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Morphological and anatomical studies on a new lepetodrilacean limpet (Gastropoda, Prosobranchia) from hydrothermal vents at the Manus Back-Arc Basin (Bismarck Sea, Papua New Guinea)

By **LOTHAR A. BECK¹⁾**

(With 5 Plates, 3 Figures and 2 Tables)

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Z u s a m m e n f a s s u n g

In der vorliegenden Studie wird eine neue *Lepetodrilus*-Art untersucht, die 1990 während der deutschen Forschungsfahrt OLGA II von aktiven hydrothermalen Quellen mit "Schwarzen Rauchern" in der Spreizungszone des Manus-Back-Arc-Beckens (Bismarck-See, Papua-Neuguinea) gesammelt wurde. Mit Hilfe von mikroskopischen und rasterelektronenoptischen Methoden gewonnene Daten zur Morphologie und Anatomie begründen die Artabgrenzung. Die neue Art ist durch eine napfförmige, mäßig hohe, ovale Schale ohne Skulptur sowie nur wenige Dorsallamellen an der Kieme, das Fehlen eines Penis beim Männchen und durch besondere Radulamerkmale gekennzeichnet. Erläuterungen zur Klassifikation und Verwandtschaft dieser Art sowie zur Speziation an hydrothermalen Tiefseequellen im Westpazifik schließen die Arbeit ab.

S u m m a r y

This study deals with the description of a new species of *Lepetodrilus* which was collected in 1990 during the German OLGA II Research Cruise to active hydrothermal vents ("black smokers") at the Spreading Center in the Manus Back-Arc Basin (Bismarck Sea, Papua New Guinea). Morphological and anatomical data gained by microscopical and SEM methods substantiate the recognition of a new species. The new taxon is characterized by a limpet-shaped, moderately elevated, oval shell without sculpture and by only a few dorsal gill lamellae, the lack of a penis in the male and also by special characters of the radula. Comments to classification and relationship of the new species and to the process of speciation at Western Pacific hydrothermal vents are included.

I n t r o d u c t i o n

Up to now, the small limpet-shaped lepetodrilacean gastropods (*Lepetodrilidae* McLEAN, 1988) are mainly known from several hydrothermal vent locations at the East Pacific Rise, the Galapagos Rift, Juan de Fuca Ridge,

¹⁾ Author's address: **LOTHAR A. BECK**, Fachbereich Biologie der Philipps-Universität Marburg, Karl-von-Frisch-Straße, D-35032 Marburg/Lahn, Federal Republic of Germany.

Guyamas Basin and Gorda Ridge (McLEAN 1985, 1988, FRETTER 1988, HICKMAN 1983). One widely distributed abundant and euryoecic species, *Lepetodrilus elevatus*, was recently also reported from the Mariana Trough (McLEAN 1990, 1993; HESSLER & LONSDALE 1991) and from the North Fiji Basin and Lau Basin (WARÉN & BOUCHET 1993). In all, 8 species have been described until now. They have been found living on hard surfaces near vents and chimneys or living epizooically on vestimentiferans (*Riftia*, *Tevnia*). Feeding is based on grazing films of chemoautotrophic bacteria and on filtering bacterial suspensions with ciliary equipment of the gill and with a food groove.

In 1990, the German OLGA II Research Cruise (Ozeanische Lagerstätten: Geologisch-Mineralogische Analyse = Oceanic Deposits: Geological-Mineralogical Analysis), under the direction of Prof. Dr. WERNER TUFAR, revealed a new *Lepetodrilus* species from active sulphide chimneys collected from Hydrothermal Field 1 "Wienerwald" ("Vienna Woods") at the Spreading Center of the Manus Back-Arc Basin. The new form is part of a faunal vent community which is dominated by mixotrophic mesogastropods described as *Alviniconcha hessleri* OKUTANI & OHTA, 1988 and *Olgaconcha tufari* BECK, 1991 (= *Ifremeria nautiliei* BOUCHET & WARÉN, 1991) (TUFAR 1990, 1992, TUFAR & JULLMANN 1991). They are accompanied by very abundant cirripeds and polychaetes and, sporadically, by several species of Cnidaria, Pogonophora, Bryozoa and Porifera. Amphipod, bresiliid, bythograeid and galatheid decapodes are likewise abundant. A preliminary list of species is given by TUFAR (1990, 1992). The archaeogastropod fauna consists of small phenacolepadid, neomphalid and fissurellid limpets (BECK 1992 a, b) and the lepetodrilacean species, forming the subject of this paper. All limpets are living in direct contact to the emanating hydrothermal solutions at the surface of sulphide chimneys (black smokers) or are living epizooically on *O. tufari* or cirripeds. The external morphology and the anatomy of the new form are treated below. Because of its similarity to *L. elevatus* and *L. ovalis* (McLEAN, 1988) the new taxon is compared with these.

Material and methods

All specimens reported here were collected by Professor TUFAR during the OLGA II Research Cruise to the Manus Basin (Fig. 1). In all, 85 specimens were found. They were recovered from the surfaces of portions of larger chimneys on board the Research Vessel Sonne. Sampling was performed with a TV-controlled electrohydraulic grab (= GTVA, GTVD). Specimens were preserved in buffered formaldehyde on board and later transferred to 70% ethanol in Marburg. 23 specimens were discovered while sorting sample buckets with preserved *O. tufari* (17 GTVA, 42 GTVD), whereas 7 specimens were still clinging to the periostracum of *O. tufari*. 4 juveniles were found on cirripeds (*Eochionelasmus* cf. *ohtai*) hidden between the tergum-scutum and the wall plates (56 GTVA). Well preserved specimens show muddy translucent shells, but most specimens were exposed to air for a short time, causing the ostracum to change to opaque white. Sampling stations (Table 1) were located at Hydrothermal Field 1 "Wienerwald"

