Phil. Trans. R. Soc. Lond. B **319**, 1–32 (1988) [1]
Printed in Great Britain

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

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(*Communicated by A. Graham, F.R.S.* – *Received* 8 *July* 1986)

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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 Symmetrocapulidae had similar shell proportions but were much larger; the Symmetrocapulidae 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, *Gorgoleptis 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, *Gorgoleptis 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, *Gorgoleptis 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 vesicomyid 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 in 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 *Leptodrilus* 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 . . . . . *L. pustulosus*
   Sculpture of imbricate radial ribs . . . . . *L. cristatus*
3. Apex $\frac{1}{3}$ shell length from posterior end . . . . . *L. ovalis*
   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 . . . . . *L. elevatus elevatus*
   Shell height approximately $\frac{1}{3}$ shell length . . . . . *L. elevatus galriftensis*
6. Apex medial or nearly so . . . . . *L. guaymasensis*
   Apex markedly displaced to the right . . . . . *L. fucensis*

Lepetodrilus pustulosus, new species

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

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

dive	depth/m	position	date	*pustulosus*	*elevatus*	*ovalis*	*cristatu*
			Alvin 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
			Cyana 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
			Alvin 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
		Lepetodrilus guaymasensis		
		Alvin 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
		Lepetodrilus fucensis		
		Pisces IV 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
		Alvin 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
		Pisces IV 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
		Alvin 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 × 7.5 mm × 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 × 4.8 mm × 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: 51294 paratype specimens from 13 *Alvin* dives in 1979 and 1982 (table 1).

East Pacific Rise at 13° N: 19200 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 × 4.6 mm × 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 μm, 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 × 4.9 mm × 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 μm, 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 × 6.0 mm × 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

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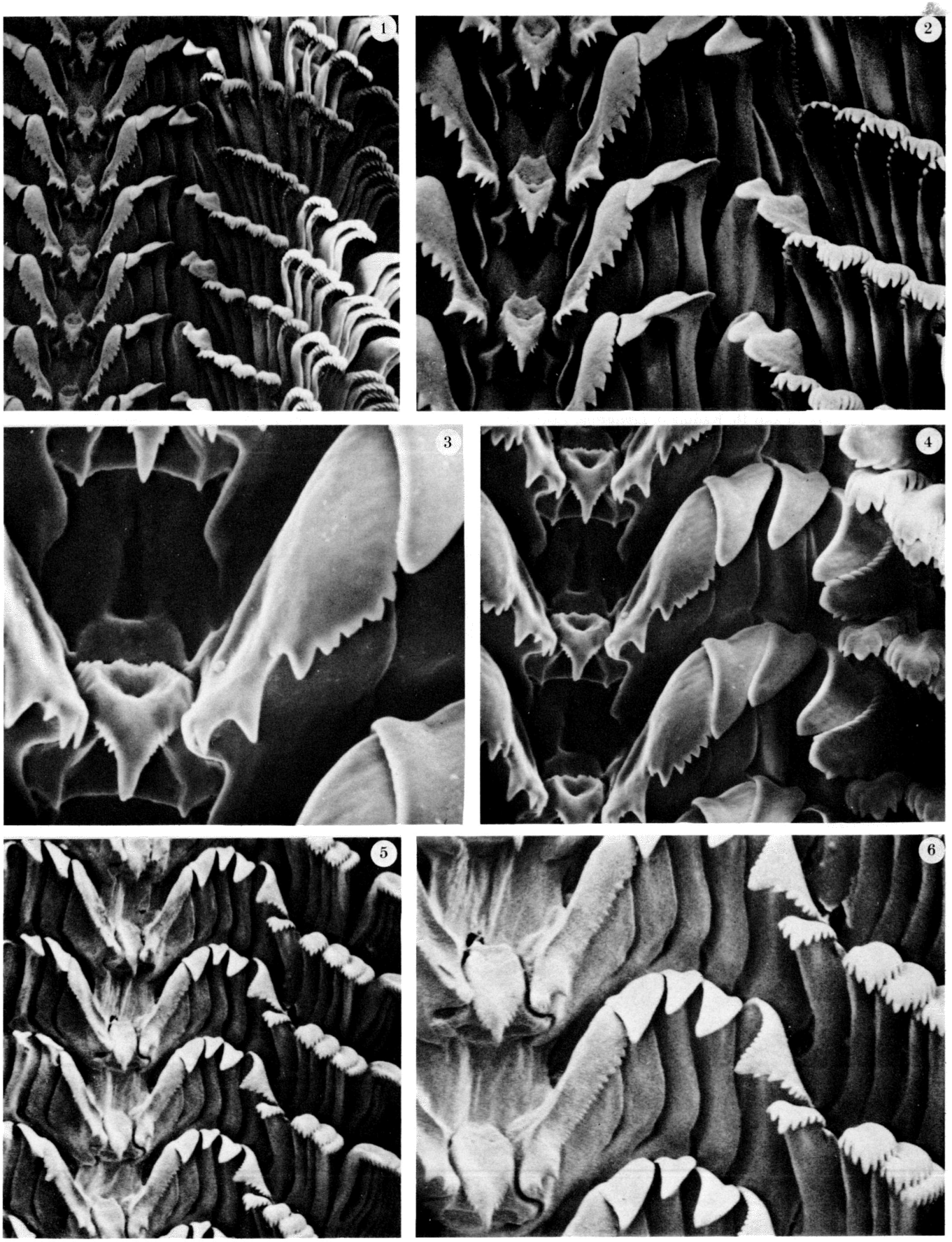
DESCRIPTION OF PLATE 1

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 × 500 and × 2000 respectively).

