes: LACM, USNM, MNHN and other designated museums.

Material

Explorer Ridge near 50° N, 31 specimens from 3 *Pisces IV* dives in 1984 (table 2).

Endeavor Segment, Juan de Fuca Ridge near 48° N, 893 specimens from 2 *Alvin* dives in 1984 (table 2).

Axial Seamount, mid Juan de Fuca Ridge near 46° N, 30 specimens from 3 *Pisces IV* dives in 1983 (table 2).

Southern Juan de Fuca Ridge near 45° N, 592 specimens from 1 *Alvin* dive in 1984 (table 2).

Additional specimens from other dives from these expeditions were collected but have not been examined.

Remarks

Although most mature specimens are about 10 mm in length, this species attains the largest size in the genus (maximum length 23 mm, holotype), approached in size only by *L. guaymasensis* with which it shares the projecting apex and a very similar radular morphology. It is evidently most closely related to that species, differing in the thinner shell and lacking the posterior thickened ridge of the shell interior, and having the apical whorl strongly recurved to the right. I have not succeeded in separating the body of a large specimen from the shell without damaging the shell; the shell of the holotype is therefore broken. Smaller shells can be separated from the body but tend to crack when dried. The fragility of the shell is due to its extreme thinness and the lack of cross-bracing provided by the interior ridge of other high-profile species (*L. elevatus* and *L. guaymasensis*). Most specimens are encrusted with an organism similar to that which encrusts *L. pustulosus* and *L. elevatus*.

This species has been treated by De Burgh & Singla (1984), who reported that masses of bacteria are present on gill surfaces, undergoing endocytosis, uptaken directly into the gill filaments (see further commentary by Fretter in part II). De Burgh & Singla (1984) reported that the 'limpets cluster adjacent to the thermal vents, predominantly in stacks of up to six individuals, with the stacks being densely aggregated. Single limpets are much less common'. Chase *et al.* (1985, p. 213) noted that the limpets cluster on the sides of active sulphide chimneys, 'stacked one above the other in numbers estimated up to 100,000' on a single chimney formation.

In its irregular outline, *L. fucensis* is the most variable member of the genus. This is no doubt due to a sedentary habit and the tendency of specimens to form clumps with individuals attached to other shells below. None of the specimens are preserved in attached condition, so the exact orientation of individuals in relation to the shell below is unknown. There is no indication that any of the other species of *Lepetodrilus* occur in stacks.

Lepetodrilus fucensis has a relatively extended distribution from the Explorer Ridge off Vancouver Island, British Columbia, and along the Juan de Fuca Ridge off Washington to central Oregon. Locations of hydrothermal activity on the Juan de Fuca and Explorer Ridges were mapped by Malahoff (1985). I expect that the distribution of *L. fucensis* is limited to those sites.

The name is based on the general locality of the Juan de Fuca Ridge. The vernacular name used earlier (McLean 1985) was 'Juan de Fuca'.

GORGOLEPTIDAE, NEW FAMILY

Characters as in genus.

GORGOLEPTIS, NEW GENUS

Type species: *Gorgoleptis emarginatus*, new species.

Shell of limpet form with long, convex anterior slope; apex posterior, below highest elevation; apical whorl positioned at less than half height of mature shell. Protoconch small,

maximum length 130 μm , right side remaining visible; surface with sculpture of fine pitting. First whorl of teleoconch evenly coiled and displaced to right; second whorl broadly expanding. Periostracum thick, slightly inturned at edge. Sculpture of beaded or imbricate radial ribs. Shell interior with strong transverse ridge away from margin at posterior (the columellar edge of aperture), over which a periostracal band passes anteriorly to terminate adjacent to operculum. Posterior slope missing below apex (to accommodate periostracal band). Muscle scar paired, elongate, not joined posteriorly, about $\frac{1}{4}$ length of shell, placed slightly anterior to centre and midway between midline and margin.

Radula rhipidoglossate, rachidian small, lateral teeth 5 pairs, marginals numerous. Rachidian with narrow overhanging cusp and fine lateral serrations; shaft broad, with projecting lateral appendages. First lateral emerging above lateral appendage of rachidian, with broad overhanging cusp and serrate denticles on inner side, distal edge of main cusp straight-edged, in close contact with similarly smooth inner edge of second lateral, which has serrations only on outer edge. Third and fourth laterals like the second, with serrate outer edges but non-serrate inner edges to their overhanging cusps. Second, third and fourth laterals rising above rachidian, but not to height of rachidian in row anterior. Shafts of laterals broad, lower ends recessed, not revealing mode of articulation with row below. Fifth lateral with long tapered overhanging cusps, both edges serrate. Marginal teeth about 10 pairs, with broad tips, nearly same size as laterals but with longer, straighter shafts; cusps serrated on both sides; cusp alignment descending away from rachidian.

Epipodial tentacles long, five on left, four on right in addition to an anterior pallial tentacle on right; tentacles nearly same length as long cephalic tentacles except for third tentacle on both sides, which is short and blunt; eyes lacking. Outer fold of mantle thin (to extend under inturned periostracum); inner fold with fine tentacles. Oral area broad, expanded laterally and posteriorly, extended in males to form penis on left side. Mouth a vertical slit with short branches; jaws with fine chitinous rods. Foot oval, broad anteriorly, with prominent anterior opening of pedal gland, tapered and blunt posteriorly; foot with metapodium and small multispiral operculum, especially prominent in juveniles but concealed beneath foot on mature specimens in ventral view. Periostracal band extends anteriorly from columellar lip, shielding posterior viscera from contact with operculum.

Mantle cavity extending to posterior end of left shell muscle. Ctenidium bipectinate for $\frac{2}{3}$ of length at free tip, where left and right lamellae are of equal size; posteriorly the left lamellae are lacking and ctenidium is monopectinate.

Nervous system hypoathroid-dystenoid. Heart with two auricles; intestine with anterior loop; rectum passing through ventricle. Left kidney within mantle skirt, relatively small. Sexes separate, gonad ventralmost in body cavity, discharging through right kidney. Gonoduct of male with vesicula seminalis and prostate; that of female lacking receptaculum seminis. Penis functions as a pipette; fertilization in mantle cavity.