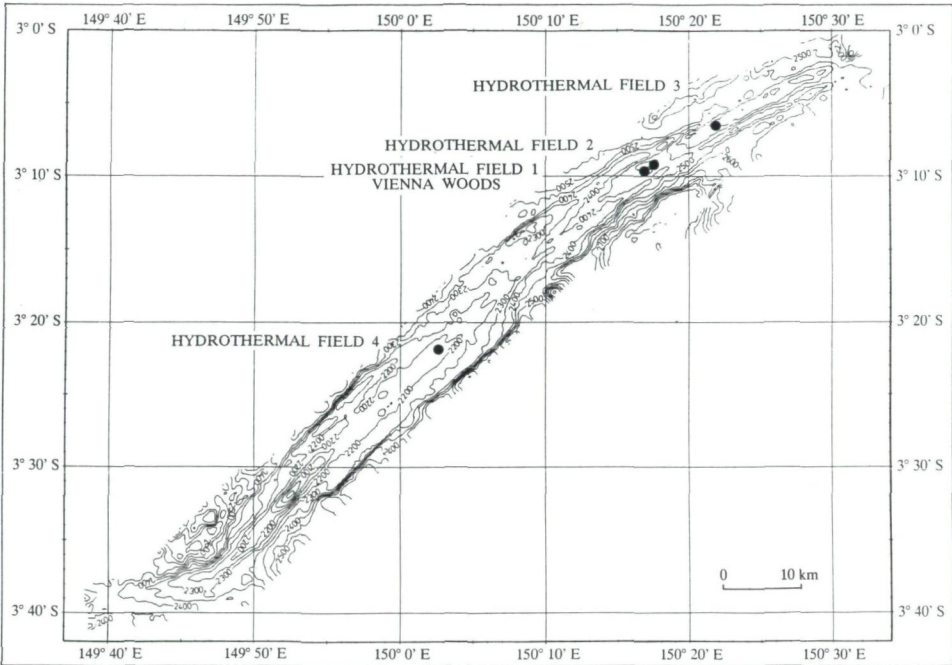


Fig. 1: Bathymetric map of the Manus Spreading Center from 3° 42' S, 149° 37' E to 3° 0' S, 150° 34' E showing the location of four major hydrothermal fields (depth in meters), Hydrothermal Field 1 “Wienerwald” (“Vienna Woods”) is the type locality of *Lepetodrilus schrolli* n. sp.

(“Vienna Woods”) with coordinates 3° 9.8 S, 150° 16.7 E at approximately 2500 m water depth (TUFAR 1990, 1992, TUFAR & JULLMANN 1991, BECK 1991, 1992 a, b). Considerations of the feeding biology and habitat of the new *Lepetodrilus schrolli* were supported by numerous photos and video-tapes taken by Prof. TUFAR during the investigation of this site in May and June 1990. 32 adult and subadult specimens were removed from their shells for morphological and anatomical studies and for determination of the sex. Radulae were extracted from preserved specimens after dissolution of tissues with 5% KOH at a temperature of 40°C for 24 hours, washed several times in distilled water, dehydrated via ethanol series and glued onto a SEM stub. To spread the radulae they were mounted on a round copper wire with 1 mm diameter. SEM shots were taken at the middle third of the radula by a Hitachi S-530 scanning electron microscope (25 kV, gold covering 6 nm). 2

Table 1: Sampling positions of *Lepetodrilus schrolli* sp. n. at Hydrothermal Field 1, “Wienerwald”, Manus Back-Arc Basin (OLGA II Research Cruise, May and June 1990)

Station N°	latitude	longitude	water depth	number
15 GTVA	3°9.88'S	150°16.79'E	2491 m	22
17 GTVA	3°9.861'S	150°16.777'E	2500 m	12
25 GTVA	3°9.86'S	150°16.79'E	2489 m	5
42 GTVD	3°9.84'S	150°16.78'E	2505 m	20
56 GTVA	3°9.801'S	150°16.768'E	1450 m	22

Table 2: *Lepetodrilus schrolli* sp. n., repository, age, shell measurements (in mm, maximum measurable), sexes and positions

Repository	age	length	width	height	sex	position
NHMW, holotype	adult	4.5	3.0	1.5	♀	56 GTVA
NHMW	adult	4.0	2.8	1.4	♀	56 GTVA
NHMW	adult	4.1	3.0	1.7	♂	56 GTVA
NHMW	juvenile	2.9	2.0	1.0	?	56 GTVA
NHMW	juvenile	1.5	1.2	0.5	?	56 GTVA
SMF	adult	5.2	4.0	2.0	♀	42 GTVD
SMF	adult	4.3	3.0	1.8	♀	42 GTVD
SMF	adult	4.1	3.1	1.5	♂	42 GTVD
SMF	juvenile	3.0	2.0	1.0	?	42 GTVD
SMF	juvenile	1.2	0.9	0.3	?	42 GTVD

NHMW = Naturhistorisches Museum Wien; SMF = Senckenbergmuseum Frankfurt

juveniles, 2 males and 2 females were critical point dried (via acetone and carbon dioxide) and examined by SEM. 2 males and 2 females were used for longitudinal and transverse sections (via paraffin, Azan staining).

For type specimens, repository and measurements see Table 2. Paratypes of *Lepetodrilus elevatus elevatus*, *L. elevatus galriftensis* (MCLEAN, 1988), *L. ovalis*, *L. pustulosus* (MCLEAN, 1988), and *L. fucensis* (MCLEAN, 1988) were available for comparative studies by courtesy of Dr. JAMES MCLEAN (Los Angeles County Museum of Natural History).

Abbreviations

(ab) afferent branchial vein, (ac) anterior odontophoral cartilage, (afg) anterior foot gland, (ai) anterior loop of intestine, (ao) anterior foot gland opening, (bc) buccal commissure, (cc) cerebral commissure, (ct) cephalic tentacle, (df) diffuse gland cells in foot sole, (dg) digestive gland, (eb) efferent branchial vein, (epa) right efferent pallial vein passing to right auricle, digitated part linked to gill lamellae (shown by transparency), (et) epipodial tentacle, (fg) food groove, (fi) gill filaments, (g) gonadal duct, (gl) gill leaflets, (inf) inner pallial fold, (j) jaws, (lau) left auricle, (lk) left kidney, (m) mantle, (mc) mantle cavity, (mf) mantle fringe, (oe) oesophagus, (oeg) oesophageal gland, (os) osphradium (shown by transparency), (ouf) outer pallial fold, (ov) ovary, (p) protoconch, (pc) posterior odontophoral cartilage, (per) periostracum, (pi) posterior loop of intestine, (pr) prostate gland, (prm) pallial retractor muscle, (pv) pallial vein, (ra) radula, (rau) right auricle, (re) rectum, (rk) right kidney, (rm) radula membran, (s) ciliated margin of the foot sole, (sev) subepipodial vein, (sc) statocyst, (sg) salivary gland, (sl) see Plate 4, section line for Fig. 3, (sm) shell muscle, (sp) sensory papilla, (spv) subpallial vein, (sto) stomach, (t) testis, (tpv) transverse pallial veins, (v) ventricle.

