The Veliger 36(1):27-35 (January 4, 1993)

THE VELIGER

New Species and Records of *Lepetodrilus* (Vetigastropoda: Lepetodrilidae) from Hydrothermal Vents

by

JAMES H. McLEAN

Los Angeles County Museum of Natural History,
900 Exposition Boulevard, Los Angeles, California 90007, USA

Abstract. Two new species of *Lepetodrilus* are described from the east Pacific hydrothermal vents: *L.* ***tevnianus*** from the East Pacific Rise near 11°N, where it is associated with the vestimentiferan *Tevnia jerichonana* Jones, 1985, and *L.* ***corrugatus*** from the Juan de Fuca Ridge, known from a single specimen, its tentative association being directly on the sulfide chimney. *Lepetodrilus elevatus* McLean, 1988, previously understood to be widely distributed at the east Pacific vents, is confirmed from the Mariana vents, where it apparently lives away from the vestimentiferans with which it is associated in the eastern Pacific. It is the only molluscan species known from both the eastern Pacific and mid-Pacific vents. *Lepetodrilus fucensis* McLean, 1988, previously known from the Explorer and Juan de Fuca Ridges, is reported at the Gorda Ridge. *Lepetodrilus guaymasensis* McLean, 1988, previously known from five specimens, is now known from 127 additional specimens from the type locality.

INTRODUCTION

Lepetodrilus McLean, 1988, family Lepetodrilidae, superfamily Lepetodrilacea, is unique among the genera of archaeogastropod limpets associated with hydrothermal vents in having three pairs of epipodial tentacles and a right cephalic-epipodial penis. Anatomy was described in a companion paper by FRETTER (1988). Relationships of the superfamily have also been discussed by HASZPRUNAR (1988), who assigned it to the suborder Vetigastropoda.

Six species of *Lepetodrilus* were initially described. In this paper I add the descriptions of two more species, and give range extensions or additional records for three of the original species. The new species and records of previously described species add new limits to the expression of morphological character states and new parameters to the understanding of biological associations and the capacity for long distance dispersal in the genus. These topics are treated in the discussion section.

MATERIALS AND METHODS

All specimens reported here were collected by expedition members on various cruises to hydrothermal vent sites that employed the deep-submersible *Alvin* or other submersibles. Limpet specimens were collected with the mechanical arm of the submersible in the course of collecting substrate samples or general collecting of all organisms. Specimens were preserved on reaching the surface and were originally fixed for 24 hr in 10% formalin-seawater buffered with sodium borate, washed in fresh water, and transferred to 70% ethanol.

Radulae were extracted from preserved specimens after dissolution of tissues with room temperature 10% NaOH for 48 hr, washed in distilled water, dried from a drop of water on a stub having a thin smear of rubber cement, and coated with gold palladium for SEM examination. Repositories of type and other material are the Los Angeles County Museum of Natural History (LACM), the United States National Museum (USNM), and the Museum National d'Histoire Naturelle, Paris (MNHN).

SYSTEMATIC DESCRIPTIONS

Order Archaeogastropoda Thiele, 1925

Suborder Vetigastropoda Salvini-Plawen, 1980

Superfamily LEPETODRILACEA McLean, 1988

Family LEPETODRILIDAE McLean, 1988

Lepetodrilus McLean, 1988

Lepetodrilus MCLEAN, 1988:6. Type species: *L. pustulosus* McLean, 1988.

Table 1

Lepetodrilus ***tevnianus***. Measurements and disposition of holotype and paratype specimens.

	Length (mm)	Width (mm)	Height (mm)	Remarks
LACM 2254	9.5	7.9	2.8	Holotype, female (Figures 1–5)
USNM 859484	8.9	7.8	2.8	Intact female
USNM 859484	8.8	7.6	2.7	Intact female
LACM 2255	8.1	7.0	—	Female, shell broken, radula preparation (Figures 7–10)
LACM 2255	6.9	5.8	2.0	Male, shell deformed (Figure 6)

Lepetodrilus species are diagnosed by differences in shell profile, sculpture, penial morphology, and radular morphology, particularly that of the rachidian and first lateral teeth. Each of the previously described species, as well as the two species described here, can be recognized on radular characters alone.

Lepetodrilus ***tevnianus*** McLean, sp. nov.

(Figures 1–10)

Description: Shell (Figures 1–3) moderately large for genus (maximum length 9.5 mm). Outline of aperture oval, anterior end markedly tapered to produce faintly angulate anterior tip. Margin of aperture not in same plane, ends raised relative to sides. Anterior slope convex except concave near margin; lateral and posterior slopes concave. Apex at one-quarter shell length from posterior margin, below highest elevation of shell, displaced slightly to right, right side of protoconch remaining visible. Periostracum moderately thick, light yellow-brown, turned in at shell edge. Early shell to 1 mm length devoid of sculpture; single mid-dorsal rib on anterior slope arising first, remaining stronger than all other ribs; fine primary ribs arising at shell length of 1–3 mm; secondary ribs arising at shell length of about 4 mm, quickly assuming strength of primary ribs. Large specimens with 6 ribs/mm at margin. Ribs minutely beaded to correspond to growth lines, remaining strong at later stages of growth. Interior surface glossy, opaque, with scattered white discolorations. Posterior half of shell interior with faintly angulate curved ridge outside of muscle scar. Muscle scar horseshoe-shaped, not deeply marked, positioned on inner surface of curved ridge midway between margin and midline; scar relatively broad, broadest anteriorly, narrow posteriorly. Apical pit prominent, not filled by deposition of callus.

