



Middle Miocene Modulidae (Gastropoda: Cerithioidea) from Indonesia, Java, Yogyakarta, near Wonosari

Bernard M. Landau

Naturalis Biodiversity Center, P.O. Box 9517, 2300 RA Leiden, The Netherlands; Instituto Dom Luiz, Faculdade de Ciências, Universidade de Lisboa, Campo Grande, 1749-016 Lisbon, Portugal; International Health Centres, Av. Infante de Henrique 7, Areias São João, P-8200 Albufeira, Portugal

bernardmlandau@gmail.com,

ORCID: <https://orcid.org/0000-0002-7768-8494>

[corresponding author]

Anton E. Breitenberger

Florastraße 8, 2540 Bad Vöslau, Austria

breitenberger@gmail.com



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ABSTRACT

Two species of the genus *Conomodulus* Landau, Vermeij & Reich, 2014 are described as new from the Middle Miocene Langhian beds from Wonosari (Indonesia, Java, Yogyakarta). Recent advances in modulid taxonomy based solely on shell characters are highlighted, both at generic level and at species level, with almost 40% of known modulid species described since the year 2000. We await molecular data to test the present generic/species concepts within the family.

Key words – Cerithioidea, Modulidae, Miocene, Indonesia, new species



INTRODUCTION

In this paper we continue the work of Dekkers et al. (2020), Merle et al. (2020), Landau et al. (2020a, 2020b, 2024) on the gastropod assemblage occurring at a locality close to the village of Wonosari, Gunung Kidul Regency, Special Region of Yogyakarta, Java, Indonesia and revisit Indonesian Miocene Modulidae, describing two new species. As discussed by Dekkers et al. (2020: 2), although the exact locality is unknown, the deposit is dated accurately to the Middle Miocene Langhian.

Until recently almost all Modulidae were placed in a single genus, *Modulus* J. E. Gray, 1842. Based on shell characters, Landau et al. (2014) proposed a supraspecific classification for the family. For the Indo-Pacific, the genus *Indomodulus* Landau, Vermeij & Reich, 2014 first appears in the early Miocene of Indonesia, after which there is no fossil record until the Pleistocene, and is today represented by a single, widely distributed Indo-Pacific species, *Indomodulus tectum* (Gmelin, 1791). Additionally, the genus *Conomodulus* Landau, Vermeij & Reich, 2014 occurs, thought to be restricted to the Miocene of Indonesia, but recently reported as still living in New Caledonia (Lozouet & Krygelmans, 2016).

In this paper we describe the modulids from the Middle Miocene Langhian locality of Wonosari and introduce two new species.

Abbreviations:

- H – height of the shell (shell length)
W – width of the shell at the broadest point
NHMW – Natural History Museum, Wien, Austria

TAXONOMY

Subclass Caenogastropoda Cox, 1960
Superfamily Cerithioidea Fleming, 1822
Family Modulidae P. Fischer, 1884
Genus *Conomodulus* Landau, Vermeij & Reich, 2014

Type species: *Modulus preangerensis* Martin, 1905, by original designation, Miocene, Indonesia. Gender masculine.

Conomodulus altispira sp. nov.

(Plate 1 Figs 1-2)

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Type species: *Strombus leurus* Woodring, 1928.

Holotype. – Indonesia, Wosonari, deposited NHMW 2024/0043/0009, H 18.7 mm, W 10.8 mm (Pl. 1 fig. 1).



Paratypes. – All from the type locality. Paratype 1 NHMW 2024/0043/0010, H 20.2 mm, width 11.9 mm (Pl. 1 fig. 2); paratype 2 NHMW 2024/0043/0011, H 18.6 mm, W 11.7 mm; paratype 3 NHMW 2024/0043/0012, subadult H 14.9 mm, W 8.9 mm; paratype 4 NHMW 2024/0043/0013, subadult H 13.8 mm, W 8.7 mm.

Other material. – NHMW 2024/0043/0014 (21).

Type locality. – Indonesia, Java, Special Region of Yogyakarta, Gunung Kidul Regency, Wonosari.

Type stratum. – Middle Miocene, Langhian portion of NN5.