T A X O N O M Y

Order Archaeogastropoda THIELE, 1925
 Suborder Vetigastropoda SALVINI-PLAWEN, 1980
 Superfamily Lepetodrilacea MCLEAN, 1988
 Family Lepetodrilidae MCLEAN, 1988
Lepetodrilus MCLEAN, 1988
 Type species: *L. pustulosus* MCLEAN, 1988: 8

Lepetodrilus schrolli sp. n.

(Plate 1–4; Figs. 2–3)

D i a g n o s i s : Shell relatively small and moderately high, with apex nearly at the posterior end, surface smooth, margin of the aperture in one plane, interior with edged ridge posteriorly, penis lacking, free tip of the gill with 3–5 dorsal lamellae only. Radula with shortened rachidians and massive overhanging cusps at the first lateral teeth.

D e s c r i p t i o n : Shell (Plate 1; Plate 5: Figs. 1, 3–4, 6). Outline of aperture oval, anterior and posterior ends slightly tapered, margin in one plane. Profile moderately high for the genus, highest point at $\frac{1}{3}$ shell length from posterior, highest elevation often spottedly eroded by corrosive hydrothermal solutions. Apex on mid line, about $\frac{1}{20}$ shell length from posterior in adults, in juveniles apex turned to right and overhanging margin of shell. Protoconch length 140 μm , its surface finely pitted; protoconch exposed on right side in juveniles, overgrown in adults from 2 mm shell length.

Periostracum light brown, enveloping extensively the shell edge (in shells larger than 0.5 mm), smaller stages with broadly overhanging periostracum not enveloping the edge; in adults it is often damaged by an unknown organism which causes roundish patches; some shells with black mineral incrustations as described for other hydrothermal gastropods. Sculpture lacking except for fine broadly spaced growth irregularities.

Shell interior not nacreous, with strong posterior transverse edged ridge subtending the apex and becoming reduced anteriorly; surface near margin shows very fine coalescent lamellae caused by crossed lamellar texture in the ostracum; muscle scar horseshoe-shaped, strongly narrowed posteriorly where it is placed on the inner side of the transverse ridge; left arm of muscle scar slightly larger than right. Apical pit remains open containing the tip of the visceral mass.

Type locality: Hydrothermal Field 1, “Wienerwald”, at Manus Back-Arc Basin, 3° 9.8' S – 150° 16.78' E (Fig. 1).

Dimensions of holotype: 4.5 mm \times 3.0 mm \times 1.5 mm, female.

Largest female: 5.5 mm \times 4.0 mm \times 2.4 mm.

Largest male: 4.1 mm \times 3.0 mm \times 1.8 mm.

Ratio of height/length: 0.391 (n = 32).

One female showed a very unusual elevated shell (4.1 mm \times 3.0 mm \times 2.1 mm; ratio of h/l: 0.512) similar to *L. elevatus*, however, evidence based on the radula and gill conditions confirmed membership of *L. schrolli*.

Animal (Figs. 2–3; Plate 2; Plate 4: Figs. 1–5; Plate 5: Fig. 2). Body whitish, without any pigmentation except the muddy haemolymphatic fluid. Head well developed, equipped with equal-sized cephalic tentacles; bases of the tentacles encircled ventrally and laterally by folds: left fold simple, right fold with deep ciliated groove (food groove); right ventral side of the neck smooth, no additional triangular epipodial fold beneath the tentacle fold (i.e. no penis), left ventral side of the neck with sensory process. Eyes lacking. Cephalic tentacles, encircling folds and lips of the snout covered with fine ciliary pouches (about 30 cilia). Snout with

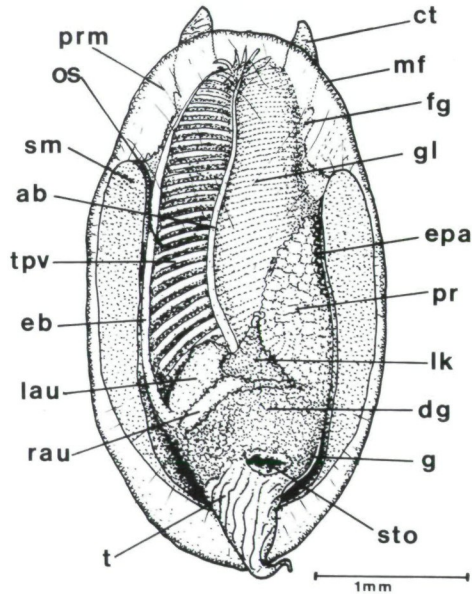


Fig. 2: *Leptodrilus schrolli* n. sp.. Male removed from shell, dorsal view (osphradium (os) and digitated part of efferent pallial vein (epa) shown by transparency, abbreviations see Material and methods).

large mouth surrounded by a rim; jaws with protruding chitinous pentagonal rods. Foot sole ovate, densely ciliated at its marginal area, anteriorly with a long transverse slit marking the opening of the pedal gland. An operculum is lacking in all stages. Epipodium with three pairs of tentacles: anterior pair with broad triangular bases, which are enlarged flaplike anteriorly to close the mantle cavity, the two posterior pairs with connected broad bases and broad flat tentacles protruding slightly over the shell margin when expanded. Compound epipodial sense organs not evident. Shell muscles horseshoe-shaped, narrowed posteriorly; left arm slightly larger and broader than right. The osphradium is marked as a dark line leading from the anterior edge of the left shell muscle to the bottom of the mantle cavity (Fig. 2).

Mantle skirt thin and translucent except for the thickened margin which shows two folds: the outer one is smooth, extending between the in-turned periostracum and the ostracum, the inner one thickened and coarsely digitated particularly at the anterior third, tips of the digitated processes covered with (sensory ?) cilia; a button-like sensory process is placed at the inner fold above the exhalant opening of the mantle cavity.