Dimensions of holotype: Length 9.5, width 7.9, height 2.8 mm.

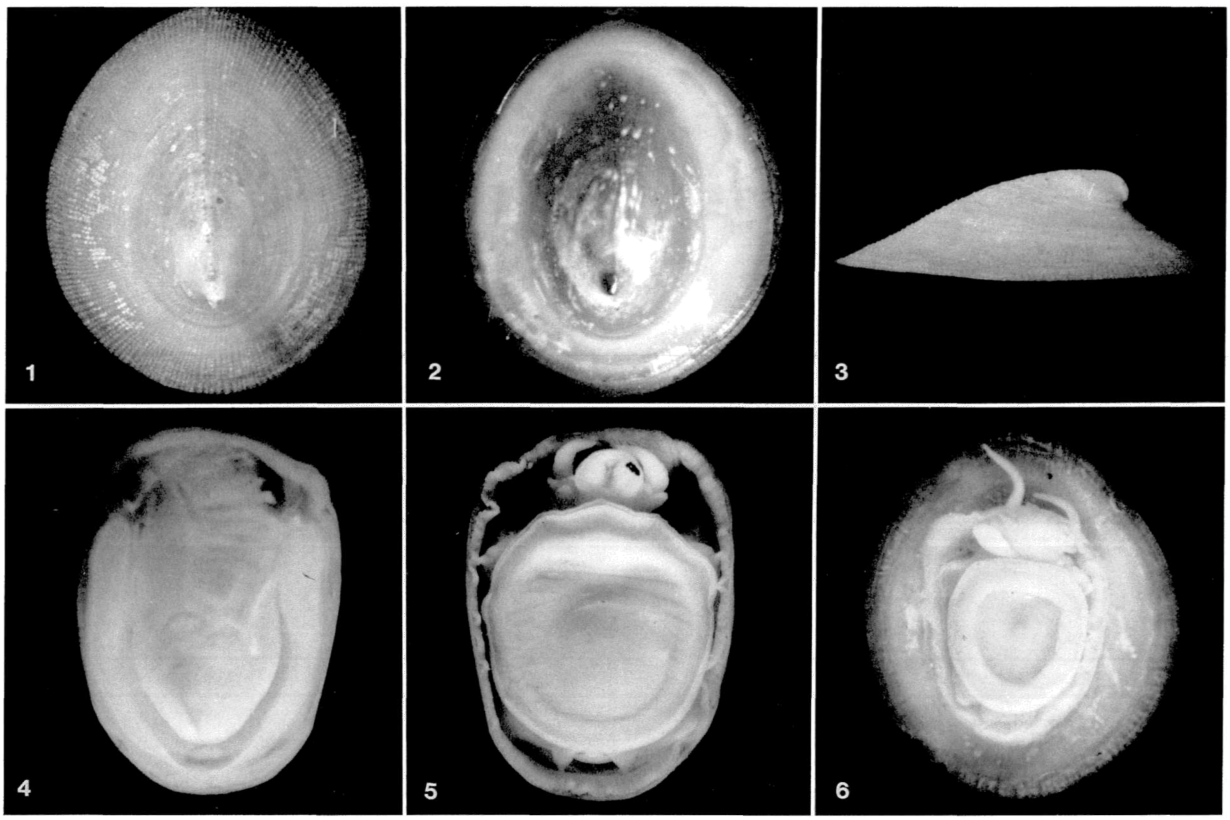
External anatomy (Figures 4–6): Typical for genus. Epipodial tentacles three pairs, one lateral pair and two posterior pairs, each with cylindrical tip and triangular base. Cephalic tentacles long, encircled laterally and ventrally by epipodial folds, eyes lacking. Oral disk broad, mouth Y-shaped. Anterior of foot with double edge, marking opening of pedal gland. Mantle edge with two folds, inner fold smooth to extend under periostracum, edge of outer fold finely divided. Penis of male (Figure 6) flaplike, its origin on right ventral neck. Mantle cavity and ctenidium typical for genus, ctenidium projecting above head in ventral view (Figure 5).