The gorgoleptid shell differs from the lepetodrilid shell in three major ways: (1) the muscle scar is not connected posteriorly to form a horseshoe; (2) the posterior emargination to accommodate the periostracal band is not known in the lepetodrilids; (3) there is an initial coiled phase of one whorl, unlike the lepetodrilid teleoconch, which has a coiled phase of less than one whorl. Lepetodrilid limpets also differ in having no operculum. Major differences in the shell muscles, epipodial elaborations, gill structure, and reproductive anatomy are further discussed in part II.

Radular differences are pronounced: the narrow cusp of the rachidian is unlike the broadly tapered cusp of lepetodrilids, the first marginal is not greatly elongate and oblique as in lepetodrilids, and the straight edges to the inner surfaces of the second, third and fourth laterals are unique. Perhaps the most characteristic and significant feature of the gorgoleptid radula is that the first and second laterals fit so closely together that they may function like a single fused tooth. However, there are points of similarity between the lepetodrilid and gorgoleptid radulae. In both families the rachidian teeth have the lateral appendages at mid-height, the laterals rise to a height above the rachidian, and the marginals have broad tips and are nearly as prominent as the laterals.

The type species *G. emarginatus*, characterized by its two strong, node-bearing ribs, is known from relatively few specimens from the East Pacific Rise at 21° N. The genus is also represented by two additional new species differing in shell sculpture and proportions: *G. spiralis* from the East Pacific Rise at 13° N and *G. patulus* from the Galapagos Rift. All known specimens of both *G. spiralis* and *G. patulus* are less than 3 mm in length. In external features these specimens resemble the juveniles of *G. emarginatus* in having the head nearly as large as the foot. It therefore seems certain that fully grown specimens of the two species are unknown.

Specific characters in the genus relate to differences in strength of the radial sculpture, breadth of the periostracal band and presence or absence of the umbilical chink in the coiled early phase.

Relatively few specimens of the gorgoleptid limpets are known (table 3), so few that notes on the particular habitat have not been made by expedition participants. Specimens tend to have more of the metallic sulphide particles trapped in the mantle cavity or mantle groove, suggesting that these limpets may live away from the *Riftia*, perhaps directly on sulphide crust deposits. Another clue to suggest that the habitat may be more cryptic than that of the

TABLE 3. STATION DATA AND NUMBER OF SPECIMENS FROM DIVES YIELDING

GORGOLEPTIS SPECIES					
dive	depth/m	position	date	number	
<i>Gorgoleptis emarginatus</i>					
<i>Alvin</i> dives, East Pacific Rise at 21° N					
1211	2615	20° 50.0' N, 109° 06' W	17 Apl 1982	3	
1219	2612	20° 50.0' N, 109° 06' W	25 Apl 1982	3	
1221	2618	20° 50.0' N, 109° 06' W	04 May 1982	18	
1222	2614	20° 50.0' N, 109° 06' W	06 May 1982	2	
1225	2618	20° 50.0' N, 109° 06' W	09 May 1982	2	
1226	2616	20° 50.0' N, 109° 06' W	10 May 1982	1	
				total	29
<i>Gorgoleptis spiralis</i>					
<i>Cyana</i> dives, East Pacific Rise at 13° N					
84-38	2630	12° 48.8' N, 103° 56.8' W	15 Mar. 1984	2	
84-46	2635	12° 48.6' N, 103° 56.7' W	28 Mar. 1984	1	
				total	3
<i>Gorgoleptis patulus</i>					
<i>Alvin</i> dives, Mussel Bed, Galapagos Rift					
989	2482	00° 48.0' N, 86° 09.0' W	06 Dec. 1979	1	
991	2490	00° 48.0' N, 86° 09.0' W	08 Dec. 1979	1	
				total	2

Lepetodrilus species is suggested by the relatively clean shells. None of the specimens have encrustations of the unknown organism that are characteristic of the lepetodrilid species.

Etymology: the name combines the Greek name *Gorgo*, for the three sisters in Greek mythology with snaky locks, with the Greek noun *lepas*, limpet. In ventral view the long epipodial and cephalic tentacles have a startling serpentine appearance.

KEY TO THE SPECIES OF *GORGOLEPTIS*

1. Radial sculpture of fine rows of beads and two prominent ridges *G. emarginatus*
 Radial sculpture of fine rows of beads only 2
2. Shell evenly expanding, umbilical chink absent *G. spiralis*
 Shell broadly inflated, umbilical chink present *G. patulus*

Gorgoleptis emarginatus, new species

(Figures 21–24, plate 4, and figures 84–92, plate 12; part II, figures 16 and 17)

Diagnosis

Shell relatively large, primary sculpture of two strongly noded ribs.

Description

Shell relatively large. Outline of aperture oval except for two indentations, the posterior indentation for the passage of the periostracal band, and a lesser indentation on right side just anterior to centre, which overlies the pallial tentacle. Margin of aperture not in one plane, sides slightly raised relative to ends. Profile of moderate height; highest elevation of shell near midpoint. Protoconch small, maximum length 120 μm , right side remaining visible. Shell apex above posterior margin, first teleoconch whorl displaced to right and extending posterior to margin except in largest shells. First whorl coiled, with umbilical chink, outer lip broadly expanding. Small multispiral operculum remaining visible through shell length of at least 3 mm; in larger specimens concealed by foot in ventral view. Periostracum thick, light greenish-brown, only slightly inturred over shell edge in mature specimens. Sculpture of imbricate radial ribs, two of which are first to appear and remain more prominent and strongly noded. Numerous lesser ribs emerge at shell length of 2–5 mm. One prominent lesser rib extends to marginal indentation on right. Concentric sculpture of growth irregularities, producing imbrications on crossing radial ribs. Interior of shell with strong transverse ridge, which is broadly separated from shell edge posteriorly, and over which periostracal band passes. Interior of shell with grooves marking position of two primary ribs and pits corresponding to exterior nodes. Muscle scars paired, not joined posteriorly, about $\frac{1}{4}$ length of shell, placed slightly anterior to centre and midway between midline and margin; anterior ends rounded, posterior ends tapered, alignment slanting posteriorly toward midline rather than parallel to margin. Dimensions of holotype: 8.9 mm \times 7.5 mm \times 2.2 mm.