Mantle cavity extending approximately $\frac{3}{4}$ length of the animal, it is narrowed posteriorly on left side. Ctenidium very large, filling the cavity, to a great extent monopectinate and fused to the mantle skirt at left side with its axis, the very short free tip showing only 3–5 dorsal lamellae. Approximately 30 gill lamellae divide the mantle cavity into a ventral inhalant chamber and a dorsal right exhalant chamber. Ctenidial sense organs (i.e. bursicles, cf. HASZPRUNAR 1987) could not be

found. The middle third of the gill is linked together with the digitated part of the right efferent pallial vein (at inner side of the right shell muscle, shown by transparency in Fig. 2, (epa)); at the posterior third the lamellae become shorter, and at the anterior third the tips of the lamellae correspond to the ciliated food groove, showing ciliary pads used for suspension collecting. Innumerable very long frontal and abfrontal cilia at the ventral part of each lamella operate as a filter for the inhalant hydrothermal solutions. Probably, these cilia are accompanied by filamentous symbiotic bacteria (cf. DEBURGH & SINGLA 1984 for *Lepetodrilus fucensis*) but TEM shots are needed to separate cilia from bacteria.

Radula (Plate 2; Plate 3: Fig. 1; Plate 4: Fig. 1; Plate 5: Fig. 5) rhipidoglossate, about 35 transverse rows of teeth (in specimen with 4.1 mm shell length); formula: about 30 + 5 + 1 + 5 + about 30. Unusual radula pattern: rachidian well developed but strongly shortened, massive cusps of the first laterals orientated about a diagonal to the longitudinal axis of the radula; cusp row of laterals forming an inverted "U", however, base-row of rachidian, laterals and marginals forming a symmetrical arc.

Rachidian less than half as long as first lateral, the sturdy base having lateral extensions corresponding to proximate notches at the bases of the large first lateral teeth; rachidian cusp sharply pointed and finely denticulated (about 8 denticles). Bases of the laterals with distal expansions fitting to notches to facilitate within-row interlocking (cf. HICKMAN 1984). First lateral cusp massive, complexly divided into a short inner area with 4–5 fine denticles, a strong pointed denticle and a long outer area serrated by coarse denticles. Bent tapered cusps of laterals 2–5 with coarse equal-sized denticles at inner and outer edge. Marginals with flattened shafts and denticulated blunt cusps: inner denticles (about 8) finer than outer (likewise about 8); outermost marginals with flap-like undenticulated cusps.

R e m a r k s

Most anatomical features (Figs. 2–3) are in accordance with genus character-states given by FRETTER (1988: 35), with the important exception that the penis is lacking in males i.e. the reproductive system is relatively simple. It consists of: a white testis underlying the digestive gland and reaching the apex of the visceral mass as a spiral white fan-like part; the gonadal duct describing a few loops, leading to the renopericardial duct and receiving the products of the prostate gland before ending at the simple urinogenital opening at the mantle roof; sperms leave the mantle cavity via the exhalant chamber; a special pallial vas deferens is hardly visible, but it is evident in transverse sections as a broad ciliated band at the mantle, roof probably used for faeces as well. The female reproduction system is composed of a large ovary lying ventrally and right of the digestive gland and stomach, with a whitish receptaculum seminis placed at the right ventral side, and a ciliated genital groove evident at the right lower side of the mantle cavity. It is assumed that ova are fertilized in the mantle cavity (cf. FRETTER 1988), but this cannot be demonstrated here.

The alimentary system, left and right kidney, the hyparthyroid-dystenoid nervous system and the circulatory system are similar to those described for *L.*

elevatus (FRETTER 1988: 49). In contracted condition (Fig. 3) all veins are tightly filled with haemolymphatic fluid. The haematocoel is not evident in serial-sectioning.

Microscopic and SEM tests of stomach and intestine contents yielded 40% mineral particles (up to 30 µm) and 60% flaky organic material; foraminifera, sponge-needles or planctonic fragments were not found, and it is therefore assumed that food is composed of globular bacteria and primary of *Hyphomonas*-like bacteria. These filamentous bacteria occurred at the food groove and the radula and over at the entire periostracum and probably even within the periostracum (Plate 5: Fig. 5).

L. schrolli certainly lives mainly as a grazer on layers of bacteria. Its nutrition is probably supported by suspension filter-feeding with the gill. Endocytosis at gill leaflets, if present, is unimportant. The life habit is controlled by the hydrothermal environment. The new species was found on hard surfaces of black smoker chimneys with diffuse venting and living epizooically on *O. tufari* and cirripeds. It is certainly not sessile or semi-sessile, like other vent limpets (eg. *Symmetromphalus hageni*).

Etymology: The species name is in honor of Univ.-Prof. Dr. ERICH SCHROLL, Wirklicher Hofrat, of the Geotechnisches Institut der Bundesversuchs- und Forschungsanstalt Arsenal, Vienna, whose scientific knowledge was of great value for the OLGA Research Project.

Discussion

Classification

Although having many similarities in shell and anatomical characters, the new species is clearly distinct from *L. elevatus* from East Pacific Rise by the following features: the smaller shell dimensions, the less elevated shell profile, the broadly overhanging cusps of the first lateral teeth (cf. Plate 3: Figs. 1–2), the reduced number of dorsal gill lamellae and the lack of a penis in males.

The same characters separate *L. schrolli* from the form of *L. elevatus* reported from the Mariana Trough by McLEAN (1990, 1993) and HESSLER & LONSDALE (1991). However, the Mariana form (though possessing a radula similar to that of the East Pacific form) seems to lack a penis, because all specimens (38 in all and probably males among them) appear to the author “to be female, none having the broad triangular penis” (McLEAN 1993: 32). Consequently, the Mariana form is neither like *L. schrolli* nor fully like *L. elevatus* from the East Pacific Rise. Further anatomical or genetical investigations are needed for a proper placement of the Mariana form.

