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THREE NEW SPECIES OF THE FAMILY NEOLEPETOPSIDAE (PATELLOGASTROPODA) FROM HYDROTHERMAL VENTS AND WHALE FALLS IN THE NORTHEASTERN PACIFIC

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ABSTRACT Three new northeastern Pacific species of the deep-sea limpet family Neolepetopsidae are described. One (*Paralepetopsis tunnicliffae*) is from the hydrothermal vent habitat, and two (*Paralepetopsis clementensis* and *Neolepetopsis nicolasensis*) are from whale bone. This is the first record of the genus *Paralepetopsis* from the eastern Pacific, and the first record of the family from whale bone, in contrast to all previous records from hydrothermal vents and seeps. The family Neolepetopsidae joins the cocculiniform Pyropeltidae in its occurrence in the vent/seep habitat and the whale-fall habitat. Unlike the Pyropeltidae, in which species may occur in both the vent/seep and the whale-fall habitat, the two new neolepetopsid species in the whale-fall habitat are not the same as the species in the nearest vent/seep habitats.

KEY WORDS: hydrothermal vents, whale-falls, new species, northeastern Pacific Neolepetopsidae

INTRODUCTION

The family Neolepetopsidae was proposed some 18 years ago (McLean 1990), at which time I proposed higher levels of classification for this family, arguing that it represented a basal sister group to all other patellogastropods. Fretter (1990) provided a report on the anatomy, finding it not unlike other patellogastropods except for the radula. Subsequently, Lindberg (1998) treated it as the most apomorphic family in Acmaeoidea; more recently, Warén & Bouchet (2005) have reinstated it at a higher level and have recognized it as the superfamily Neolepetopsoidea. Sasaki & Warén (2007, abstract), have suggested "possible relationships with deep-sea Acmaeoidea." Kiel (2004) reported that the outer layer of neolepetopsid shell structure is "prismatic complex crossed lamellar," a combination shown by Hedegaard (1990) to be entirely calcitic. This was considered by Kiel to provide "further evidence for their position as sister group of the Acmaeidae." My original observation (McLean 1990) was that the individual teeth of the radula of the Neolepetopsidae were unmineralized, considering that the teeth are not darkly opaque, as observed in the shallow-water patellogastropods. However, Cruz & Farina (2005), have shown that the teeth are in fact mineralized, making them less unique than they may seem to be.

Additional species of Neolepetopsidae have been described by Beck (1996) and by Warén & Bouchet (2001). Beck extended the distribution to the Edison Seamount in the western Pacific with the description of *Paralepetopsis rosemariae*. Warén & Bouchet (2001) provided notes on eastern Pacific species of *Neolepetopsis*, and described two additional species of *Paralepetopsis*: *P. ferrugivora*, from the Mid-Atlantic Ridge and *P. lepichoni* from the Nankai Trench, off Southeastern Honshu, Japan.

Here I take the opportunity to describe three additional northeastern Pacific species of the family Neolepetopsidae, including two species of the genus *Paralepetopsis* and one new species of *Neolepetopsis*. One of the species, a new *Paralepetopsis*, is from the hydrothermal vent habitat; another new *Paralepetopsis* and a new *Neolepetopsis* are from whale bone, which is an hitherto unknown habitat for the family, although

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the whale bone habitat is known for the cocculiniform families Pyropeltidae, Cocculinidae (see McLean 1992), and Osteopeltidae (see Marshall 1994). Only the family Pyropeltidae has previously been known from both the vent/seep and whale bone habitat.

METHODS

Shells of the new species were photographed with three views. The radula from the single specimen of *Paralepetopsis tunnicliffae* was mounted for SEM; radulae of the two other new species were whole-mounted in stain-suffused, nonresinous mounting medium. For these two new species, the entire radular ribbon was digitally photographed through a light microscope, which enabled a count of the tooth rows and, at higher resolution enabled confirmation of the generic identification indicated by the shell morphology.

Specimens are deposited in the type collection of the Natural History Museum of Los Angeles County (LACM).