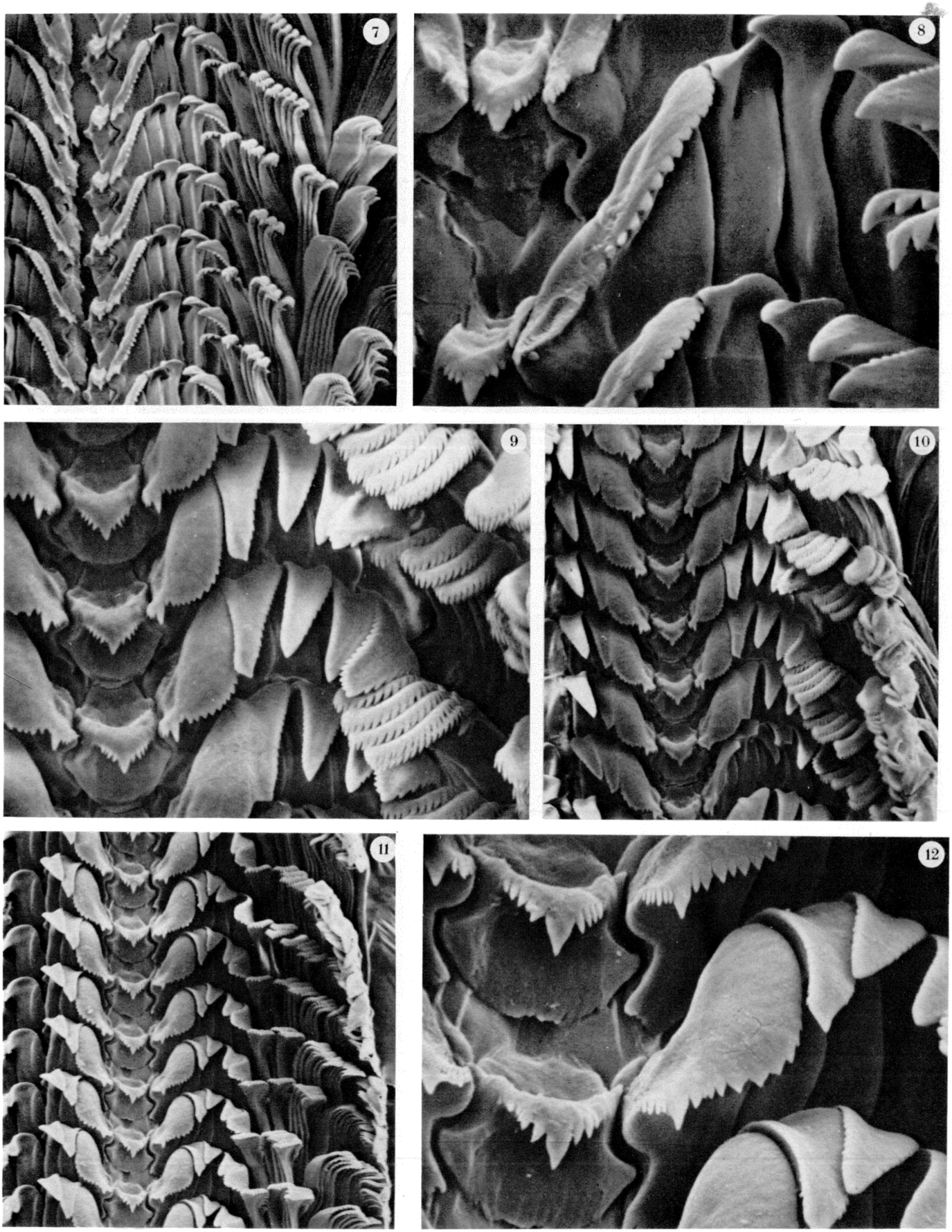
Figures 9–12. Radula of *Lepetodrilus ovalis*, new species. Figures 9 and 10: East Pacific Rise at 21° N, *Alvin* dive 1219 (magns × 1000 and × 500 respectively). Figures 11 and 12: East Pacific Rise at 13° N, *Cyana* dive 82–35 (magns × 500 and × 2000 respectively).

Description of plate 3

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

Figures 15 and 16. Radula of *Lepetodrilus guaymasensis*, new species. Guaymas Basin, *Alvin* dive 1170 (magns × 200 and × 1000 respectively).

Figures 17 and 18. Radula of *Lepetodrilus fucensis*, new species. Juan de Fuca Ridge, *Alvin* dive 1419 (magns × 2000 and × 500 respectively).



FIGURES 7–12. For description see opposite.