Radula (Figures 7–10): Rhipidoglossate; laterals five pairs, cusp rows of first and second laterals forming inverted-U; marginals numerous, cusp rows descending. Rachidian broad at base, shaft shorter than that of laterals, rachidian with very long, tapered central cusp, edges with about six sharply pointed denticles; shaft of rachidian with projecting lateral extension fitting against edge of first lateral. First lateral large and complex, curved overhang broad at its distal edge. Inner edge of shaft of first lateral continuous with main cusp, projecting so that it appears to be a long pointed denticle like that of rachidian; outer edge of shaft with hooked projection that articulates with shaft of second lateral. Overhanging edge of first lateral with about eight long, unseparated denticles on inner edge, followed by a major denticle and at least three shorter denticles on outer edge. Second, third, and fourth laterals similar to each other, cusps long, tapered, with serrate edges; fifth lateral broader. Marginal teeth similar to each other, tips with numerous, deeply cut serrations.

Type locality: On vestimentiferan *Tevnia jerichonana* Jones, 1985, living on basalt cliff overhanging low temperature venting water, East Pacific Rise near 11°N (10°56.3′N, 103°41.4′W), 2536 m.

Type material: 5 specimens (4 females, 1 male) from the type locality, recovered from washings of specimens of *Tevnia jerichonana, Alvin* dive 1986, 8 March 1988. Received from Cindy Lee Van Dover. Holotype, LACM 2254; 2 paratypes, LACM 2255; 2 paratypes, USNM 859484. Dimensions and disposition of all specimens are given in Table 1.

Remarks: *Lepetodrilus* ***tevnianus*** is easily distinguished from the other species of *Lepetodrilus* in characters of the shell, penial morphology, and radula. The shell most resembles that of *L. pustulosus,* but has the strong anterior rib, is broader, has a more angulate anterior (dorsal view), and lacks the diverging curves in the alignment of the beads on the radial ribs, as well as lacking the two supporting



Explanation of Figures 1 to 6

Figures 1–6. *Lepetodrilus* ***tevnianus*** McLean, sp. nov. *Alvin* dive 1982, East Pacific Rise near 11°N, 2536 m. Anterior at top in vertical views. Figures 1–3. Holotype shell, LACM 2254. Length 9.5 mm. Exterior, interior, and left lateral views. Figures 4, 5. Holotype body (female). Dorsal and ventral views. Figure 6. Paratype, male body attached to shell, LACM 2255. Length 6.9 mm.

ridges below the apex on the posterior slope of that species. The flat, non-elbowed morphology of the penis is characteristic. The radula of *L.* ***tevnianus*** is unlike that of any other species of *Lepetodrilus.* The rachidian is unique in having a very long cusp and large, conspicuous flanks to the shaft; the first lateral is unique in its prominent inner edge of the shaft.

The significance of the association of this species with a vestimentiferan other than *Riftia pachyptila* is treated further in the discussion section.

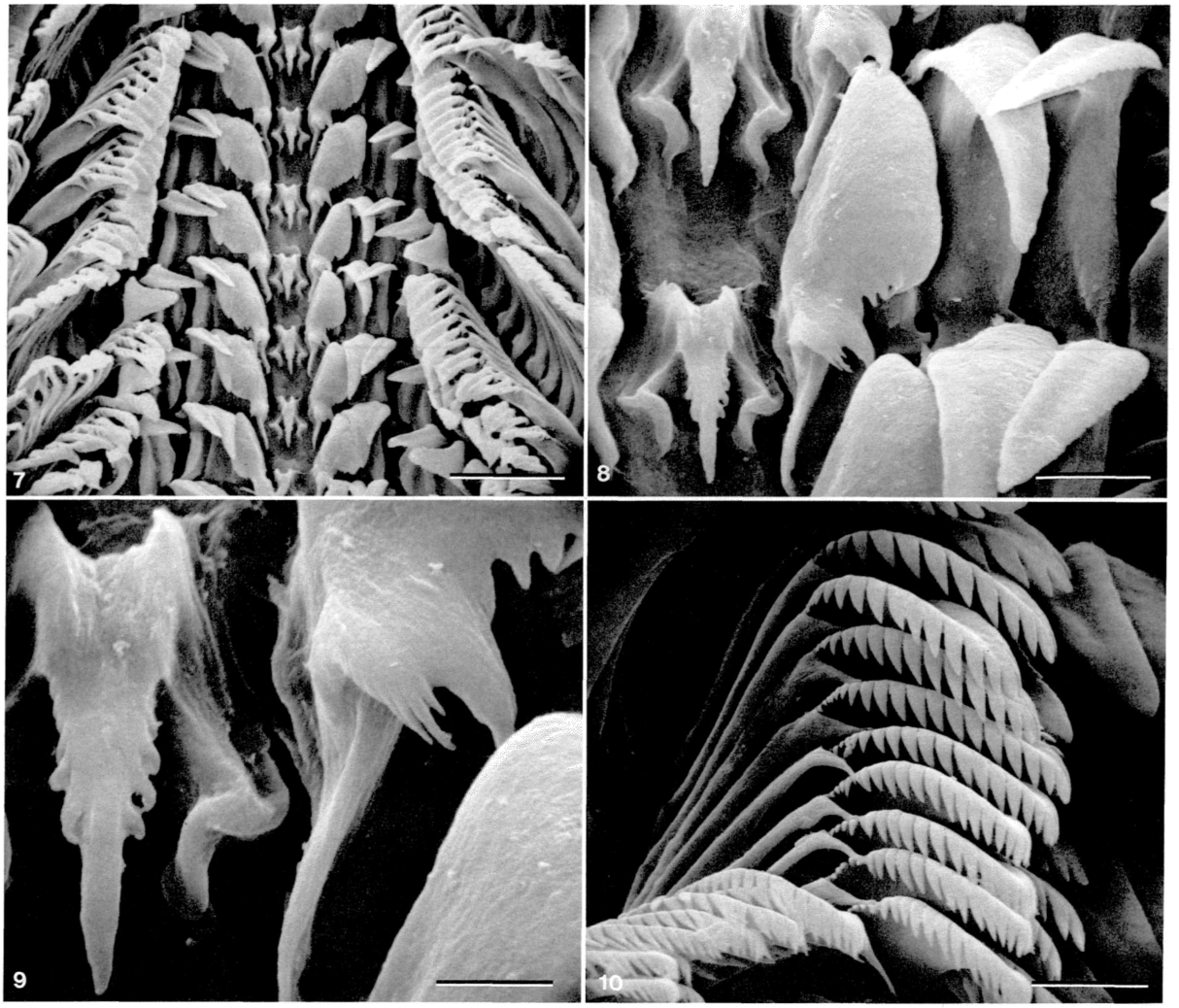
Etymology: The name ***tevnianus,*** means *of Tevnia,* the vestimentiferan on which this species lives.

