Liralithes, a new genus of Clavalithidae (Neogastropoda) from the Indo-West Pacific, with comments on the late evolution of apertural lirae

Geerat J. Vermeij
Department of Geology, University of California at Davis, One Shields Avenue, Davis, CA 95616; gjvermeij@ucdavis.ed [corresponding author]

J.G.M. Raven
Naturalis Biodiversity Center, Leiden, P.O. Box 9517, 2300 RA Leiden, The Netherlands; han.raven@naturalis.com

Mathias Harzhauser
Natural History Museum Vienna, Burgring 7, 1010 Vienna, Austria; mathias.harzhauser@nhm-wien.ac.at

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In the Clavilithidae Vermeij & M. A. Snyder, 2018, here raised from subfamily to family status in Neogastropoda, we name *Liralithes* gen. nov. (type species: *Fusus tjidamarensis* K. Martin, 1879) from the Early Miocene to Early Pleistocene of the Indo-Malayan region. It differs from other clavilithids by having lirae on the inner side of the outer lip and by having columellar folds. Lirae evolved very late in this family as well as in Muricidae, Fasciolariidae (Fusininae), Melongenidae, and Dolicholatiridae. In Dolicholatiridae, the genus *Latirofusus* Cossmann, 1889 (lirae absent) from the Paleocene and Eocene differs from the post-Eocene *Dolicholatirus* Bellardi, 1884 (lirae present).

Key words: *Liralithes*, *Fusus*, Clavalithidae, Miocene, Pleistocene, Indo-Malayan region

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INTRODUCTION

The Clavilithidae (for revised status see below) comprises a diverse extinct clade of Cenozoic neogastropods usually associated with the family Fasciolariidae. Its genus-level taxonomy has been controversial largely owing to insufficient attention to diagnostic shell characters and confusion about type species (see Grabau, 1904; Wrigley, 1927; Snyder, 1999; Beu & Marshall, 2011). Part of the confusion stemmed from inclusion of the extant genus *Cyrtulus* Hinds, 1845 (type species: *C. serotinus* Hinds, 1845), which is confirmed now to belong to the fasciolariid subfamily Fusininae (Vermeij & Snyder, 2018).

Although it is not our intention to attempt a full genus-level revision of the Clavilithidae, our aim here is to clarify the taxonomic unity of a group of Miocene to Pleistocene species from the Indo-Malayan region that diverge from all other known Clavilithidae. Vermeij & Snyder (2018) already hinted at the unique features of this group but did not formalize their suspicions by taking taxonomic action. Here we erect the new genus *Liralithes* and comment on character evolution in the Clavilithidae, with special reference to apertural characters. We also take this opportunity to comment on the late evolution of apertural lirae in this group and in several other neogastropod families, and recommend reinstatement of the genus *Latirofusus* Cossmann, 1889 in Dolicholatiridae.

SYSTEMATICS

Family Clavilithidae Vermeij & M. A. Snyder, 2018, stat. nov.

Remarks. — The group of genera in the so-called *Clavilithes* group has long been associated with the family Fasciolariidae J.E. Gray, 1853 (or Fusidae Swainson, 1840). Vermeij & Snyder (2018) formalized this group's name as Clavilithinae within Fasciolariidae. Besides a generalized resemblance to the fusiform Fasciolariidae, there is no

character that convincingly links the Clavilithinae more to this family than to other buccinoidean or turbinelloidean neogastropods. Moreover, there is no obvious neogastropod ancestor for the group, which appears as small but otherwise typical species in the Early Paleocene. Accordingly, we elevate the *Clavilithes* group to family status as Clavilithidae.

Genus *Liralithes* gen. nov.

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Type species: *Fusus tjidamarensis* K. Martin, 1879, Miocene, Indonesia.

Diagnosis. — Clavilithidae with axially and spirally smooth last whorl, erect inner lip, lirate inner side of outer lip, and one or two folds near junction between columella and siphonal canal.

Etymology. — lira, Latin, referring to the ridges inside the aperture, and lithos, Greek, stone.