Radula (figures 21–24) and external features as described above for genus. Penis continuous with left oral lobe, usually retained in mantle groove; tip blunt, expanded (figures 87 and 89).

Type material

Holotype (male), LACM 2133, East Pacific Rise at 21° N (20° 50.0' N, 109° 06.0' W), *Alvin* dive 1225, 2618 m, 9 May 1982. The holotype is the largest known specimen. Paratypes: LACM, USNM, and MNHM.

Material

East Pacific Rise at 21° N, 28 paratype specimens from 6 *Alvin* dives in 1982 (table 3). Of these, only 7 specimens had shell lengths greater than 3 mm.

Remarks

Gorgolettis emarginatus, the type species, is the largest member of the genus and the only one with sculpture of two prominent carinations. It is also the only species exhibiting the marginal indentation of the right side. The shell of the holotype retains the brown inorganic encrustation characteristic of this species. The shell of this species can not be confused with that of any other limpet, as the two marginal indentations are unique.

The name is a Latin adjective meaning notched, with reference to the posterior notch. The vernacular name used earlier for this species (McLean 1985) was 'emarginate'. Turner *et al.* (1985, figures 1a-1c) illustrated the protoconch and early juvenile, identified only as 'unnamed limpet'.

Gorgolettis spiralis, new species

(Figures 93-97, plate 13; part II, figure 18a)

Diagnosis

Known only from small specimens, but differing from other members of genus in lacking the broad umbilical chink in specimens of 2.4-3.3 mm in length.

Description

Shell known only from three poorly preserved small female specimens of 3.3 mm in maximum length, decalcified at the margin, though the periostracum remains extended to former position of margin. These specimens are identified as *Gorgolettis* in having long epipodial tentacles, a wide periostracal band, and in having a small multispiral operculum comparable to the same stage of development in *G. emarginatus*. Protoconch concealed by encrusting deposits. First whorl of teleoconch coiled, the suture with the second whorl (which forms anterior slope of limpet) deeply impressed. Posterior margin of aperture lacking the umbilical chink of *G. emarginatus* at the same stage. The posterior periostracal band extends across the entire posterior end of the aperture where it makes contact with the foot dorsal to the area of opercular attachment. Sculpture of fine radial ribs having fine nodes or imbrications, not the bicarinate early sculpture of *G. emarginatus*. Dimensions of holotype: 3.3 mm × 2.5 mm × 1.0 mm.

Type material

Holotype (figures 93-97) (female), MNHN, East Pacific Rise at 13° N (12° 48.6' N, 103° 56.7' W), *Cyana* dive 84-46, 2635 m, 28 March 1984. The specimen is generally free of encrustations. The body is separated from the shell but the shell remains preserved in alcohol, lest the shell crack further on drying.

Material

Two paratypes, MNHN, East Pacific Rise at 13° N (12° 48.8' N, 103° 56.8' W), *Cyana* dive 84-38, 2630 m, 15 March 1984. These specimens are smaller than the holotype (lengths 2.6

and 2.4 mm) but have thick inorganic encrustations. Spiral sculpture appears to be more pronounced, although the actual sculpture is concealed by the deposits.

Remarks

Although the material is sparse, not fully grown and in poor condition, its description enables formal recognition of the fact that *Gorgoleptis* is a genus that has speciated at distant sites. *Gorgoleptis spiralis* is unique in the extreme breadth of the periostracal band. It differs from *G. emarginatus* in lacking the two strong carinations and lacking the umbilical chink.

The name is a Latin noun for coil or spiral, with reference to the even coil of the early whorls. The vernacular name used earlier for this species (McLean 1985) was 'micro-emarginate'.

Gorgoleptis patulus, new species

(Figures 98–102, plate 13; part II, figure 18*b, c*)

Diagnosis

Differing from *G. spiralis* in having an umbilical chink and from *G. emarginatus* in lacking the two strongly noded carinations.

Description

Shell known only from two poorly preserved small specimens of 2.8 mm in maximum length, both specimens decalcified at the margin but with periostracal remains extended to former position of the margin. As with *G. spiralis*, these specimens are identified as *Gorgoleptis* by having the long epipodial tentacles, the wide posterior periostracal band, and a small multispiral operculum, as in similarly sized specimens of *G. emarginatus* and *G. spiralis*. Protoconch and first teleoconch whorl of both specimens decalcified and torn to some extent, concealed by encrusting deposits. First whorl coiled, suture with second whorl (the inflated portion forming anterior slope of the limpet) deeply impressed. Smaller specimen with clearly defined umbilical chink; the ridge that defines this also apparent on the larger holotype specimen. Holotype specimen (in ventral view) showing a broader and more extended development of the posterior margin than in *G. spiralis*. In dorsal view this produces a posterior slope to the limpet lateral to the early whorl at both sides, unlike the more even spiral form of *G. spiralis*. Periostracal band present but only as broad as that portion of the early shell that shows in ventral view, less broad than the periostracal band of *G. spiralis*. Sculpture of finely beaded radial ribs, not the bicarinate early sculpture of *G. emarginatus*. Dimensions of holotype: 2.8 mm × 2.1 mm × 0.7 mm.

Type material

Holotype (figures 98–102) (male), LACM 2134, Mussel Bed vent field, Galapagos Rift (0° 48.0' N, 86° 09.0' W), *Alvin* dive 989, 2482 m, 6 December 1979. Removal of the body from the shell resulted in further damage to the shell and the early whorl (figures 101 and 102), but the specimen was photographed before this damage was done (figures 98 and 99), showing the intact early whorl. The shell remains preserved in alcohol.

Material

Paratype, LACM, same vent field, Galapagos Rift, *Alvin* dive 991, 2490 m, 8 December 1979. Length 1.5 mm.

Remarks

Like *Gorgolettis spiralis*, this species is described to document speciation in the genus, despite the small size, few specimens, and poor preservation of the material. Although shell characters of full grown specimens remain unknown, there should be no difficulty in distinguishing this species from its congeners. The holotype specimen may be sexually mature, however, as the labial penis of the male holotype has comparable development to that of the illustrated juvenile specimen of *G. emarginatus* (figure 89).