L. schrolli is similar to *L. ovalis* in same characters of the radula and the gills. In *L. ovalis* (Plate 3: Fig. 3) the first lateral teeth show the same triple division of overhanging cusps (inner 4–5 denticles, strong pointed denticle, outer serrated area). However, the rachidian is much broader. While most species of *Lepetodrilus* possess many dorsal gill lamella (e. g. about 25 in *L. elevatus*, FRETTER 1988), they are reduced in number in *L. schrolli* and *L. ovalis*. However, *L. schrolli* still

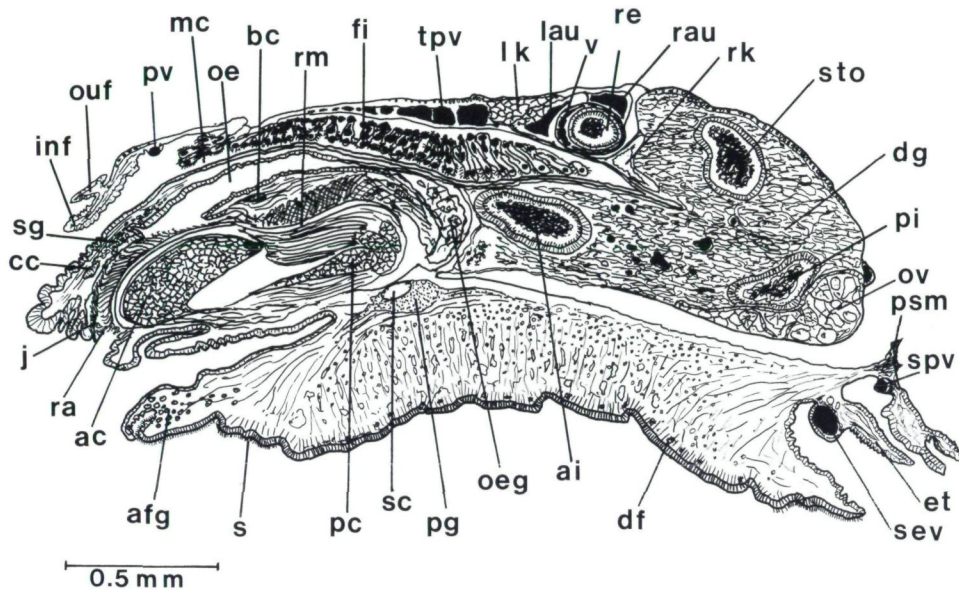


Fig. 3: *Lepetodrilus schrolli* n. sp. Female with odontophore retracted and circulatory system tightly filled with haemolymphatic fluid, oblique longitudinal section (cf. Plate 4 Fig. 3; abbreviations see Material and methods).

has 3–5 lamella, while *L. ovalis* has none (FRETTER 1988). In addition, obvious differences between the two species exist with respect to shell characters: position of the apex ($\frac{1}{3}$ shell length from posterior margin in *L. ovalis*) and basal outline (more oval in *L. ovalis*) are different. The new taxon is thus well separated from other *Lepetodrilus*-species by morphological characters.

The character “lack of a penis in males” needs more comment because all *Lepetodrilus*-species from the East Pacific Rise have a well developed penis and reproduction probably happens all the year round as FRETTER (1988) deduces from anatomical data. It is conceivable that the lack of penes in *Lepetodrilus* species from the West Pacific is caused by seasonal effects. In some shallow water gastropods the reproductive apparatus becomes much reduced outside the breeding season (e. g. in *Littorina*, cf. FRETTER & GRAHAM 1962: 23). But are there comparable periodic seasons at deep-sea hydrothermal vents? We know of variations in vent flow which effect differences in shell growth or faunal change and replacement (HESSLER et al. 1985, HESSLER et al. 1988, ROUX et al. 1989). Short-time temperature periods, such as reported by CHEVALDONNE et al. 1991, certainly have no influence on the anatomical characters of reproduction apparatus. But long-term cycles of vent activity might do so. However, three-year cycles of this activity were deduced only from shell microstructure of *Calyptogena magnifica* from the East Pacific Rise 21° N until now, i.e. from the region where a lack of penes was never observed. Rhythms of vent activity may occur in the West as lack of penes may be found in the East one day. At present, absence or presence

of a penis cannot be considered a reliable taxonomic character allowing the recognition of a special subgenus or even genus.

Relationship

Lepetodrilacean limpets are easy to determine by characters of the radula. The radula pattern follows the principle: shortening of the rachidian, accompanied by enlargement and obliquity of the first laterals. This would appear to be unique (MCLEAN 1988). However, there are some examples from other rhipidoglossate archaeogastropod groups which share this genetically coded basic ground plan: Phenacolepadidae (OKUTANI et al. 1988, BECK 1992 b), Neritidae (THIELE 1866–1893), and to a certain extent Pyropeltidae (MCLEAN & HASZPRUNAR 1987), Pseudococculinidae (MCLEAN 1991) and Tricoliinae (HICKMAN & MCLEAN 1990). In addition, we can find special flap-like outer marginal teeth in Lepetodrilidae as well as in Pleurotomariacea and Neritacea (BECK 1992 b). Such conformity in all these rather different groups points out that there must have been a common ancestor that invented this radula pattern and/or flap-like teeth. In any case, these special features are not caused by constructional, ecological or mechanical factors (sensu HICKMAN 1980), but are certainly of phylogenetic relevance. The phylogram proposed by HASZPRUNAR (1988: 424), which places the Lepetodrilioidea within the Vetigastropoda away from Neritimorpha, has to be reconsidered taking into account this radular evidence. But the comments of MCLEAN (1988, 1993) that Lepetodrilacea are an offshoot from a late Palaeozoic to early Mesozoic archaeogastropod stock is supported by this. Likewise, the wide distribution of the genus *Lepetodrilus*, ranging from the East Pacific Rise System to the Mariana Trough, the Manus Back-Arc Basin and, as recently reported, to the North Fiji and Lau Basin (WARÉN & BOUCHET 1993: 88) makes us assume that there has been a very early radiation. In the sense of HESSLER & LONSDALE (1991: 176 and Fig. 7) a radiation could have also been possible about 60, 55 or 43 m.y. ago when the gap between the East Pacific Rise and Western Pacific Spreading Centers could probably be bridged. It is likely that more recent tectonic events (formation and fading of several active spreading centers, cf. HESSLER & LONSDALE 1991) caused the recent biogeography of hydrothermal vent fauna of the Western Pacific complex.