SYSTEMATICS

Family Neolepetopsida (McLean, 1990) Genus Neolepetopsis (McLean 1990)

Neolepetopsis McLean, 1990: 492. Type species (OD): Neolepetopsis gordensis McLean, 1990. Type locality: Escanaba Trough, Gorda Ridge, off northern California (41°29'N, 128°29'W), 3,271 m.

Shell sculpture coarsely clathrate, shell interior with transparent zones. Radula with well-formed rachidian, two pairs of laterals, paired pluricuspid teeth, and two pairs of marginals.

Four species, all from abyssal depths at hydrothermal vents, were originally described by McLean (1990). Two of these species, *N. verruca* from the East Pacific Rise at 21°N, and *N. occulta* from the Green Seamount at 21°N have not been subsequently reported. The species *N. densata* from the East Pacific Rise at 12°N was reported by Gustafson & Lutz (1994) from the Galapagos Rift; Warén & Bouchet (2001) illustrated the shell and radula of *N. densata*, with figures that closely matched my original figures.

The type species N. gordensis has been extended by Warén & Bouchet (2001) to the Jalisco Block Seeps at 20°N, and tentatively to 5°S, off the coast of Peru at. They noted that the identity of the Peruvian specimens as N. gordensis was uncertain because of the high variability of the type species, corroded condition of the material from Peru, and distance from the type locality; no illustrations of shells or radulae from Peru were provided. They illustrated the shell and radula for material from the Jalisco Block Seeps, which they considered most likely to be conspecific with N. gordensis. There is an error in the figure lettering because the radula figured by Warén & Bouchet (2001, Fig. 2d) from the Jalisco Block Seeps shows a broad, rounded pluricuspid, unlike my original illustration (McLean 1990, Fig. 11f), and it is clear that this represents a switch of their Figures c and d, because c is closely similar to Figure 11f of McLean (1990) for gordensis and their Figure d is evidently that of their new species Paralepetopsis lepichoni, in which the pluricuspid tooth is large and broad as in most species of Paralepetopsis. On the basis of shell characters, I notice that their illustration of a shell from the Jalisco Block Seeps (Figs. 3f,g) does not show the sharply projecting radial ribs at the margin to match specimens from the type locality (shown here again in Fig 1A,B), so I do not accept that it is *gordensis*; I consider it an undescribed new species.

The new species of *Neolepetopsis* described here was collected from whale bone, in contrast to the original records of other species from hydrothermal vents. *Neolepetopsis* remains known only from abyssal depths in the eastern Pacific, as yet unreported from other vent/seep sites elsewhere.

Neolepetopsis nicolasensis McLean, New Species (Figs. 1C, 3A, 3C)

Holotype LACM 3089, paratype LACM 3,090, 960 m on whale skeleton, NW of San Nicolas Island, CA (33°20.35'N, 119°58.85'W), collected by Craig Smith (ATV 113), April 30, 1995. Two specimens. For further information on the habitat and collecting records, see Smith & Baco (2003) and Baco & Smith (2003).

Shell (Fig. 1C): Sturdy, oval to oblong, slightly narrower anteriorly, profile low, highest elevation at apex; shell margin in



Figure 1. Shells of *Neolepetopsis*. (A) *Neolepetopsis gordensis* McLean, 1990, 3,200–3,250 m, Escanaba Trough, Gorda Ridge, off northern California (LACM 2404, paratype), length 8.7 mm (laterally compressed form). (B) *Neolepetopsis gordensis* McLean, 1990, 3,271 m, Escanaba Trough, Gorda Ridge, off northern California (LACM 2401, holotype), length 7.6 mm. C. *Neolepetopsis nicolasensis* McLean, new species, 960 m, on whale bone, NW of San Nicolas Island, CA (LACM 3089, holotype), length 7.5 mm.