The name is a Latin adjective meaning open or spread out, with reference to the more inflated shell form, compared with that of *G. spiralis*. The vernacular name used earlier for this species (McLean 1985) was 'Galapagos-emarginate'.

DISCUSSION

Potential distribution of Lepetodrilacea

Although relatively few hydrothermal sites have been explored, some generalizations about the distribution of lepetodrilaceans can be made. Lepetodrilaceans of the East Pacific Rise and Galapagos Rift are associated with the three large invertebrate species treated by Hessler & Smithey (1983) and Hessler *et al.* (1985): *Riftia pachyptila*, *Calyptogenia magnifica* and *Bathymodiolus thermophilus*, each of which is positioned in the path of warm effluent. Cavanaugh (1985) considered these species each to harbour chemoautotrophic symbionts, although Morton (1986) did not support that argument for *C. magnifica*. The limpets live in close association with these species but have not been shown to have bacterial symbionts.

Other unexplored vent fields are known along these ridges; their locations were treated by Crane (1985) and Malahoff (1985). These vent fields are likely to yield the four broadly distributed species of *Lepetodrilus*. No information is yet available on the potential presence of limpets on the southern portion of the East Pacific Rise between 17° S and 20° S, which has been explored by the French submersible *Cyana* (Desbruyères *et al.* 1985), although it is likely that lepetodrilaceans are present. As noted by the last author, 'our knowledge of the hydrothermal ecosystems along the fast-spreading ridges, even their distribution and locations, is still in its infancy.' However, to my knowledge, there are no deep-sea, hydrothermally active sites in the eastern Pacific at which lepetodrilaceans have not been found, once sampling has been done.

Unlike two of the new superfamilies remaining to be treated, the group is known only from thermally active vent fields, not from the cold seeps or cold subduction zones that have yielded some invertebrates related to the taxa known from hydrothermal vents. Only the new 'symmetrical' superfamily of McLean (1985) is known from the cold Florida Escarpment Site (see Paull *et al.* 1984; Hecker 1985); there are no limpets at the Oregon subduction site described by Suess *et al.* (1985). Turner (1985) noted that predators from adjacent communities can invade cold seep sites because the water column is less toxic than at hydrothermal vent sites; she considered that vulnerability to predators could explain the poor representation of limpets at seep sites.

Lepetodrilaceans have apparently not adapted to the more extreme temperature and chemical conditions of the 'black smoker' vents that are known from some of the hydrothermal sites. Only the new 'tapersnout' superfamily of McLean (1985) is associated with the hotter

black smoker habitat; Baross & Deming (1985, figure 6) illustrated one of the two 'tapersnout' species associated with the black smokers.

Comparisons based on shell characters

Fretter (part II) amply shows that anatomy of the lepetodrilacean limpets differs at the superfamily level from other archaeogastropods. Even if the anatomy of these limpets were unknown, the shells could not be assigned to an established superfamily. The patellacean limpets have nothing in common with lepetodrilacean shells, as the shell apex of patellaceans is anterior and the shell structure has complex layers (MacClintock 1967). Trochacean limpets of the subfamily Stomatellinae differ in their asymmetry and having a nacreous interior layer. Closer comparisons are warranted with limpet families having a posterior apex and non-nacreous interior: the phenacolepadid, cocculinid, pseudococculinid, and capulid limpets. Capulids differ in having a projecting apex with early teleoconch sculpture of strong radial ribs, and most are markedly irregular in outline as a result of their sessile habit. The muscle scar eliminates the cocculinid and pseudococculinid limpets, as the anterior tips of the muscle scar are greatly expanded and project inwardly, whereas the entire remaining portion of the muscle is narrow and constricted into bundles in these two families (J. H. McLean, unpublished observation).

On shell characters, the phenacolepadid neritaceans are the closest to the lepetodrilaceans, for both groups have the horseshoe-shaped muscle scar narrow posteriorly and both may have a posterior transverse ridge on the shell interior (compare figure 37 for *L. elevatus* with figure 7 of Fretter (1984) for *Phenacolepas*). However, the narrow posterior muscle scar is not a feature of major taxonomic significance in limpets with a posterior apex, because shell muscle never fills the apical pit in limpets, which leaves little space for a broad posterior muscle between the apex and shell margin. Of more importance is the unique configuration of the phenacolepadid muscle scar: its two arms are constricted at half the distance from the anterior tips, as illustrated by Thiele (1909, plate 5, figure 6a) and Fretter (1984, figure 1). How this outline relates to phenacolepadid anatomy is clearly shown by Fretter (1984, figure 4). Another major difference between shells of phenacolepadids and lepetodrilaceans is the inturned periostracum of the latter.

Lepetodrilacean shells most resemble those of the 'tapersnout' superfamily (yet to be described) of rift-vent limpets (McLean 1985) in having similar shell structure, the inturned periostracum, the posterior apex offset to the right, the highest elevation of the shell anterior to the apex, the horseshoe-shaped muscle narrow posteriorly, and the transverse, posterior ridge on the interior of some species. However, one shell character can apparently be used to distinguish between the two groups: the pitted surface of the protoconch of lepetodrilacean species (see especially Turner *et al.* 1985, figures 1c, 2c, 6c, 7c and 8c), in contrast to the strong ridges on the protoconch of a tapersnout limpet (see Turner *et al.* 1985, figure 5c). These characters can only be seen with SEM.