Speciation

Hydrothermal vent sites are rather patchy in distribution and speciation could be influenced by many factors: e.g. geographical (tectonic) isolation, long-time eustatic oscillation of the sea level accompanied by changes of water current which hinders or promotes larval dispersal, ecological specifics (pH-value, concentrations of sulphides, methane, heavy metals, radioactivity etc.) or genetic founder effects. Recently published genetical evidence (DENIS, JOLLIVET & MORAGA 1993, in print) for the mesogastropod *Alviniconcha hessleri* point out that there are strong genetical differences between populations of two neighbouring vent sites (North Fiji and Lau Basin) and that reproductive isolation is strongly suggested, though morphological differences are recognizable only in shell sizes

and length of periostracum spicules. Although these two morphs were considered as cryptic species these authors waver to draw taxonomic consequences as do MORAGA, JOLLIVET & DENIS (1993, in print) for the hydrothermal vent bivalve *Bathymodiolus*. In view of the genetic differences found in neighbouring morphs of *A. hessleri* cited above, these forms (from North Fiji and Lau Basin, WARÉN & BOUCHET 1993) could well be considered separated species, and this view would also refer to the pertinent morphs from the Mariana Trough (OKUTANI & OHTA 1988), the Manus Back-Arc Basin (TUFAR 1990, 1992, TUFAR & JULLMANN 1991, BECK 1991) and the Woodlark Basin (S. D. SCOTT, University of Toronto, pers. comm.). The same view can be applied to the morphs of the black mesogastropods *Olgacocha tufari* (= *Ifremeria nautilei* BOUCHET & WARÉN, 1991) from Manus Basin, Woodlark Basin, North Fiji Basin and Lau Basin. It is also suggested that the speciation of *Lepetodrilus* species from Western Pacific is influenced in a similar way. MCLEAN's *Lepetodrilus elevatus* from Mariana Trough as well as *L. elevatus* from North Fiji and Lau Basin consequently require further study, both morphological and genetical.

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Plate explanations

(Abbreviations see Material and methods)

Plate 1: *Lepetodrilus schrolli* n. sp. Figs. 1–2, 4. Holotype, female (length 4.5 mm); Fig. 3. Empty shell ventrally viewed (length 4.1 mm).

Plate 2: *Lepetodrilus schrolli* n. sp. Male, critical point dried specimen, ventral view on head and foot, buccal mass with radula totally protruded.

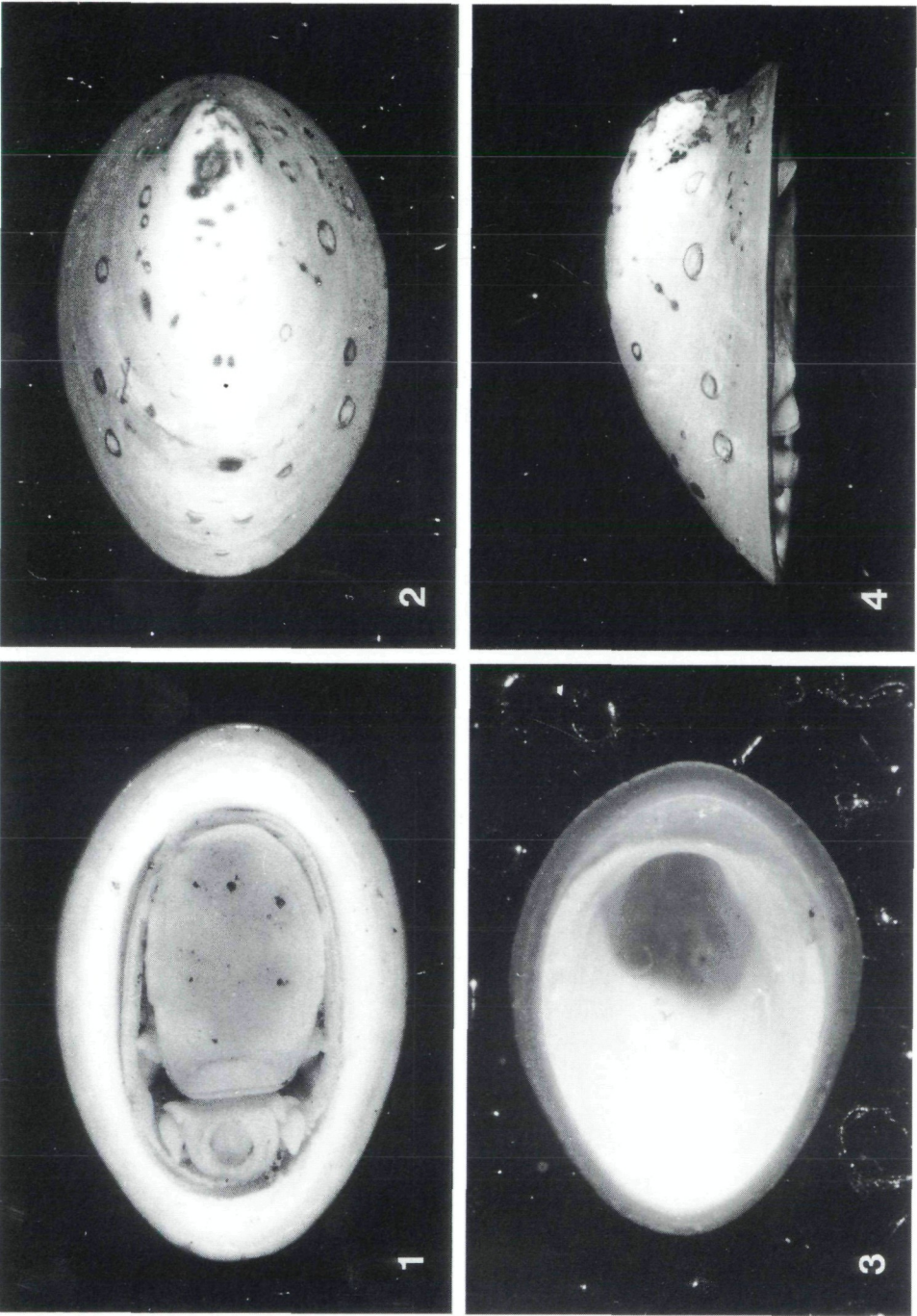
Plate 3: Radulae. Fig. 1. Radula of *Lepetodrilus schrolli* n. sp. Fig. 2. Radula of *L. elevatus* from East Pacific Rise (20° 50.0' N, 109° 6.0' W). Fig. 3. Radula of *L. ovalis* from East Pacific Rise (20° 50.0' N, 109° 6.0' W).

Plate 4: *Lepetodrilus schrolli* n. sp. Animal. Fig. 1. Mouth with jaws and radula, ventral view. Fig. 2. Dorsal view on the tip of the gill, mantle removed. Note reduced number of dorsal gill lamellae. Fig. 3. Female removed from shell, dorsal view. Fig. 4. Frontal view into mantle cavity, mantle removed. Note the digitated part of the efferent pallial vein (arrow). Fig. 5. Right cephalic tentacle with encircling fold and food groove (arrow points to a bundle of Hyphomonas-like bacteria).