Figure 2. Shells of *Paralepetopsis*. (A) *Paralepetopsis tunnicliffae* McLean, new species, 2,145 m, Middle Valley Segment, Juan de Fuca Ridge, off Washington (LACM 3091, holotype), length 8.2 mm. (B) *Paralepetopsis clementensis* McLean, new species, 1,800 m, on whale bone, San Clemente Seep, SW of San Clemente Island, CA (LACM 3092, holotype), length 5.9 mm.

same plane (ends not raised). Apex on midline, nearly central but slightly closer to anterior end. Apex eroded, lacking protoconch; periostracum lacking. Sculpture reticulate, concentric ridges well-defined, about equal in strength to radial ribs, producing nodes on crossing radial ribs; radial and concentric sculpture diminishing in strength near margin; radial ribs not projecting at margin. Shell interior opaque white in area corresponding to apex; outline of muscle scar not well marked, sides of interior translucent, revealing concentric sculpture of exterior; shell margin translucent, with dark line at 0.4 mm from edge marking transition to thicker inner layer. Length 7.5 mm, width 5.7 mm, height 2.1 mm (holotype), length 6.6 mm, width 4.6 mm, height 1.9 mm (paratype).

Radula prepared as whole mount (Fig. 3A): Length of ribbon 0.7 mm, estimated number of tooth rows 240. Cusps taking stain faintly, detectable as five dark markings that indicate the bending region of the overhanging cusps. There are clearly five cusped teeth in each row, in contrast to the expected seven (rachidian, two pairs of laterals and the pluricuspid) as shown in previous illustrations for the species gordensis and densata, as originally illustrated by McLean (1990). The centermost bending cusp is positioned above two shaft units, suggesting that this represents a fusion of the rachidian and adjacent first pair of laterals, with loss of the shaft of the rachidian. This is flanked by another pair of laterals with similar bending cusps, outside of which there is a pair of cusped teeth with very long, dark staining, pointed shafts that taper at the base. These large fang-like basal shafts have laterally extending branches leading to two tooth plates regarded as the marginal teeth. The radula of N. nicolasensis is incompletely understood in the absence of an SEM illustration, but it is clear that this is an entirely novel pattern that expands the possible conditions for the genus Neoleptopsis.

The shell of *N. nicolasensis* is not like that of *N. gordensis*, because the radial sculpture does not have the sharp projections of the radial ribs at the margin, showing in both forms, the regular (Fig. 1B) and the laterally compressed (Fig. 1A). The

shell is not comparable to that of N. *densata*, which has a much lower profile and fully transparent interior. The shell interior is most like that of N. *verruca* in having a dark band along the margin in interior view, but the band is a line, rather than the broader band of N. *verruca*. The concentric sculpture of N. *verruca* is much more pronounced in lateral view. There was no original radular preparation for N. *verruca*. The shell interior is not like that of N. *occulta*, which is fully transparent except in the central area.

Genus Paralepetopsis (McLean 1990)

Paralepetopsis McLean 1990: 510. Type species (OD): *Paralepetopsis floridensis* McLean 1990. Type locality: Florida Escarpment Seeps (26°03' N, 84°54' W), 3270 m.

Shell sculpture of radial ribs and concentric growth lines weak, shell interior fully opaque. Radula with rachidian and two pairs of laterals with straight shafts, cusps usually broad.

The weak radial and concentric sculpture differs from the strongly clathrate sculpture of *Neolepetopsis*; the shell interior is opaque, rather than partially transparent.

When the genus was proposed one species was known. Now, however, it is known to be broadly distributed. Three additional species have subsequently been named. Beck (1996) described *P. rosemariae* from the central Pacific Edison Seamount (3°S, 152°E), 1,483 m. Warén & Bouchet (2001) described *P. ferrugivora* from the Mid-Atlantic Ridge (37°18' N, 32°17' W), 1,665–1,728 m, and *P. lepichoni* from the Nankai Trench Seeps, off southeastern Honshu, Japan (33°50'N, 137°55'E), 2,140 m.

Paralepetopsis tunnicliffae McLean, New Species (Figures 2A, 3D)

Holotype LACM 3,091; 2,145 m, Clam Bed, Chowder Hill, Middle Valley Segment, Juan de Fuca Ridge west of Juan de Fuca Strait (48°27.5'N, 128°42.5'W) (station HS 192), collected by Verena Tunnicliffe, June 26, 1992. Single specimen. For collection details see Juniper et al. (1992).