Included species. — *Fusus tjidamarensis* K. Martin, 1879 (Figs 1-2), Late Miocene, Java, Borneo, and Phillipines; *Fusus* (*Clavella*) *tjaringinensis* K. Martin, 1895, Pliocene, Java; *Fusus* (*Clavella*) *verbeeki* K. Martin, 1895 (Figs 3-4), Early Miocene-Early Pleistocene, Southeast Asia.

Remarks. — We propose the new genus *Liralithes* for three extinct species collectively ranging from the Early Miocene to Early Pleistocene of the Indo-Malayan region. The character that immediately distinguishes *Liralithes* gen. nov. from all other clavilithids except one is the presence of lirae (spiral ridges) on the inner side of the outer lip. Most other clavilithids are smooth on the inner side of the outer lip. In having one or two folds near the entrance of the siphonal canal, *Liralithes* gen. nov. resembles the genera *Clavilithes* Swainson, 1840 (= *Rhopalithes* Grabau, 1904) (type species: *Murex noae* Lamarck, 1803, Middle Eocene of France) and *Cosmolithes* Grabau, 1904 (type species: *Fusus uniplicatus* Lamarck, 1803, Middle Eocene, France). As with numerous other mollusk groups, the Clavilithidae originated in the Tethys Ocean with ample representation of fossils in the Paleocene to Miocene of Europe, whereas the family survived longer in the Indo-West Pacific where *Liralithes* gen. nov. is known until the Early Pleistocene.

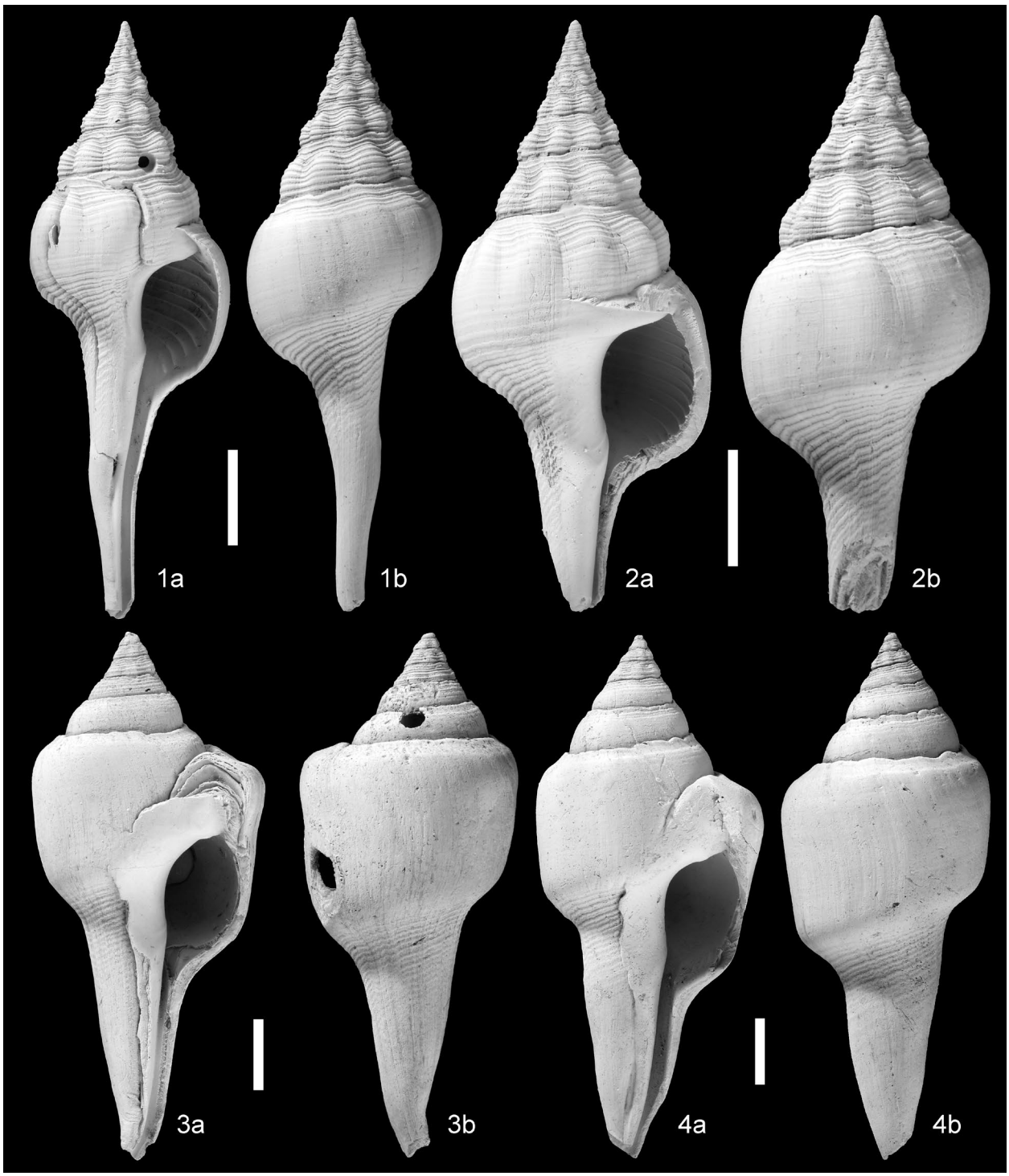
Liralithes gen. nov. also resembles the fusinine fasciolariid genus *Cyrtulus*, whose type (*C. serotinus*) is endemic to the Marquesas Archipelago, but which also contains other species broadly distributed in the Indo-West Pacific (Vermeij & Snyder, 2018). Like *Liralithes* gen. nov. , *Cyrtulus* has a lirate outer lip, but it differs from *Liralithes* gen. nov. by lacking folds near the entrance of the siphonal canal, by having an adherent (instead of an erect) inner lip, by having a conspicuous broad spiral bulge on the siphonal process, and by having the axial side of the siphonal canal separated from the rest of the siphonal process by a very deep, very narrow umbilicus.