Plate 5: *Lepetodrilus schrolli* n. sp. Fig. 1. Very young specimen showing the pitted protoconch and the broadly overhanging periostracum (folded during preparation). Fig. 2. Left first epipodial tentacle in ventral view. Fig. 3. Young shell viewed from right, densely coated with bacteria, protoconch still visible and exposed to right. Fig. 4. Shell, broken at middle third of shell, showing overhanging periostracum and shell structure. Fig. 5. Large globular and fine filamentous bacteria on the radula. Fig. 6. Shell, detail of Fig. 4, periostracum with porous outer surface.

L. A. BECK: Morphological and anatomical studies on a new lepetodrilacean limpet (Gastropoda, Prosobranchia) from hydrothermal vents at the Manus Back-Arc Basin (Bismarck Sea, Papua New Guinea)

Plate 1



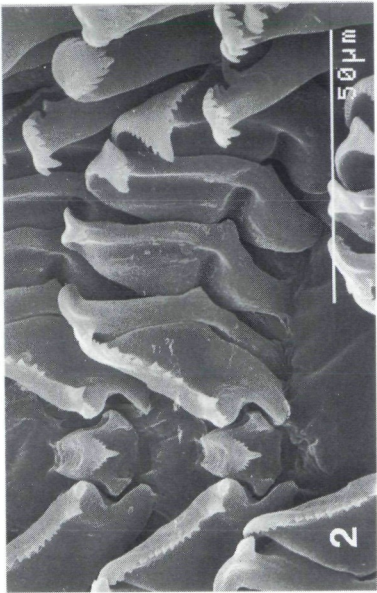
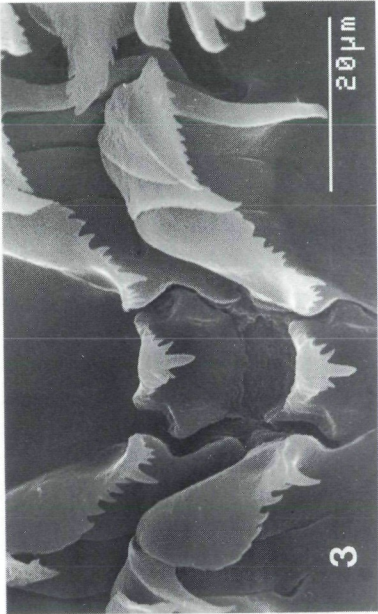
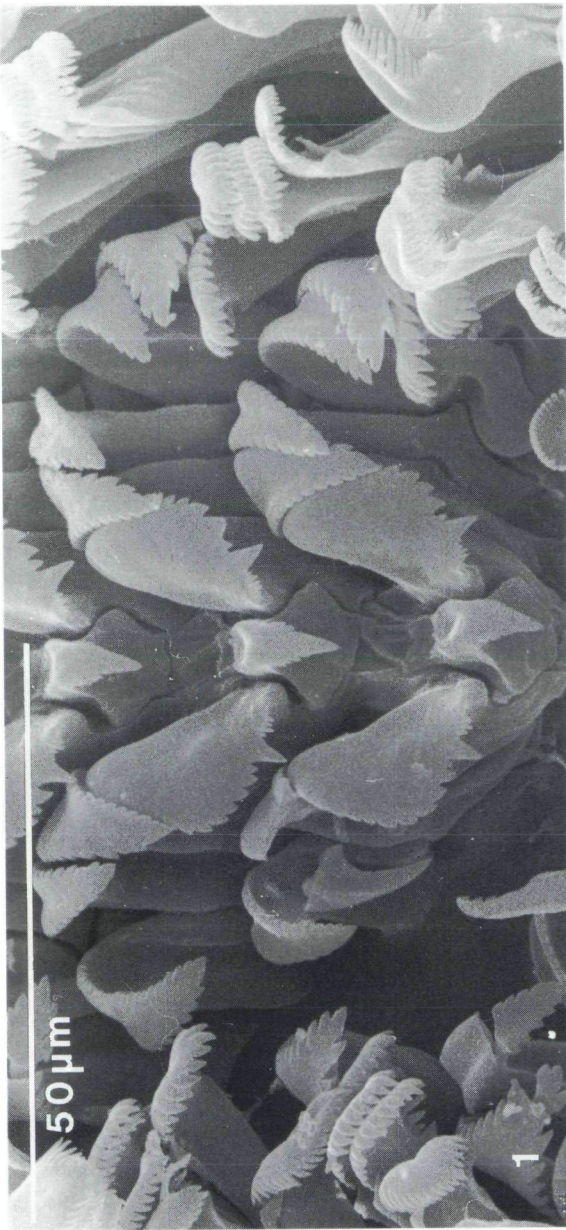
L. A. BECK: Morphological and anatomical studies on a new lepetodrilacean limpet (Gastropoda, Prosobranchia) from hydrothermal vents at the Manus Back-Arc Basin (Bismarck Sea, Papua New Guinea)