Lepetodrilus ***corrugatus*** McLean, sp. nov.

(Figures 11–16)

Description (based on single female specimen): Shell (Figures 11–13) medium-sized for genus (length 6.1 mm). Outline of aperture oval, anterior end slightly narrower than posterior. Margin of aperture not in same plane, ends raised relative to sides. Anterior slope convex, lateral slopes flat, posterior slope convex below apex. Apex at one-eighth shell length from posterior margin, below highest elevation of shell, apex displaced slightly to right; protoconch surface eroded, not visible on right side. Periostracum moderately thick, light greenish-brown, turned in at shell edge. Early shell to 1 mm length devoid of sculpture. Mature sculpture dominated by about six irregularly formed concentric swellings, producing a wrinkled appearance; additional concentric sculpture of fine growth lines on periostracum. Radial sculpture of low ribs, strongest posteriorly and laterally, interspaces broader than ribs. Ribs only faintly beaded to correspond to growth lines. Interior surface opaque, chalky (probably etched by preservation fluids), showing the coarse, irregular concentric sculpture of the exterior. Posterior half of shell interior with strongly angulate, curved ridge outside of muscle scar. Muscle scar horseshoe-shaped, not deeply marked, positioned on inner surface of curved ridge midway between margin and midline; scar relatively broad, broadest anteriorly, narrow posteriorly. Apical pit prominent, not filled by deposition of callus.

Dimensions of holotype: Length 6.1, width 4.7, height 2.2 mm.