Possible fossil affinity

No fossil limpets can be related to the Lepetodrilacea, although there is a clade having similar shell proportions: the Jurassic to early Cretaceous *Symmetrocopus* (see Knight *et al.* 1960, p. 232, figure 144). The muscle scar of that relatively large-shelled genus has recently been unknown (McLean 1985), but, based on a new illustration of Kase (1984, plate 24,

figure 6), is now known to have a general horseshoe configuration: narrow posteriorly, the two limbs broadest anteriorly (though not to the extent of cocculinaceans), not constricted on the sides (as in phenacolepadids). Kase (1984) cited an earlier illustration of a protoconch in an unidentified species of *Symmetrocapulus* figured by Gründel (1977, plate 1, figure 1 and text figure 1), in which the protoconch is shown tilted to the right, resembling that of lepetodrilacean limpets (and 'tapersnout' limpets as well). Species of *Symmetrocapulus* attained 98 mm in length (Kase 1984) and were associated with shallow-water environments. The size difference between lepetodrilaceans and *Symmetrocapulus* and the lack of congruence between general outlines of muscle scars argues against drawing conclusions about affinity between the two, especially because of the close resemblance between the new 'tapersnout' superfamily and the lepetodrilaceans on shell characters.

Another genus, the Triassic *Phryx*, assigned to the Symmetrocapulidae by Knight *et al.* (1960, figure 144, 2) is not so large as *Symmetrocapulus* and has a general resemblance to one of the new 'tapersnout' limpets. The protoconch is unknown, making further comparisons unproductive.

The subfamily Symmetrocapulinae had been assigned by Wenz (1938) to the Patellidae, in the mistaken belief that the apex is anterior. Kase (1984) assigned *Symmetrocapulus* to the mesogastropod Capulidae without discussion. That assignment is not supported here, as the asymmetry of Recent capulids and their appearance in the Cretaceous with the significant radiation taking place in the Tertiary (Wenz 1938) suggest no connection between the two. Asymmetry is likely to be a primitive character of capulids, as the earliest members would be expected to partly retain the asymmetry of their coiled predecessors.

In my opinion, *Symmetrocapulus* is better classed as an archaeogastropod, considering that its protoconch characters are similar to those of lepetodrilaceans and 'tapersnout' limpets. I provisionally rank Symmetrocapulidae as a sister group to lepetodrilaceans and to the 'tapersnout' limpets.

Another possibility is an affinity of the lepetodrilaceans with the Cretaceous *Damesia*, assigned by Knight *et al.* (1960, figures 181–186) to the Neritopsidae. *Damesia* has an inflated aperture recalling the juvenile stage of *Lepetodrilus* (compare figure 33 herein). Further comparisons with *Damesia* may be productive.

Hypothesis of origin and age

Limpet-derivatives of coiled gastropods have arisen in a number of superfamilies of gastropods, primarily in the Archaeogastropoda, but also in the Mesogastropoda, Neogastropoda, Opisthobranchia and Pulmonata. The Lepetodrilacea, as well as the Neomphalacea (and the remaining new families yet to be described), have many advanced features, but all have arisen from an archaeogastropod stock (McLean 1985; Fretter, part II and personal communication). This is consistent with the hypothesis of archaic origin, as has been previously discussed (McLean 1981, 1985). Archaeogastropods were the dominant gastropods in shallow waters of the Palaeozoic and early Mesozoic (Knight *et al.* 1960). Numerous radiations took place, although we can only speculate as to their anatomies. Many evolutionary stocks would have been available to enter the hydrothermal-vent community during that time. Submergence to the deep-sea hydrothermal community would have protected these clades from the late Permian and late Cretaceous extinctions. The only satisfactory explanation for the unique anatomies and radular morphologies in the

hydrothermal-vent limpets is that these are conservative characters that were present in their extinct predecessors in the shallow marine environment of the late Palaeozoic and early Mesozoic. The anatomical evidence relates the Lepetodrilacea at the superfamily level to the living archaeogastropod superfamilies, with which they had common ancestry. It is, therefore, necessary to place their origin within the period – late Palaeozoic to early Mesozoic – in which the actual common ancestors are presumed to have lived.

Rocks that provide evidence of 'submarine volcanic exhalations' are available over a time span of 3.5 billion years (Skinner 1983). Tectonic activity in the Mesozoic Tethys Ocean has been documented (Robertson & Boyle 1983). Haymon *et al.* (1984) and Haymon & Koski (1985) have described fossil worm tubes in late Cretaceous deposits of the Samail Ophiolite, Oman, a remnant of a spreading centre in the Tethyan Sea. The fossil worm tubes of the Samail Ophiolite resemble those of vestimentiferans that have been fossilized *in situ* in sulphide deposits on the Juan de Fuca Ridge. Considering that the hydrothermal-vent habitat has been available throughout geological time, I think it likely that traces of limpets and other molluscs will be found in ancient hydrothermal deposits. Shell dissolution takes place in the hydrothermal habitat (see Lutz *et al.* 1985), but the rapid process of fossilization at the black smokers described by Desbruyères *et al.* (1985) should enable trace fossils to be recognized.

Although the hydrogen sulphide of the hydrothermal-vent environment is toxic to most marine animals (Powell & Somero 1983), the species living in close proximity to the vents have mechanisms by which they avoid sulphide poisoning (Felbeck *et al.* 1985). However, the toxicity of the environment prevents the encroachment of species from the ambient deep-sea fauna into this community (Hessler & Smithey 1983). Successful invasions of life forms new to the community, particularly predators, have evidently been infrequent. The limpets need no defence against such usual molluscan predators as drill snails, as these are unknown in the rift-vent habitat. Seastar predators are unknown, except for rare occurrences at the Juan de Fuca Ridge (M. L. Jones, personal communication). Sulphide toxicity, with respect to new immigrants should, therefore, promote stability and longevity within the community over long periods of geological time.

Molluscs have been shown to have an unusual ability to adapt to sulphide environments in shallow water. Some shallow water bivalves have been reported to harbour sulphur-oxidizing bacteria in their gills (Dando *et al.* 1985, 1986). Stein (1984) found that such archaeogastropod grazers as *Haliotis*, *Megathura* and *Norrisia*, as well as acmaeid limpets, thrive by feeding upon mats of filamentous sulphur-oxidizing bacteria that surround hydrothermal vents in shallow water in southern California (Kleinschmidt & Tschauder 1985). Stein (1984) found that shallow-water echinoids could not withstand the toxicity of vent water. That observation is in keeping with the lack of echinoderms, at least on the vent walls, in the deep-sea hydrothermal vents. The macroevolutionary origin and subsequent radiations of the limpet families may well have been a phenomenon of the hydrothermal environment, given the ease with which living archaeogastropods appear to adapt to an H₂S environment in shallow water. Shallow-water vents like those reported by Stein (1984) and Kleinschmidt & Tschauder (1985) may have been sufficiently widespread in the past to have offered sites for macroevolution.