Figure 3. Radulae of new species of *Neolepetopsis* and *Paralepetopsis*. (A) *Neolepetopsis nicolasensis*. Whole mount of radular ribbon, scale bar = 1,000 μ m. (B) *Paralepetopsis clementensis*. Whole mount of radular ribbon, scale bar = 1,000 μ m. (C) *Neolepetopsis nicolasensis*. Enlarged view of tooth rows, scale bar = 100 μ m. (D) *Paralepetopsis tunnicliffae*. SEM view of tooth rows, scale bar = 50 μ m. (E) *Paralepetopsis clementensis*. Enlarged view of ribbon with damaged teeth, scale bar = 100 μ m.

Shell (Fig. 2A): Elliptical in outline, anterior end slightly narrower, profile moderately high, highest elevation of shell at apex; shell margin in same plane. Apex on midline, closer to anterior edge. Apex eroded, protoconch missing. Periostracum thin, light tan. All slopes moderately convex. Sculpture of fine radial striae and concentric growth irregularities. Shell interior with thickened opaque area at apex, slopes of interior translucent, revealing faint indications of radial and concentric irregularities of exterior; inner margin of lip 0.5 mm broad, thinner and more translucent than thicker part of interior slope. Muscle scar not well marked, but faintly indicated if the shell is tilted for viewing. Length 10.6 mm, width 8.2 mm, and height 3.6 mm (holotype).

Radula prepared for SEM (Fig. 3F). The radular SEM shows two pairs of lateral teeth and the broad overhanging cusps expected in *Paralepetopsis*. The shafts of the rachidian and inner pair of lateral are narrow; the cusp of the second pair is larger than that of the first pair; the shaft of the second pair is hidden behind the larger pluricuspid. The shafts of the marginals are not differentiated from the base of the ribbon, but the cusps are in their expected positions and may be distinguished from debris on the outer edge of the ribbon that shows in Figure 3D.

The undifferentiated shafts of the marginals are unique in the genus. However, this could mean that the tooth rows examined came from the developing end of the ribbon. The cusps have a rounded edge, unlike the square rachidian of *Paralepetopsis floridensis* and the acutely pointed outline of the other cusps of *P. floridensis*.

The shell profile is lower than that of the type species *P*. *floridensis.* Shell sculpture is similar, but the interior differs in having the muscle scar weakly indicated.

Paralepetopsis clementensis McLean, New Species (Figures 2B, 3B, 3E)

Holotype, LACM 3092, paratype LACM 3093, 1,800 m, on whale skeleton, San Clemente Seep, SW of San Diego, CA

(32°12′N, 117°44′W), collected by Craig R. Smith, *Alvin* dive 3534, March 29, 2000. Two specimens. For further information on the habitat and collecting records, see Smith & Baco (2003) and Baco & Smith (2003).

Shell (Fig. 2B): Outline elongate elliptical, anterior slightly narrower, profile high, ends strongly raised relative to sides (even in smaller specimen), apex at highest point of shell. Apex eroded, outer shell layer in apical area missing (even in smaller specimen); periostracum not detected. All slopes convex, more so at margin of large specimen. Radial and concentric sculpture lacking except for fine microscopic, interrupted, concentric ripples. Muscle scar of interior not marked, interior of larger holotype with darker margin, 0.3 mm wide, adjacent slope opaque white, inner slope darker. Length 5.9 mm, width 4.8 mm, height 2.7 mm (holotype); length 4.8, width 2.7, height 1.2 mm (paratype).

Radula prepared as whole mount, but cusps of teeth lost during preparation (Fig. 3E): Length of ribbon 0.9 mm, estimated number of tooth rows 270. The shafts of the rachidian and laterals are straight, the shafts of the first pair of marginals are tapered toward the tip. The shaft of the second pair of marginals is larger at the tip and flexed toward the outer side at the base. The inner edge to the shaft of the pluricuspid has a broad embayment and is relatively narrow; the shafts of the pluricuspid is narrow toward the base. The shafts of the shafts of the shafts of the shafts agrees with the radular illustrations for the other four species of the genus, including *P. tunnicliffae* described here.