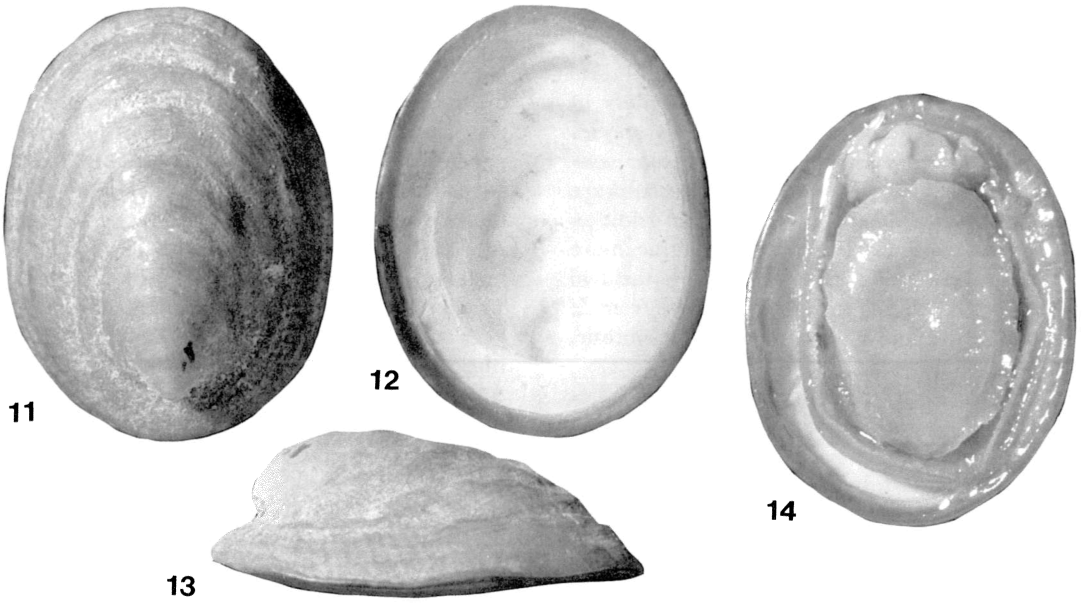
Explanation of Figures 7 to 10

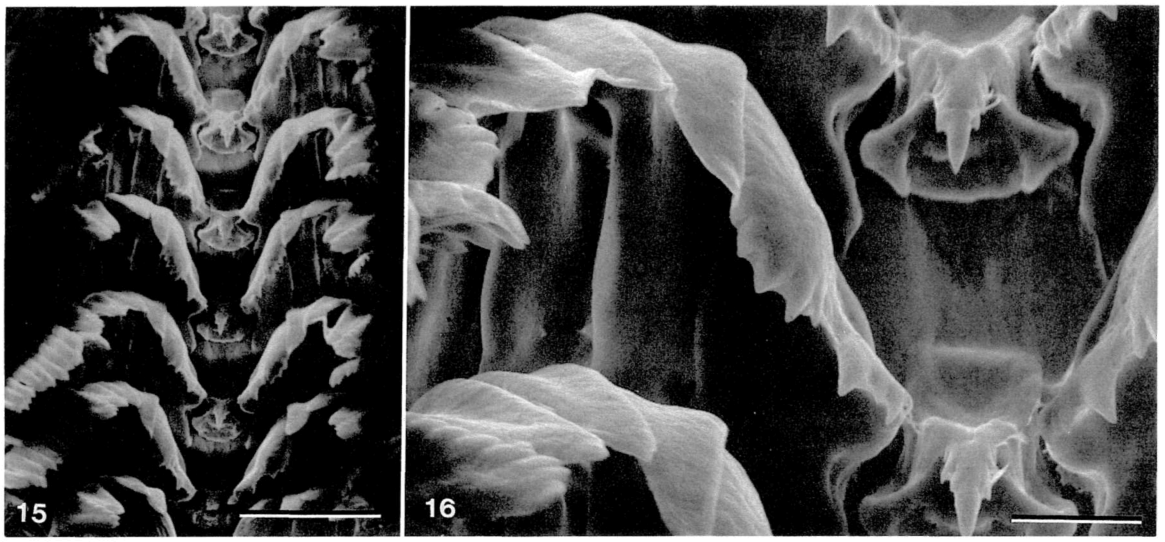
Figures 7–10. *Lepetodrilus* ***tevnianus*** McLean, sp. nov. SEM views of radula of paratype, LACM 2255. Figure 7. Full width of ribbon. Scale bar = 40 μm. Figure 8. Rachidian and first three laterals. Scale bar = 10 μm. Figure 9. Rachidian and adjacent edge of first lateral. Scale bar = 4 μm. Figure 10. Detail of serrations on marginal teeth. Scale bar = 10 μm.

External anatomy (Figure 14): Typical for genus. Epipodial tentacles three pairs, one lateral pair and two posterior pairs, each with cylindrical tip and triangular base. Cephalic tentacles short (preserved condition), encircled laterally and ventrally by epipodial folds, eyes lacking. Oral disk broad, mouth Y-shaped. Foot anterior with double edge, marking opening of pedal gland. Mantle edge with two folds, edge of outer fold smooth to extend under periostracum, edge of inner fold finely divided. Mantle cavity and ctenidium typical for genus, ctenidium not projecting above head in ventral view (Figure 14).

Radula (Figures 15, 16): Rhipidoglossate; lateral teeth five pairs, cusp rows of first and second laterals forming inverted-U; marginals numerous, cusp rows descending. Rachidian broad at base, shaft shorter than that of laterals, with tapered central cusp, edges with about three sharply pointed denticles; shaft of rachidian with projecting lateral extension fitting against edge of first lateral. First lateral large and complex, shaft broad, curved overhang broader distally from rachidian, distal portion bearing about six sharp denticles, inner portion with one major and two or three minor denticles. Second, third, and fourth laterals similar to each other, cusps long, tapered, edges not serrate; fifth lateral with deeply serrate edges. Marginal teeth similar to each other, tips with numerous, deeply cut serrations.

Type locality: Heinecken Hollow, Middle Valley, Juan de Fuca Ridge, west of Washington (48°25.8′N, 128°40.9′W), 2420 m.





Explanation of Figures 11 to 16

Figures 11–16. *Lepetodrilus* ***corrugatus*** McLean, sp. nov. *Alvin* dive 2252. Middle Valley, Juan de Fuca Ridge off Washington, 2420 m. Anterior at top in vertical views. Figures 11–14. Holotype, LACM 2256. Length 6.1 mm. Exterior, interior, right lateral, and body (female) before detachment from shell. Figures 15, 16. SEM views of radula of holotype. Figure 15. Width of ribbon. Scale bar = 20 μm. Figure 16. Rachidian and lateral teeth. Scale bar = 10 μm.

Type material: 1 specimen (female) from the type locality, recovered from sample containing broken pieces of sulfide chimney, *Alvin* dive 2252, 5 August 1990. Recognized during sample sorting by K. Wilson and forwarded by Verena Tunnicliffe. Holotype, LACM 2256. The holotype body is intact except for removal of the radula.

