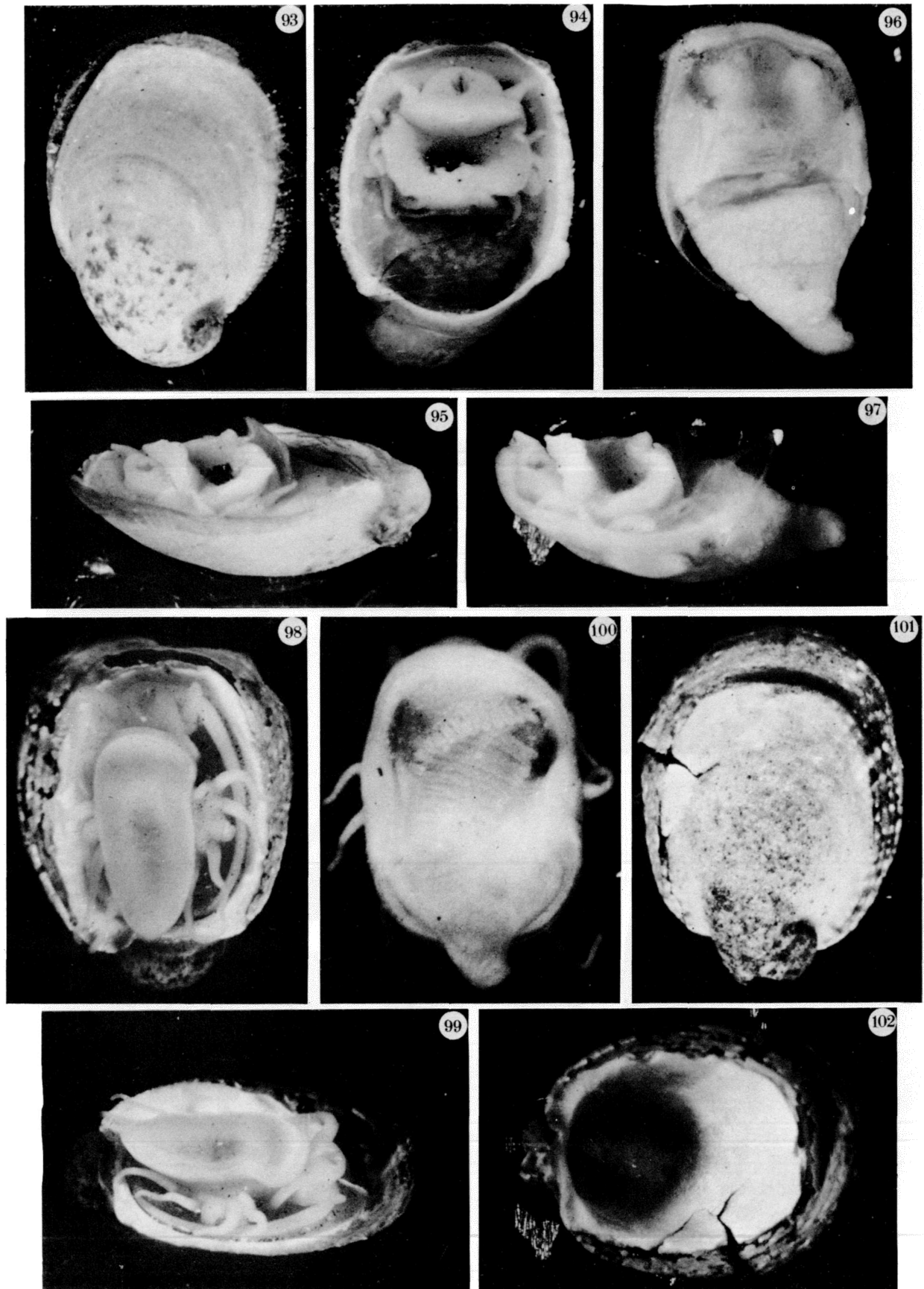FIGURES 84–92. For description see opposite.

DESCRIPTION OF PLATE 12

FIGURES 84–92. *Gorgoleptis 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. × 7.1). Figures 87 and 88: ventral and dorsal views of body of holotype (magn. × 10.3). Figure 89: left ventral view of immature male in shell showing periostracal band and penis. Same locality, *Alvin* dive 1221 (magn. × 16.2). Figure 90: apex of immature shell showing protoconch. Same locality, *Alvin* dive 1221 (magn. × 95). Figure 91: exterior view of shell, sex unknown (body lost at preservation). Same locality, *Alvin* dive 1211 (magn. × 15.6). Figure 92: apertural view of juvenile with dried body and operculum. Same locality, *Alvin* dive 1221 (magn. × 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 × 8.8 mm × 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 × 7.7 mm × 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. *Gorgoleptis 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. × 18.5). Figures 96 and 97: dorsal and left lateral views of holotype specimen removed from shell (magn. × 21.4).

FIGURES 98–102. *Gorgoleptis 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. × 22.5). Figure 100: dorsal view of holotype body (magn. × 27.2). Figures 101 and 102: exterior and interior views of holotype shell preserved in alcohol, damaged after removal of body (magn. × 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 × 9.0 mm × 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
		Gorgoleptis emarginataus		
		Alvin 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
		Gorgoleptis spiralis		
		Cyana 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
		Gorgoleptis patulus		
		Alvin 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 inturned 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. Dimenions of holotype: 8.9 mm × 7.5 mm × 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

Gorgoleptis 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'.

Gorgoleptis 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 *Gorgoleptis* 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'.

<div align="center">

Gorgoleptis patulus, new species

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

</div>

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 *Gorgoleptis 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*, *Calyptogena 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 *Symmetrocapulus* (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 H_2S 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 zevinae* 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.

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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