It is clear that the radula differs from the more northern *P. tunnicliffae* because the pluricuspid has a narrower base and the marginal teeth are well marked, quite unlike the condition in *P. tunnicliffae*, in which only the tips are revealed.

DISCUSSION

The composition of the family Neolepetopsidae with the three original genera *Neolepetopsis*, *Paralepetopsis*, and *Eulepetopsis* has remained unchanged for 18 years. Four species of *Neolepetopsis* were previously known and a fifth is here added. *Paralepetopsis* was originally known from a single species; other authors have added three species of *Paralepetopsis* and I am here adding the fifth and sixth species. The genus *Eulepetopsis* remains monotypic. The eastern Pacific seems to be the center of distribution, but that may be because of the more extensive sampling in the eastern Pacific.

The whale-fall habitat in the eastern Pacific has been known for at least 15 years, and has been reported on by Smith et al. (1989), Smith (1992), Smith & Baco (1998), Baco & Smith (2003), Smith & Baco (2003), Bennett et al. (1994). Elsewhere, whale-bone associated molluscs have been reported from New Zealand (Marshall 1987, Marshall 1994), from Japan by Okutani et al. (2003), and by Fujiwara et al. (2007). The mytilid mussel *Ides washingtonia* is the most abundant northeastern Pacific molluscan species known from whale bone, sunken wood, and seeps. The whale-fall habitat has also been reported from Oligocene deposits (Squires, et al. 1991, Goedert et al. 1995), and widely from Cenozoic fossil deposits (Kiel & Goedert 2006). Kiel & Goedert considered the modern whale fall species community to have arisen in the early Miocene.

Cocculiniform limpets associated with the whale-fall habitat in southern California have previously been described (McLean 1992). It is noteworthy that only two of the vent-limpet families, the Pyropeltidae and the Neolepetopsidae are now known to occur in the hydrothermal vent habitat and the whale-fall habitat. The whale bone oil and the ubiquitous chemosynthetic bacterial mats are not the same, but two species of *Pyropelta* have colonized both habitats, as reported by McLean (1992).

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LITERATURE CITED

- Baco, A. R. & C. R. Smith. 2003. High species richness in deep-sea chemoautotrophic whale skeleton communities. *Mar. Ecol. Prog. Ser.* 260:109–114.
- Beck, L. 1996. Morphology and anatomy of new species of neolepetopsid, acmaeid, fissurellid and pyropeltid limpets from Edison Seamount off Lihir Islands (West Pacific). *Archiv für Molluskenkunde* 125:87–103.
- Bennett, B. A., C. R. Smith, B. Glaser & H. L. Maybaum. 1994. Faunal community structure of a chemoautotrophic assemblage on whale bones in the deep northeast Pacific Ocean. *Mar. Ecol. Prog. Ser.* 108:205–223.
- Bouchet, P. & J-P. Rocroi. 2005. Classification and nomenclator of gastropod families. Malacologia, 47(1–2): 1–397 [Part 1. Nomenclator of Family-Group Names (Bouchet & Rocroi). Part 2. Working Classification of the Gastropoda (modern "archaeogastropods" by Warén & Bouchet)].
- Cruz, R. & M. Farina. 2005. Mineralization of major lateral teeth in the radula of a deep-sea hydrothermal vent limpet (Gastropoda: Neolepetopsidae). *Mar. Biol. (Berlin)* 147:163–168.