Remarks: *Lepetodrilus* ***corrugatus*** is known from a single female specimen. The morphology of the penis, an important external character in members of this genus, is therefore unknown. Attempts by K. Wilson to locate additional specimens in samples from the Middle Valley site on the Juan de Fuca Ridge have been unsuccessful (V. Tunnicliffe, personal communication). The type locality is a new site on the northern Juan de Fuca Ridge for which there are faunal and structural differences from

other sites that will be described by V. Tunnicliffe. The species is described from a single specimen in order to update knowledge of the family.

Lepetodrilus ***corrugatus*** differs from its congeners in both shell and radular characters. It is the only species having the sculpture dominated by deep, irregular concentric undulations. In general proportions and sculpture it is most similar to *L. pustulosus*. Differences, in addition to the corrugate sculpture, are its more oval outline, more posterior apex, coarser radial ribs, and lack of the two strong radial ribs that subtend the apex. It differs from *L. elevatus* in its sculpture and its broader anterior outline, as well as radular characters.

The radula of *Lepetodrilus* ***corrugatus*** requires comparison with that of *L. pustulosus* and *L. fucensis*, both of which have similarly proportioned first lateral teeth. The rachidian of *L.* ***corrugatus*** differs from that of *L. pustulosus* in having fewer serrations and not having the concave depression on the overhanging surface; details in the placement of cusps of the elongate first lateral also differ. Similar differences separate the radulae of *L.* ***corrugatus*** from that of *L. fucensis*; the latter species also differs in having a marked concavity on the overhanging surface of the rachidian.

The occurrence of this species on the sulfide chimney microhabitat is unique in the genus and needs to be verified by the collection of further specimens. It occurs sympatrically with the abundant species *Lepetodrilus fucensis*.

Etymology: The name ***corrugatus*** is a Latin adjective meaning "wrinkled" or "ridged," with reference to the dominant shell sculpture.

Lepetodrilus elevatus McLean, 1988

(Figures 17–25)

Lepetodrilus elevatus McLean, 1988:11, figs. 5,5, 36–44; McLean, 1990a:84.

Lepetodrilus cf. *elevatus:* Hessler & Lonsdale, 1991a:190; Hessler & Lonsdale, 1991b:171.

New records: 29 specimens from *Alvin* dive 1837, Burke Field vents, Mariana Trough spreading center (18°10.9′N, 144°43.2′E), 3660 m, 28 April 1987. Received from Robert R. Hessler. Disposition: 14 specimens LACM 146884; 10 specimens USNM 882027; 5 specimens MNHN.

Nine specimens from *Alvin* dive 1843, Alice Springs vents, Mariana Trough spreading center (18°12.6′N, 144°42.4′E), 3640 m, 4 May 1987. Received from Robert R. Hessler. Disposition: 5 specimens LACM 146885; 4 specimens USNM 882028.

Remarks: The presence of this species at the Mariana Trough vents has previously been reported by McLean (1990a) and by Hessler & Lonsdale (1991a, b), but detailed commentary and illustrations have not been given. Material from the Mariana Trough (Figures 17–25) matches that illustrated by McLean (1988) for specimens of the typical subspecies *Lepetodrilus elevatus elevatus* from the East Pacific Rise at 21°N. All specimens of the present material have surficial markings on the periostracum made by an unknown organism, but this does not penetrate the periostracum and has no significance for taxonomic comparison. Specimens originally described from the Galapagos Rift were consistently lower in profile (at two-thirds the height of the typical subspecies) and were given the subspecific name *L. elevatus galriftensis*, but the present material has the high profile of the typical subspecies. All specimens of the material from the Mariana Trough appear to be famale, none having the broad triangular penis illustrated by McLean (1988:pl. 6, fig. 39). The significance of this is unknown and needs to be further investigated. Genetic (electrophoretic) evidence that the two populations represent the same species would also be of interest.

Lepetodrilus guaymasensis McLean, 1988

Lepetodrilus guaymasensis McLean, 1988:16, figs. 15, 16, 66–74.

New records: 98 small to medium-sized specimens (not sexed) from *Alvin* dive 1613, Guaymas Basin (27°00.5′N, 111°24.6′W), 2007 m, 5 August 1985. Received from Meredith R. Jones. Disposition: 48 specimens LACM 146886; 30 specimens USNM 882029; 20 specimens MNHN.

Twenty-nine specimens (21 male, 8 female) from *Alvin* dive 1615, Guaymas Basin (27°00.5′N, 111°24.6′W), 2000 m, 7 August 1985. Received from Meredith R. Jones. Disposition: 13 specimens LACM 146887; 10 specimens USNM 882030; 6 specimens MNHN.

Remarks: *Lepetodrilus guaymasensis* was described originally from five specimens; the 127 specimens reported here from the 1985 expedition to the Guaymas Basin (Fred Grassle, Chief Scientist) are a significant increase in the number known. Both samples were recovered from washings of *Riftia pachyptila*.