It is unlikely that the ancestors of the rift-vent limpets came from the deep sea, as there should be a few survivors elsewhere in the deep sea if this were the case. Clarke (1962) found no evidence that any molluscan families originated in the deep sea. Recently, Jablonski *et al.* (1983) showed that throughout the Phanerozoic the first occurrences, i.e. macroevolution, of

higher taxa in all groups with fossil records are in nearshore, stressful environments with low species diversity. The deep-sea hydrothermal-vent community is also an environment with low species diversity; on this basis it could be argued that the vent environment might be favourable for macroevolution. However, shallow-water species are broadly tolerant and, therefore, more likely to make the stressful transfer to the toxic hydrothermal environment than are the relatively unstressed inhabitants of the deep sea. After a macroevolutionary origin in shallow water, migration and submergence to the deep-sea hydrothermal habitat could then take place, once the ancestral founder-stocks had become adapted to sulphide régimes in shallow water. This explanation was first postulated by Newman (1979) to explain the origin of the scalpellid *Neolepas zeviniae* at 21° N.

There are examples in other phyla of living members of the rift-vent communities that have Mesozoic affinities: the Cretaceous worm tubes (Haymon *et al.* 1984) and three barnacle genera of Mesozoic affinity (Newman 1985). Newman discusses still other examples of archaic origins for hydrothermal-vent invertebrates, based on degree of endemism and generic age. Hickman's (1984, p. 24) explanation for the uniqueness of rift-vent taxa: 'a relatively recent *in situ* adaptive radiation' fails to explain how the archaeogastropod features of these taxa could be derived from living archaeogastropods (for further discussion see McLean (1985); Newman (1985)).

In an earlier account of the Galapagos Rift limpet *Neomphalus* (McLean 1981), I proposed that it represents a highly specialized limpet-derivative of a group of coiled gastropods that was prolific in shallow Palaeozoic seas, with a minor record in the Mesozoic. Other new limpet families, restricted to the hydrothermal-vent community, also are derived from archaeogastropod stocks and I now apply similar arguments to explain the origin of the Lepetodrilacea.

I hypothesize that the ancestors of the living hydrothermal-vent limpets entered the community, first by colonizing hydrothermal sites in shallow water and then dispersing to successively deeper hydrothermal-vent sites. Essential features of anatomy and radulae were shared by their extinct predecessors. Subsequent evolution is considered to be a radiation at the level of genera and species within this community. I suggest that the hydrothermal-vent limpets are living derivatives of families that once were distributed more broadly in the shallow seas of the late Palaeozoic and Mesozoic. Evidence in support of this may best be sought through a better understanding of the fossil record of archaeogastropods.

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National Museum of Natural History, Washington, sent limpets from the Juan de Fuca and Explorer Ridges collected by the *Pisces IV* and the *Alvin*.

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REFERENCES

- Baross, J. A. & Deming, J. W. 1985 The role of bacteria in the ecology of black smoker environments. In *The hydrothermal vents of the Eastern Pacific: an overview* (ed. M. L. Jones) (*Bull. biol. Soc. Wash.* **6**), pp. 355–371.
- Berg, C. J. Jr 1985 Reproductive strategies of mollusks from abyssal hydrothermal vent communities. In *The hydrothermal vents of the Eastern Pacific: an overview* (ed. M. L. Jones) (*Bull. biol. Soc. Wash.* **6**), pp. 185–197.
- Cavanaugh, C. M. 1985 Symbioses of chemoautotrophic bacteria and marine invertebrates from hydrothermal vents and reducing sediments. In *The hydrothermal vents of the Eastern Pacific: an overview* (ed. M. L. Jones) (*Bull. biol. Soc. Wash.* **6**), pp. 373–388.
- Chase, R. L., Delaney, J. R., Karsten, J. L., Johnson, H. P., Juniper, S. K., Lupton, J. E., Scott, S. D., Tunnicliffe, V., Hammond, S. R. & McDuff, R. E. 1985 Hydrothermal vents on an axis seamount of the Juan de Fuca Ridge. *Nature, Lond.* **331**, 212–214.
- Clarke, A. H. Jr 1962 On the composition, zoogeography, origin and age of the deep-sea mollusk fauna. *Deep Sea Res.* **9**, 291–306.
- Corliss, J. B., Dymond, J., Gordon, L. I., Edmond, J. M., Herzen, R. P. von, Ballard, R. D., Green, K., Williams, D., Bainbridge, A., Crane, K. & Andel, T. H. van 1979 Submarine thermal springs on the Galapagos Rift. *Science, Wash.* **203**, 1073–1083.
- Crane, K. 1985 The distribution of geothermal fields along the mid-ocean ridge: an overview. In *The hydrothermal vents of the Eastern Pacific: an overview* (ed. M. L. Jones) (*Bull. biol. Soc. Wash.* **6**), pp. 3–18.
- Dando, P. R., Southward, A. J., Southward, E. C., Terwilliger, N. B. & Terwilliger, R. C. 1985 Observations on sulphur-oxidising bacteria and haemoglobin in the gills of the bivalve mollusc *Myrtea spinifera* and their ecological significance. *Mar. Ecol. Prog. Ser.* **23**, 85–98.
- Dando, P. R., Southward, A. J. & Southward, E. C. 1986 Chemoautotrophic symbionts in the gills of the bivalve mollusc *Lucinoma borealis* and the sediment chemistry of its habitat. *Proc. R. Soc. Lond. B* **227**, 227–247.
- De Burgh, M. E. & Singla, C. L. 1984 Bacterial colonization and endocytosis on the gill of a new limpet species from a hydrothermal vent. *Mar. Biol.* **84**, 1–6.
- Desbruyères, D., Crassous, P., Grassle, J., Khrpounoff, A., Reyss, D., Rio, M. & van Praet, M. 1982 Données écologiques sur un nouveau site d'hydrothermalisme actif de la ride du Pacifique oriental. *C. r. Séanc. Acad. Sci., Paris III*, **295**, 489–494.
- Desbruyères, D. & Laubier, L. 1983 Primary consumers from hydrothermal vent animal communities. In *Hydrothermal processes at seafloor spreading centers* (ed. P. A. Rona, K. Bostrom, L. Laubier & K. L. Smith, Jr), pp. 711–734. New York: Plenum.
- Desbruyères, D., Gaill, F., Laubier, L. & Fouquet, Y. 1985 Polychaetous annelids from hydrothermal vent ecosystems: an ecological overview. In *The hydrothermal vents of the Eastern Pacific: an overview* (ed. M. L. Jones) (*Bull. biol. Soc. Wash.* **6**), pp. 103–116.
- Felbeck, H., Powell, M. A., Hand, S. C. & Somero, G. N. 1985 Metabolic adaptations of hydrothermal vent animals. In *The hydrothermal vents of the Eastern Pacific: an overview* (ed. M. L. Jones) (*Bull. biol. Soc. Wash.* **6**), pp. 261–272.
- Fretter, V. 1984 The functional anatomy of the neritacean limpet *Phenacolepas omanensis* Biggs and some comparison with *Septaria*. *J. mollusc. Stud.* **50**, 8–18.
- Fretter, V. 1988 New archaeogastropod limpets from hydrothermal vents; superfamily Lepetodrilacea. II. Systematic descriptions. *Phil. Trans. R. Soc. Lond. B* **318**, 33–82. (Following paper.)
- Fretter, V., Graham, A. & McLean, J. H. 1981 The anatomy of the Galapagos Rift limpet, *Neomphalus fretterae*. *Malacologia* **21**, 337–361.