- Fretter, V. 1990. The anatomy of some new archaeogastropod limpets (Order Patellogastropoda, Suborder Lepetopsina) from hydrothermal vents. J. Zool. 222:529–526.
- Fujiwara, Y., M. Kawato, T. Yamamoto, T. Yamanaka, W. Sato-Okoshi, C. Noda, S. Tsuchida, T. Komai, S. S. Cubelio, T. Sasaki, K. Jacobsen, K. Kubokawa, K. Fujikura, T. Maruyama, Y. Furushima, K. Okoshi, H. Miyake, M. Miyazaki, Y. Noqi, A. Yatabe & T. Okutani. 2007. Three-year investigations into sperm whale-fall ecosystems in Japan. *Mar. Ecol.* 28:219– 232.
- Goedert, J. L., R. L. Squires & L. B. Barnes. 1995. Paleoecology of whale-fall habitats from deep-water Oligocene rocks, Olympic Peninsula, Washington state. *Palaeogeogr. Palaeoclimatol. Palaeoecol.*, 118:151–158.
- Gustafson, R. G. & R. A. Lutz. 1994. Molluscan life history traits and deep-sea hydrothermal vents and cold methane/sulphide seeps. In: C. M. Young & K. J. Eckelbarger, editors. Reproduction, larval biology, and recruitment of the deep-sea benthos. New York: Columbia University Press. pp. 76–97.

- Hedegaard, C. 1990. Shell structure of the Recent Vetigastropoda. J. Mollus. Stud. 63:369–377.
- Juniper, S. K., V. Tunnicliffe & E. C. Southward. 1992. Hydrothermal vents in turbidite sediments on a northeast Pacific spreading centre: organisms and substratum at an ocean drill site. *Can. J. Zool.* 70:1792–1809.
- Kiel, S. 2004. Shell structures of selected gastropods from hydrothermal vents and seeps. *Malacologia* 46:169–183.
- Kiel, S. & J. L. Goedert. 2006. Deep-sea food bonanzas: early Cenozoic whale-fall communities resemble wood-fall rather than seep communities. Proc. Roy. Soc., Biol. Sci., Ser. B, 273. pp. 2625–2631.
- Lindberg, D. R. 1998. Comments on "Lepetopsina." In P. L. Beesley, G. J. B. Ross & A. Wells, editors. Mollusca: the southern synthesis. Fauna of Australia, Vol. 5. Melbourne: CSIRO Publishing, Part B, i-vii. pp. 565–1234.
- Marshall, B. A. 1987. Osteopeltidae (Mollusca: Gastropoda): a new family of limpets associated with whale bone in the deep-sea. *J. Mollus. Stud.* 53:121–127.
- Marshall, B. A. 1994. Deep-sea gastropods from the New Zealand region associated with Recent whale bones and an Eocene turtle. *Nautilus* 108:1–8.
- McLean, J. H. 1990. Neolepetopsidae, a new docoglossate limpet family from hydrothermal vents and its relevance to patellogastropod evolution. J. Zool. 222:485–528.

- McLean, J. H. 1992. Cocculiniform limpets (Cocculinidae and Pyropeltidae) living on whale bone in the deep sea off California. *J. Mollus. Stud.* 58:401–414.
- Okutani, T., Y. Fujiwara, K. Fujikura, H. Miyage & M. Kawato. 2003. Venus. *Japanese J. of Malac.* 63:61–64.
- Sasaki, T. & A. Warén. 2007. Anatomy of *Eulepetopsis vitrea* McLean, 1990 (Patellogastropoda: Neolepetopsidae). In: K. Jordaens, N. Van Houtte, J. Van Geothem & T. Backeljau, editors. Abstracts, World congress of malacology. Antwerp, Belgium, July 15–20, 2007. pp. 195.
- Smith, C. R. 1992. Whale falls. Chemosynthesis on the deep seafloor. Oceanus 35:74–78.
- Smith, C. R. & A. R. Baco. 1998. Phylogenetic and functional affinities between whale-fall, seep, and vent chemoautotrophic communities. *Cah. Biol. Mar.* 39:345–346.
- Smith, C. R. & A. R. Baco. 2003. Ecology of whale falls at the deep-sea floor. Oceanogr. Mar. Biol. Ann. Rev. 41:311–354.
- Smith, C. R., H. Kulkert, R. A. Wheatcroft, P. A. Jumars & J. W. Deming. 1989. Vent fauna on whale remains. *Nature* 341:27–28.
- Squires, R. L., J. L. Goedert & L. G. Barnes. 1991. Whale carcasses. *Nature* 349:574.
- Warén, A. & P. Bouchet. 2001. Gastropoda and Monoplacophora from hydrothermal vents and seeps; new taxa and records. *Veliger* 44:116–231.