We include *Fusus (Clavella) verbeeki* K. Martin, 1895 in *Liralithes* gen. nov. despite the fact that most specimens are smooth on the inner side of the outer lip. Martin (1895) and Vredenburg (1925) stated that their specimens of this species are internally lirate. It is therefore possible that this species is variable with respect to apertural sculpture. *Liralithes tjidamarensis* and *Liralithes verbeeki* are characterized by a change in shape from a fusinid outline with convex periphery in subadult shells to a thick-shelled last whorl with subcylindrical periphery. Lirae are developed during the early stage of growth but may become subobsolete in fully grown specimens (e.g., Martin, 1895; pl. 13, fig. 193 versus Figs 3-4). In both species, the protoconch has about 2.5 whorls with few axial ribs close to the transition into the teleoconch. Syntypes of all *Liralithes* gen. nov. species are illustrated in Leloux & Wesselingh (2009: pl. 108 fig. 10 to pl. 111 fig. 1).

Similar variability (presence or absence of lirae, or discontinuous lirae) occurs among extant populations of the genera *Fulguropsis* Marks, 1951 and *Sinistrofulgur* Hollister, 1958 and the extinct *Pyruella* Petuch, 1982 (Busyconidae) and the extant *Volema* Röding, 1798 (Melongenidae) and *Triplofusus* Olsson & Harbison, 1953 (Fasciolariidae).

We have not included *Clavilithes fennemai* (K. Martin in K. Martin & Icke, 1906) from the Early Miocene to the Pliocene of Java and Borneo in *Liralithes* gen. nov. This species, which as an adult has a massive, broadly expanded and thick inner-lip callus, shares with *Liralithes* gen. nov. the presence of folds near the entrance of the siphonal canal, as well as the smooth last whorl, but the inner side of the outer lip is smooth instead of lirate. It is possible that *C. fennemai* is transitional from a *Clavilithes*-like ancestor to *Liralithes* gen. nov., and that juveniles (which we have not seen) could be lirate. The highly developed callus of adults is certainly more extreme than anything observed in the species we include in *Liralithes* gen. nov., perhaps implying that species in the latter genus are paedomorphic. Likewise, we exclude *C. noetlingi* Vredenburg, 1925, from the Oligocene to Early Miocene of Myanmar and India. We cannot evaluate the generic status of *C. africanicus* Harzhauser, 2009, from the Aquitanian (Early Miocene) of Tanzania, because apertural characters remain obscured by matrix.