Distribution. – Middle Miocene: central Java, Yogyakarta (this paper).

Description. – Shell large for genus, biconic; spire relatively tall, regularly conical; apical angle about $57-67^\circ$. Protoconch abraded in all specimens. Teleoconch of up to seven whorls. First 4-5 teleoconch whorls convex, bearing six primary spiral cords, abapical cord slightly stronger forming periphery just above suture; single narrow secondary cord intercalated in primary interspaces from fourth whorl. Suture linear, deeply impressed, narrowly canaliculate. On fifth whorl poorly defined axial folds appear, strengthening abapically to form about ten broad, low, opisthocline axial ribs on penultimate whorl, overrun by weakening spirals; spirals fade again before last whorl. Last whorl about 66-68% of total height, biconic, sharply angled at basal keel forming periphery; above keel very weakly convex, surface smooth in fully adult specimens; keel strengthened by cord in some specimens; below about ten very fine spiral cords to stronger mid-basal cord, 4-5 further cords from mid-basal cord to umbilicus of irregular strength; basal cords corrugated by weak axial collabral growth lines in some specimens. umbilicus very narrow, reduced to narrow chink in some specimens. Aperture ovate, outer lip sharp, prosocline in lateral view, weakly angled at peribasal cord, extremely finely and deeply liriate within; anal canal not developed; siphonal canal represented by broad, deep, rounded groove in columellar callus placed below columellar tooth. Columella moderately excavated in mid-portion, with strong, sharp, abapical columellar tooth. Columellar callus very narrow, erect, forming medial border of umbilicus, thin and adherent, poorly delimited in parietal area.



Plate 1. *Conomodulus* species. Figs 1-2. *C. altispira* sp. nov. Fig. 1. Holotype NHMW 2024/0043/0009, height 18.7 mm, width 10.8 mm. Fig. 2. Paratype 1 NHMW 2024/0043/0010, height 20.2 mm, width 11.9 mm. Figs 3-4. *C. forticostatus* sp. nov. Fig. 3. Holotype NHMW 2024/0043/0015, height 23.1 mm, width 13.6 mm. Fig. 4. Paratype 1 NHMW 2024/0043/0016, height 20.3 mm, width 13.4 mm. Figs 5-6. *C. preangerensis* (K. Martin, 1905). Fig. 5. NHMW 2024/0043/0018, height 11.7 mm, width, 10.9 mm. Fig. 6. NHMW 2024/0043/0019, height 11.8 mm, width 10.0 mm. All specimens from Indonesia, Java, Special Region of Yogyakarta, Gunung Kidul Regency, Wonosari, Middle Miocene, Langhian.

Etymology. – Name reflecting the unusually tall spire for the genus.

Comparison. – This new species is most like its older congener *Conomodulus renemai* Landau, Vermeij & Reich, 2014 from the Lower Miocene Burdigalian of Java, but differs in its larger maximum size (maximum height 20.2 mm vs. 6.8 mm), with more numerous spire whorls of which fewer (usually only one or two) have axial sculpture, and in its taller last whorl, which is smooth above the basal angulation, whereas the last whorl in *C. renemai* bears strong axial and spiral sculpture.



Conomodulus preangerensis (Martin, 1905) from the Middle and Upper Miocene of Indonesia is less closely similar to the new species, with a much lower spire and ovate last whorl only weakly angled mid-whorl, axial sculpture is weak throughout and close-set spiral cords persist onto the last whorl.

Discussion. – *Conomodulus altispira* sp. nov. is somewhat variable in adult sculpture but changes importantly with ontogeny. Subadult shells are similar in profile to *C. renemai* but can be distinguished by having axial ribs only on the last whorl (penultimate whorl of fully adult specimens). As the shell grows, axials and spirals fade, so that the last whorl is smooth above the basal keel, or almost so, and the last whorl becomes relatively tall biconic. In all fully adult specimens, axials have disappeared on the last whorl; a few weak spiral cords may persist in some, but in most the surface is smooth. The basal keel can be sharp or strengthened by a narrow peribasal cord. Basal sculpture is relatively constant; a stronger mid-basal cord, very fine cords between the peri- and mid-basal cords, a few stronger cords of irregular strength between mid-basal cord and umbilicus. The umbilicus is narrow in all specimens, in some reduced to a narrow groove. Apertural characters are constant; the lirae are very fine in all specimens.