Plate 2

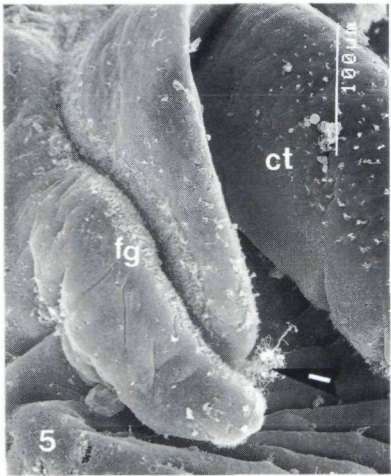
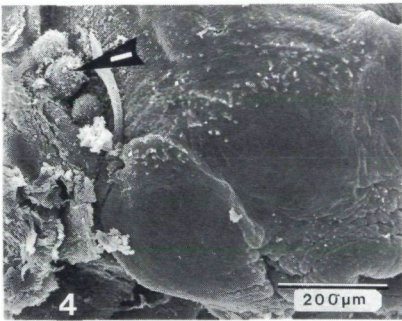
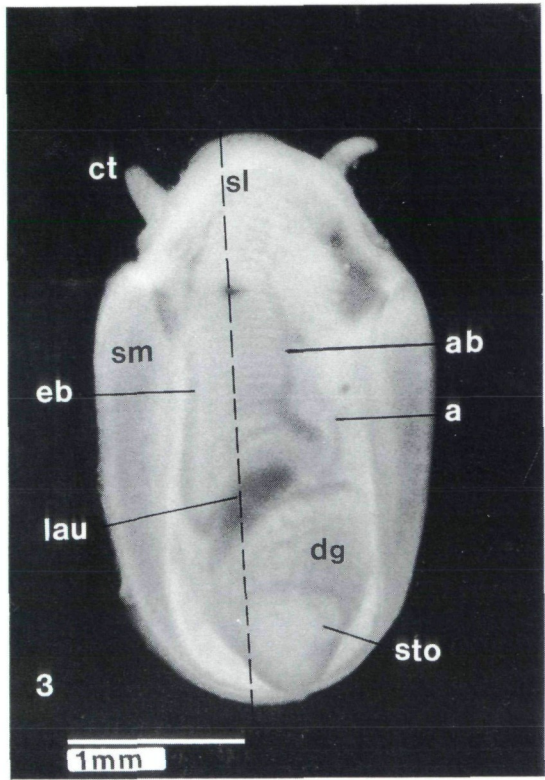
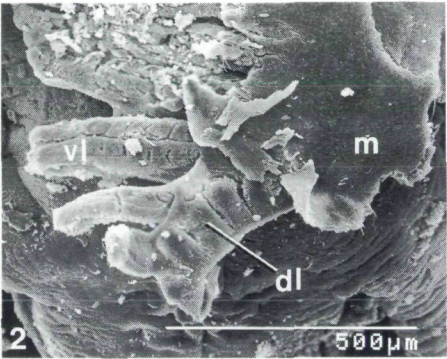
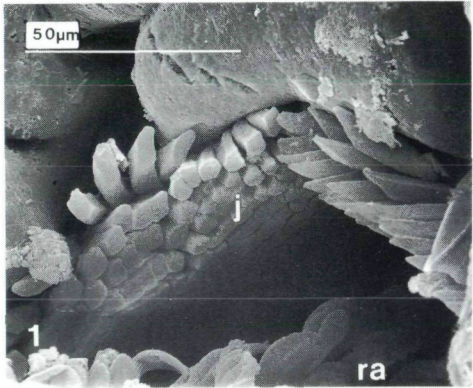


L. A. BECK: Morphological and anatomical studies on a new lepetodrilacean limpet (Gastropoda, Prosobranchia) from hydrothermal vents at the Manus Back-Arc Basin (Bismarck Sea, Papua New Guinea)

Plate 3

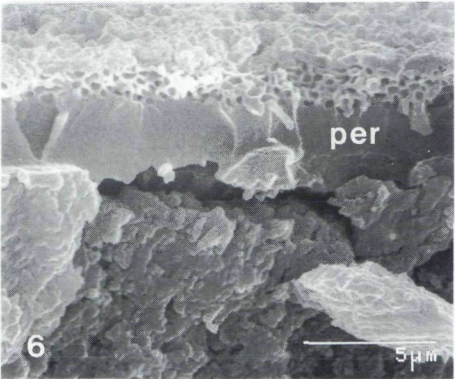
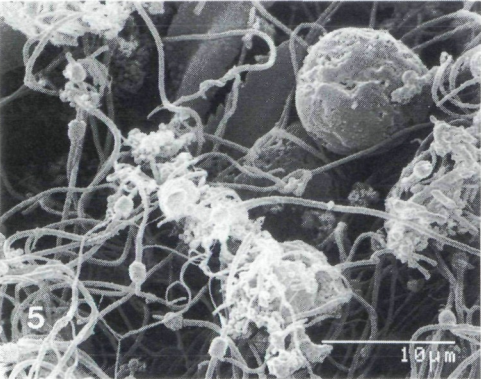
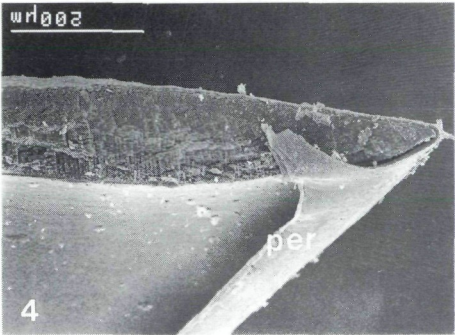
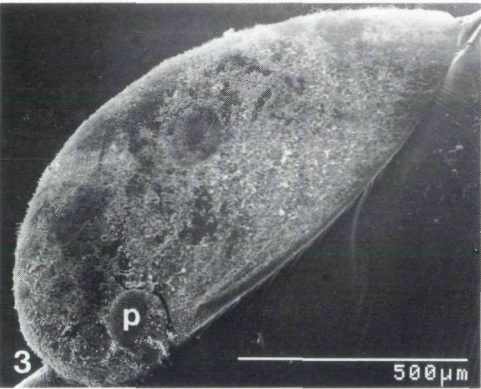
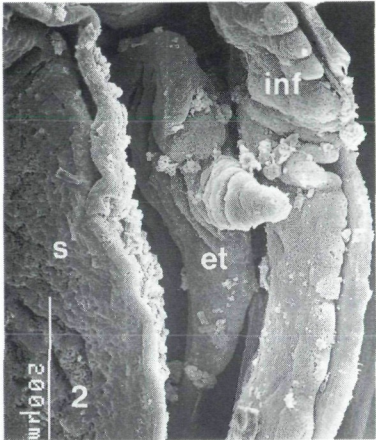
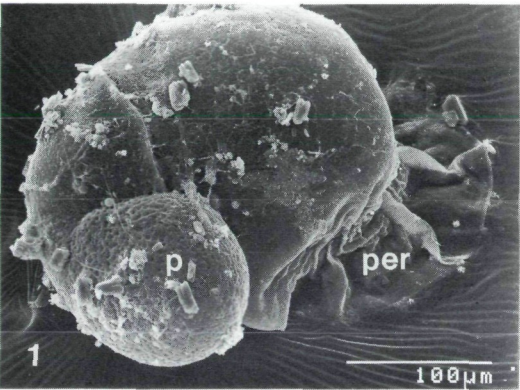


L. A. BECK: Morphological and anatomical studies on a new lepetodrilacean limpet (Gastropoda, Prosobranchia) from hydrothermal vents at the Manus Back-Arc Basin (Bismarck Sea, Papua New Guinea)



L. A. BECK: Morphological and anatomical studies on a new lepetodrilacean limpet (Gastropoda, Prosobranchia) from hydrothermal vents at the Manus Back-Arc Basin (Bismarck Sea, Papua New Guinea)

Plate 5



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