We also exclude *Clavilithes klipsteini* (Michelotti, 1847) from the Tortonian (Late Miocene) of Italy. This species, the only post-Early Oligocene clavilithid in Europe, has short lirae on the inner side of the outer lip, but it lacks columellar folds. Ruggieri & Davoli (1984) assigned it to *Rhopalithes* (= *Clavilithes*), but that assignment is inconsistent with the absence of columellar folds in *C. klipsteini*.



Figs 1-2. *Liralithes tjidamarensis* (K. Martin, 1879), NHMW 1902/0005/0068, 'Martin-collection', Java, Miocene. **Figs 3-4.** *Liralithes verbeeki* (K. Martin, 1895), NHMW 1902/0005/0106, 'Martin-collection', Java, Miocene. Scale bars: 10 mm. NHMW = Natural History Museum, Wien.

DISCUSSION

The late evolution of apertural lirae on the inner side of the outer lip characterize numerous marine gastropods, particularly in warm shallow marine gastropods from the Oligocene onward. Although a survey of lirate gastropods is far beyond the scope of this paper, we note here that the Clavilithidae are not alone among gastropod clades in evolving lirae late in their history. In Clavilithidae, which date back to the Early Paleocene (Glibert, 1973; Adegoke,

1977), lirae did not appear until the Early Miocene, some 45 million years later. Similarly, in the Muricidae, a family known since at least the Maastrichtian stage of the Late Cretaceous, the first lirate genus (*Cymia* Mörch, 1860) (Rapaninae) evolved during the Late Eocene, more than 35 million years later, (Vermeij, 2024). Early fusinine fasciolariids, represented by the Eocene genera *Eofusus* Vermeij & Snyder, 2018 and *Lamarckofusus* Vermeij & Lozouet, 2012, evolved a lirate outer lip only after the Eocene. In the Strombidae, lirae are known in several Neogene to present-day genera but in no Paleogene taxa. Eocene genera assigned to Melongenidae have a smooth surface on the inner side of the outer lip; the consistently lirate genus *Pugilina* Schumacher, 1817 and some species of *Volema* Röding, 1798 can be traced back to the Early Oligocene (see Vermeij & Raven, 2009). In the cerithioidean family Modulidae, the earliest genus (*Incisilabrum* Cossmann, 1918), ranging from the Early to Late Eocene of France, has a smooth inner side of the outer lip. Lirae characterize all subsequent modulids, beginning with the genus *Trochomodulus* Landau, Vermeij & Reich, 2014 in the Early Oligocene (see Landau et al., 2014; Lozouet et al., 2020).

The family Dolicholatiridae (see Kantor et al., 2022) is an enigmatic buccinoidean group with columellar folds. All Oligocene and later members have a lirate outer lip, as in *Dolicholatirus* Bellardi, 1884, *Crassicantharus* Ponder, 1972, *Dulaiania* Harzhauser, Landau & Vermeij, 2024, and *Teralatirus* Coomans, 1965. This condition, which appeared first in the Early Oligocene *Dolicholatirus gaasensis* (Vergneau, 1963) in France, contrasts with all Paleocene and Eocene species, for which Cossmann (1889) erected the genus *Latirofusus* (Type species: *Fusus funiculosus* Lamarck, 1803, Middle Eocene of France). Although most authors considered *Latirofusus* to be a subjective junior synonym of *Dolicholatirus* (see e.g. Vokes, 1977), the consistent absence of lirae in the former taxon leads us to recommend that the Paleocene and Eocene species should be assigned to *Latirofusus*, and that *Dolicholatirus*, with its lirate outer lip, is distinct from *Latirofusus*.

The function of apertural lirae remains entirely unstudied. Apertural lirae are secondarily produced features and are not simply expressions of external spiral sculpture, suggesting that they do have a function. Lirae extending deep into the aperture might facilitate extension and retraction or the soft parts. This possibility is consistent with the glossy-smooth nature of most lirae, including those of *Liralithes* gen. nov., but beaded or discontinuous lirae are known in many fasciolarids. Work in progress by one of us (GJV) will elucidate the taxonomic, geographical, and temporal distribution of lirate gastropods and compare lirae with columellar folds.

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