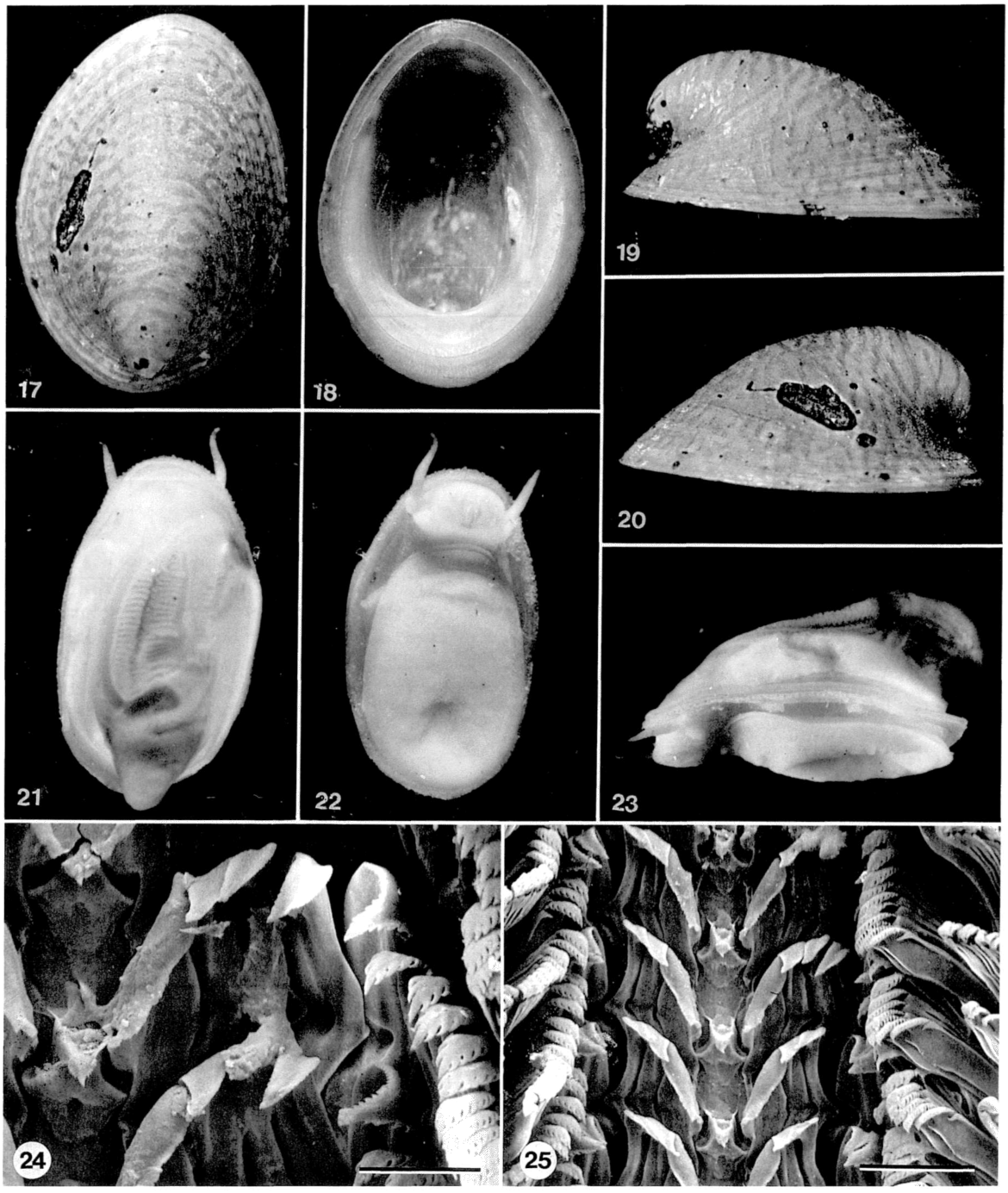
Lepetodrilus fucensis McLean, 1988

Lepetodrilus fucensis McLean, 1988:18, figs. 17–20, 75–83; McLean, 1990b:496.

New records: 15 specimens (9 male, 6 female) from *Sea Cliff* dive 764, Escanaba Trough, Gorda Ridge (41°00′N, 127°29′W), 3200–3250 m, 3 September 1988. Received from Robert R. Hessler. Disposition: 7 specimens LACM 146888; 5 specimens USNM 882031; 3 specimens MNHN.

Twenty-three specimens (12 male, 11 female) from *Alvin* dive 2036, Escanaba Trough, Gorda Ridge (41°00.4′N, 127°29.3′W), 3240 m, 6 June 1988. Received from Cindy Lee Van Dover. Disposition: 9 specimens LACM 146889; 8 specimens USNM 882032; 6 specimens MNHN.