Generic placement is based on its turbiniform biconic shape, tall spire, sculpture of axial folds that become subobsolete, and the presence of a marked groove delimiting the siphonal depression, characteristic of the genus *Conomodulus* Landau, Vermeij & Reich, 2014.

Conomodulus neocaledonensis Lozouet & Krygelmans, 2016, recently described from the extant faunas of New Caledonia, Ouen Island, is most like *C. renemai* in size, profile and sculpture, but differs in lacking the broad groove delimiting the siphonal depression characteristic of the genus. Nevertheless, we agree with Lozouet & Krygelmans (2016) in this generic placement being the least problematic. One further difference is that the extant species from New Caledonia seems to lack lirae within the outer lip. However, the presence/absence of lirae is of dubious generic and even species specific value in many gastropod groups. Petuch & Berschauer (2023) placed two extant species from the western Atlantic Florida Keys in *Conomodulus*; *Modulus lindae* Petuch, 1987 ([holotype](#) USNM 859825) and *Conomodulus lambi* Petuch & Berschauer, 2023 (2023, pl. 1 figs A-C). Both of these lack the groove delimiting the siphonal depression and, in our opinion, are more likely to represent somewhat derived *Modulus* species.

***Conomodulus forticostatus* sp. nov.**

(Plate 1 Figs 3-4)

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Holotype. – Indonesia, Wosonari, deposited NHMW 2024/0043/0015, height 23.1 mm, width 13.6 mm (Pl. 1 fig. 3).



Paratypes. – All from the type locality. Paratype 1 NHMW 2024/0043/0016, height 20.3 mm, width 13.4 mm (Pl. 1 fig. 4); paratype 2 NHMW 2024/0043/0017, height 15.7 mm, width 11.2 mm.

Other material. – Known from the type series only.

Type locality. – Indonesia, Java, Special Region of Yogyakarta, Gunung Kidul Regency, Wonosari.

Type stratum. – Middle Miocene, Langhian portion of NN5.

Distribution. – Middle Miocene: central Java, Yogyakarta (this paper).

Description. – Shell large for genus, biconic; spire relatively tall, coeloconoid in profile; apical angle initially 56-57°, later 63°. Protoconch abraded in all specimens. Teleoconch of up to seven angular whorls. First four teleoconch whorls convex, bearing five primary spiral cords, abapical cord forming periphery just above suture, with very fine secondary and tertiary spirals intercalated in primary interspaces from third whorl, interrupted or crossed by fine irregular collabral axial growth lines. Suture linear, narrowly impressed. On fourth whorl, abapical two cords equal in strength, forming periphery. On second half of fourth whorl axial ribs appear, strengthening rapidly abapically. Last three whorls with broad, flattened subsutural ramp, roundly angled at shoulder placed at about one-third whorl height, tapering rapidly below to suture. Axials weakly opisthocline, ten on penultimate whorl, narrow at adapical suture, widening towards shoulder, most prominent and swollen at periphery without tubercles. Last whorl 67-69% of total height, biconic, roundly angled at periphery; axial ribs tubercular at periphery, stopping abruptly just below periphery; base delimited by two stronger peribasal cords, equal strength mid-basal cord, cords of alternating strength between mid-basal cord and umbilicus. Finer spiral threads of secondary strength intercalated between peribasal cords and mid-basal cord; collabral axial growth lines weak; umbilicus narrow, widening with ontogeny. Aperture ovate, outer lip sharp, prosocline in lateral view, weakly angled at periphery, extremely finely and deeply lirate within; anal canal not developed; siphonal canal represented by broad, deep, rounded groove in columellar callus placed below columellar tooth. Columella weakly excavated in mid-portion, with strong, sharp, abapical columellar tooth. Columellar callus very narrow, strongly thickened in fully adult specimens, erect, forming medial border of umbilicus, continuing thickened and detached in parietal area.

Etymology. – Name reflecting the strong axial sculpture for the genus.