- Gründel, J. 1977 Gastropoden aus dem Dogger. *Z. Geol. Wiss.* **5**, 129–264.
- Haymon, R. M., Koski, R. A. & Sinclair, C. 1984 Fossils of hydrothermal vent worms discovered in Cretaceous sulfide ores of the Samail Ophiolite, Oman. *Science, Wash.* **223**, 1407–1409.
- Haymon, R. M. & Koski, R. A. 1985 Evidence of an ancient hydrothermal vent community: fossil worm tubes in Cretaceous sulfide deposits of the Samail Ophiolite, Oman. In *The hydrothermal vents of the Eastern Pacific: an overview* (ed. M. L. Jones) (*Bull. biol. Soc. Wash.* **6**), pp. 57–67.
- Hecker, B. 1985 Fauna of a cold sulfur-seep in the Gulf of Mexico: comparison with hydrothermal vent communities and evolutionary implications. In *The hydrothermal vents of the Eastern Pacific: an overview* (ed. M. L. Jones) (*Bull. biol. Soc. Wash.* **6**), pp. 465–474.
- Hessler, R. W. & Smithey, W. M. Jr 1983 The distribution and community structure of megafauna at the Galapagos Rift hydrothermal vents. In *Hydrothermal processes at seafloor spreading centers* (ed. P. A. Rona, K. Bostrom, L. Laubier & K. L. Smith, Jr), pp. 735–770. New York: Plenum.
- Hessler, R. W., Smithey, W. M. Jr & Keller, C. H. 1985 Spatial and temporal variation of giant clams, tube worms and mussels at deep-sea hydrothermal vents. In *The hydrothermal vents of the Eastern Pacific: an overview* (ed. M. L. Jones) (*Bull. biol. Soc. Wash.* **6**), pp. 411–428.
- Hickman, C. S. 1983 Radular patterns, systematics, diversity, and ecology of deep-sea limpets. *Veliger* **26**, 73–92.
- Hickman, C. S. 1984 A new archaeogastropod (Rhipidoglossa, Trochacea) from hydrothermal vents on the East Pacific Rise. *Zool. Scr.* **13**, 19–25.
- Jablonski, D., Sepkoski, J. J. Jr, Bottjer, D. J. & Sheehan, P. M. 1983 Onshore-offshore patterns in the evolution of Phanerozoic shelf communities. *Science, Wash.* **222**, 1123–1125.
- Jones, M. L. 1981 *Riftia pachyptila*, new genus, new species, the vestimentiferan worm from the Galapagos Rift geothermal vents (Pogonophora). *Proc. biol. Soc. Wash.* **93**, 1295–1313.
- Jones, M. L. 1985 On the Vestimentifera, new phylum; six new species, and other taxa from hydrothermal vents and elsewhere. In *The hydrothermal vents of the Eastern Pacific: an overview* (ed. M. L. Jones) (*Bull. biol. Soc. Wash.* **6**), pp. 117–158.
- Jones, M. L. & Bright, C. F. 1985 Bibliography of hydrothermal vents and related areas, their biotas, ecological parameters and ancillary data. In *The hydrothermal vents of the Eastern Pacific: an overview* (ed. M. L. Jones) (*Bull. biol. Soc. Wash.* **6**), pp. 495–538.
- Jones, M. L., Bright, C. F. *et al.* [sic] 1985 Dive data of certain submersibles, hydrothermal and other sites. Appendix 2. In *The hydrothermal vents of the Eastern Pacific: an overview* (ed. M. L. Jones) (*Bull. biol. Soc. Wash.* **6**), pp. 539–545.
- Kase, T. 1984 *Early Cretaceous marine and brackish-water Gastropoda from Japan*. (199 pages.) Tokyo: National Science Museum.
- Kenk, V. & Wilson, B. R. 1985 A new mussel (Bivalvia, Mytilidae) from hydrothermal vents in the Galapagos Rift zone. *Malacologia* **26**, 253–271.
- Kleinschmidt, M. & Tschauder, R. 1985 Shallow-water hydrothermal vent systems off the Palos Verdes Peninsula, Los Angeles County, California. In *The hydrothermal vents of the Eastern Pacific: an overview* (ed. M. L. Jones) (*Bull. biol. Soc. Wash.* **6**), pp. 485–489.
- Knight, J. B., Cox, L. R., Keen, A. M., Batten, R. L., Yochelson, E. L. & Robertson, R. 1960 Systematic descriptions (Archaeogastropoda). In *Treatise on invertebrate paleontology*, vol. I (1) (*Mollusca*) (ed. R. C. Moore), pp. 169–310. Geological Society of America and University of Kansas Press.
- Lonsdale, P. 1984 Hot vents and hydrocarbon seeps in the Sea of Cortez. In *Deep-sea hot springs and cold seeps* (ed. P. R. Ryan) (*Oceanus* **27**), pp. 21–24.
- Lutz, R. A., Fritz, K. W. & Rhoads, D. C. 1985 Molluscan growth at deep-sea hydrothermal vents. In *The hydrothermal vents of the Eastern Pacific: an overview* (ed. M. L. Jones) (*Bull. biol. Soc. Wash.* **6**), pp. 199–210.
- Lutz, R. A., Bouchet, P., Jablonski, D., Turner, R. D. & Warén, A. 1986 Larval ecology of mollusks at deep-sea hydrothermal vents. *Am. malac. Bull.* **4**, 49–54.
- MacClintock, C. 1967 Shell structure of patelloid and bellerophonoid gastropods (Mollusca). *Bull. Peabody Mus. nat. Hist.* **22**, 1–140.
- Malahoff, A. 1985 Hydrothermal vents and polymetallic sulfides of the Galapagos and Gorda/Juan de Fuca Ridge systems and of submarine volcanoes. In *The hydrothermal vents of the Eastern Pacific: an overview* (ed. M. L. Jones) (*Bull. biol. Soc. Wash.* **6**), pp. 19–41.
- 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. 1985 Preliminary report on the limpets at hydrothermal vents. In *The hydrothermal vents of the Eastern Pacific: an overview* (ed. M. L. Jones) (*Bull. biol. Soc. Wash.* **6**), pp. 159–166.
- Morton, B. 1986 The functional morphology of the organs of feeding and digestion of the hydrothermal vent bivalve *Calyptogena magnifica* (Vescicomidae). *J. Zool.* **A 208**, 83–98.
- Newman, W. A. 1979 A new scalpellid (Cirripedia): a Mesozoic relic living near an abyssal hydrothermal spring. *Trans. S. Diego Soc. nat. Hist.* **19**, 153–167.
- Newman, W. A. 1985 The abyssal hydrothermal vent invertebrate fauna: a glimpse of antiquity? In *The hydrothermal vents of the Eastern Pacific: an overview* (ed. M. L. Jones) (*Bull. biol. Soc. Wash.* **6**), pp. 231–242.