Remarks: This species, which is abundantly known from the Explorer and Juan de Fuca Ridges, was reported by McLean (1990b) from Escanaba Trough on the Gorda Ridge. Disposition of the material is given here. As re-



Explanation of Figures 17 to 25

Figures 17–25. *Lepetodrilus elevatus* McLean, 1988. *Alvin* dive 1837. Burke Field, Mariana vents, 3660 m. Anterior at top in vertical views. Figures 17–20. LACM 146884. Length 6.8 mm. Figures 17–20. Exterior, interior, right, and left lateral views. Markings on shell produced by unknown organism. Figures 21–23. Detached body of same specimen as in Figures 17–20. Dorsal, ventral, and lateral views. Figures 24, 25. SEM views of radula, LACM 146884. Figure 24. Rachidian, lateral, and inner marginal teeth. Scale bar = 20 μm. Figure 25. Full width of ribbon. Scale bar = 40 μm.

ported initially, there is no known association with vestimentiferans. A general description of the biotic community of the Escanaba Trough was given by VAN DOVER *et al.* (1990).

DISCUSSION

The discription of two additional species brings the total number of described species of *Lepetodrilus* to eight. The genus remains the most speciose of limpet genera in the hydrothermal-vent habitat. Eight of the species are known from eastern Pacific vents; one of these species, *L. elevatus,* is also known from the Mid-Pacific Mariana vents (the only mollusk with such a distribution).

Until now, the only association between species of *Lepetodrilus* and vestimentiferans had been with the vestimentiferan *Riftia pachyptila.* MCLEAN (1988) reported that washings of retrieved specimens of that vestimentiferan were highly productive in collecting *L. pustulosus, L. elevatus, L. ovalis,* and *L. cristatus. Lepetodrilus* ***tevnianus*** is the only species yet reported to be associated with the vestimentiferan *Tevnia jerichonana,* a vestimentiferan previously reported by JONES (1985) as occurring only at the French expedition site at 13°N. *Lepetodrilus* ***tevnianus*** is yet unknown from 13°N, although its vestimentiferan associate is present at that site. *Riftia pachyptila* was not recorded from the type locality of *Tevnia jerichonana* (*Alvin* dive 1986). The only other *Lepetodrilus* species occurring with *L. tevnianus* was *L. elevatus.* This pattern of distribution suggests that *L.* ***tevnianus*** depends on the presence of *Tevnia jerichonana,* and that the most abundant species, *L. elevatus,* can be associated with either species of vestimentiferan, whereas three other species of *Lepetodrilus* are associated only with *Riftia pachyptila.*

The two northernmost occurring species, *Lepetodrilus fucensis,* which occurs clustered on hard surfaces near vents and chimneys, and *L.* ***corrugatus,*** which is now known from a single specimen, but may prove to be associated with the hard surface deposits of sulfide chimneys, differ from other eastern Pacific species in having no known association with vestimentiferans. The physical and biological parameters of the sulfide chimney habitat have been discussed by TUNNICLIFFE (1990), although the limpets were not mentioned.

Lepetodrilus elevatus, the most broadly distributed species of the genus, is also the most diverse in its substrate associations. At the eastern Pacific vents it occurs with two different species of vestimentiferans, yet it appears to be capable of living away from vestimentiferans, there being no reported vestimentiferans at the Mariana Trough.

HESSLER & LONSDALE (1991a, b) have recently discussed the biogeographic implications of the species known from the Mariana Trough and the eastern Pacific. The fact that one species of *Lepetodrilus* has bridged the gap seems difficult to explain. However, HESSLER & LONSDALE (1991) noted that "two now-extinct portions of the mid-ocean ridge system would have allowed comparatively easy interchange 43 and 55 million years ago."

In the genus *Lepetodrilus* the biogeographic affinity between the East Pacific Rise and the Juan de Fuca Ridge extends only to the generic level, as no species are shared between the two systems. Biogeographic affinity of these two systems has been treated by TUNNICLIFFE (1988).

My earlier assessment (MCLEAN, 1988) that the lepetodrilaceans may represent limpet derivatives of unknown Paleozoic or Mesozoic archaeogastropods has not been challenged nor supported with further evidence. Additional arguments in support of the concept that the hydrothermal-vent fauna as a whole represents an ancient relict fauna have been given by TUNNICLIFFE (1991; in press). A concerted effort to apply the techniques of molecular genetics will be necessary to test this hypothesis of antiquity, but that is left to future investigators.

ACKNOWLEDGMENTS

For providing material of the new species and new records reported here I thank: Cindy Lee Van Dover of Woods Hole Oceanographic Institution; Verena Tunnicliffe and K. Wilson of the University of Victoria, British Columbia; Bob Hessler and Michel Boudrias of Scripps Institution of Oceanography, Fred Grassle and Rosemarie Petrecca of Rutgers University, New Jersey; and Meredith Jones of the U.S. National Museum of Natural History. Photographs are the work of Bertram C. Draper. SEM work was done by C. Clifton Coney, using the CEMMA facility of the University of Southern California. For helpful commentary I thank Anders Warén of the Swedish Museum of Natural History, Stockholm, and two anonymous reviewers.

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