Comparison. – In sculpture the new species is most like *Conomodulus renemai* Landau, Vermeij & Reich, 2014, but is much larger (maximum height 23.1 mm vs. 6.8 mm), its last three whorls are roundly but strongly angled at the shoulder, and the axial ribs form tubercles at the shoulder of the last whorl. *Conomodulus altispira* sp. nov., with which it co-occurs, has a regularly conical spire and is immediately separated by the lack of sculpture on the last whorl, being smooth above the basal angulation.



Discussion. – *Conomodulus forticostatus* sp. nov. shows little intraspecific variability, mainly reflected in the changes that occur with ontogeny. As the shell grows, the columellar lip thickens and becomes sharply delimited from the base, detached in the parietal area and erect in the umbilical area.

This species is very characteristic, with its strongly biconic profile, coeloconoid spire, and strongly shouldered last three whorls with the axial ribs forming tubercles at the periphery. The generic description “Sculpture of axial folds not forming tubercles at shoulder,...” (Landau et al., 2014: 17) must be revised with the addition of this new species to the genus. Notwithstanding, the other shell characters agree well with this generic placement.

Conomodulus preangerensis (K. Martin, 1905)
(Plate 1 Figs 5-6)

Modulus preangerensis Martin, 1905: 221, pl. 46 fig. 671; Martin, 1928: 127.

Modulus preangerensis Martin – Van der Vlerk, 1931: 252; Ladd, 1972: 24, pl. 5 figs 19-21.

Modulus spec. nov. – Beets, 1941: 37.

Modulus preangerensis Martin, 1905 – Dharma, 2005: 306, pl. 118 fig. 15; Leloux & Wesselingh, 2009: 142, pl. 275 figs 14-15.

Conomodulus preangerensis (Martin, 1905) – Landau et al., 2014: 18, pl. 1 figs 99-108.

Material seen. – Indonesia, Wosonari. Maximum H 11.7 mm, W 10.1 mm. NHMW 2024/0043/0018-0019 (2), NHMW 2024/0043/0020 (16).

Distribution. – Middle Miocene: Kalimantan (Beets, 1941), central Java, Yogyakarta (this paper); late Middle Miocene: Java (Martin, 1905). Upper Miocene: Palau (Ladd, 1972), Kalimantan (new data, Throughflow Project).

Discussion. – As discussed by Landau et al. (2014: 17), this species is rather variable in profile and sculpture. The specimens from Wonosari are similar in size to specimens from other localities but have a more rounded last whorl, weaker spiral sculpture, and weaker lirae within the outer lip than the holotype (Landau et al., 2014: figs 99-100). Similar weakly sculptured specimens with rounded rather than angular last whorls were also reported from the Middle Miocene, lower Menkrawit beds, East Kalimantan (Landau et al., 2014: figs 103-104). We consider these forms to represent a single, rather variable, species.

CONCLUSIONS

Historically, modiolid taxonomy has been rather conservative, almost all species placed in the single genus *Modulus* J. E. Gray, 1842. Following the familial generic revision of Landau et al. (2014) based solely on shell characters, there has been renewed interest in the family with the description of both further fossil and extant taxa. WoRMS (consulted 08-02-2024) lists 49 modiolid species as being valid, of which 19 (39%) have been described since the year 2000 (excluding the two species described as new herein).



This has led to further insights in modolid palaeobiogeography. For example, the genus *Trochomodulus* Landau, Vermeij & Reich, 2014, when erected, was considered a Tropical American genus with a geological history ranging back to the early Miocene in the Caribbean (Landau et al., 2014: 7). Lozouet et al. (2020) showed it to have an eastern Atlantic origin, with one species present in the Lower Oligocene Rupelian and one in the Upper Oligocene Chattian of France.

Two genera were considered exclusively Indo-West Pacific by Landau et al. (2014): *Conomodulus* and *Indomodulus* Landau, Vermeij & Reich, 2014. In the Wonosari assemblage only *Conomodulus* is so far known. However, the two species described herein show the genus to be more diverse than previously thought (3 IWP species listed in WoRMS), and as these Pacific fossil assemblages become better known, this diversity is likely to increase. We are not aware of any molecular studies on this family to date to test these taxonomic hypotheses.

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