- Paull, C. K., Hecker, B., Commeau, R., Freeman-Lynde, R. P., Neumann, C., Corso, W. P., Golubic, S., Hook, J. E., Sikes, E. & Curray, J. 1984 Biological communities at the Florida escarpment resemble hydrothermal vent taxa. *Science, Wash.* **226**, 965-967.
- Powell, M. A. & Somero, G. N. 1983 Blood components prevent sulfide poisoning of respiration of the hydrothermal vent tube worm *Riftia pachyptila*. *Science, Wash.* **219**, 297-299.
- Robertson, A. H. F. & Boyle, J. F. 1983 Tectonic setting and origin of metalliferous sediments in the Mesozoic Tethys Ocean. In *Hydrothermal processes at seafloor spreading centers* (ed. P. A. Rona, K. Bostrom, L. Laubier & K. L. Smith, Jr), pp. 595-633. New York: Plenum.
- Skinner, B. J. 1983 Submarine volcanic exhalations that form mineral deposits: an old idea now proven correct. In *Hydrothermal processes at seafloor spreading centers* (ed. P. A. Rona, K. Bostrom, L. Laubier & K. L. Smith, Jr) pp. 557-569. New York: Plenum.
- Spieß, F. N., Macdonald, K. C., Atwater, T., Ballard, R., Carranza, A., Cordoba, D., Cox, C., Diaz Garcia, V. M., Francheteau, J., Guerrero, J., Hawkins, J., Haymon, R., Hessler, R., Juteau, T., Kastner, M., Larson, R., Luyendyk, B., Macdougall, J. D., Miller, S., Normark, W., Orcutt, J. & Rangin, C. 1980 East Pacific Rise: hot springs and geophysical experiments. *Science, Wash.* **207**, 1421-1433.
- Stein, J. L. 1984 Subtidal gastropods consume sulfur-oxidizing bacteria: evidence from coastal hydrothermal vents. *Science, Wash.* **223**, 696-698.
- Suess, E., Carson, B., Ritger, S., Moore, J. C., Jones, M. L., Kulm, L. D. & Cochrane, G. R. 1985 Biological communities at vent sites along the subduction zone off Oregon. In *The hydrothermal vents of the Eastern Pacific: an overview* (ed. M. L. Jones) (*Bull. biol. Soc. Wash.* **6**), pp. 475-484.
- Thiele, J. 1909 Cocculinoidea und die Gattungen *Phenacolepas* und *Titiscania*. *Systematisches Conchylien-Cabinet von Martini und Chemnitz*, 2nd edn, vol. 2, no. 11a. (48 pages.)
- Tunnicliffe, V., Juniper, S. K. & de Burgh, M. E. 1985 The hydrothermal vent community on Axial Seamount, Juan de Fuca Ridge. In *The hydrothermal vents of the Eastern Pacific: an overview* (ed. M. L. Jones) (*Bull. biol. Soc. Wash.* **6**), pp. 453-464.
- Turner, R. D. 1985 Notes on mollusks of deep-sea vents and reducing sediments. *Am. malac. Bull.* (spec. edn) **1**, 23-34.
- Turner, R. D. & Lutz, R. A. 1984 Growth and distribution of mollusks at deep-sea vents and seeps. *Oceanus* **27**, 54-62.
- Turner, R. D., Lutz, R. A. & Jablonski, D. 1985 Modes of molluscan larval development at deep sea hydrothermal vents. In *The hydrothermal vents of the Eastern Pacific: an overview* (ed. M. L. Jones) (*Bull. biol. Soc. Wash.* **6**), pp. 167-184.
- Wenz, W. 1938 Gastropoda. Allgemeiner Teil und Prosobranchia. *Handb. Paläozool.* **6** (1), 1-1639.