Caenogastropoda and Stylommatophora (Gastropoda) from the mid-Miocene Zhangpu amber of East Asia

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Received 12 May 2022; received in revised form 12 July 2022; accepted 26 July 2022

Abstract

Four gastropod species including two new species (?Tinnyea sp., Cyclophoridae gen. et sp. indet., Metalycaeus fossilis n. sp., and Tortaxis zhangpuensis n. sp.) are described from the mid-Miocene Zhangpu amber. Among them, ?Tinnyea sp. is potentially the first fossil record of this group in lake systems of East Asia, outside of Mediterranean and Paratethys areas. Tortaxis zhangpuensis n. sp. and Metalycaeus fossilis n. sp. are likely the oldest representatives of respective genera. Despite Tortaxis zhangpuensis n. sp. being a juvenile shell, its whorls are taller and more convex in comparison to congeners, and from around 3.75th whorl onwards the sub-sutural area of whorls displays a crenulated pattern. Metalycaeus fossilis n. sp. has a spirally striated protoconch (the key diagnostic character of the genus), and with strong, widely spaced R1 ribs, short R2, which distinguishes it from its congeners.

Keywords: fossil Gastropoda; Metalycaeus fossilis n. sp.; Cyclophoroidea; Tortaxis zhangpuensis n. sp.

1. Introduction

The Miocene Zhangpu biota (~14.7 Ma) is hailed as one of the top four amber biotas worldwide and is the richest Cenozoic megathermal seasonal rainforest paleobiota. The preservation of inclusions is usually excellent, with specimens displaying colors and three-dimensional (3D) details. The inclusions mainly include arthropods and abundant plants, fungi, snails, and even feathers (Wang et al., 2021). Among the recognizable fossils, the most diverse and abundant plant fossils are those of the Dipterocarpaceae, Fabaceae, Lauraceae, and Clusiaceae; arthropod inclusions cover an impressive array of more than 250 families of all major terrestrial groups (Shi et al., 2014a, 2014b; Wang et al., 2021). The Zhangpu amber biota offers a unique window through which the tropical ecosystem of an Asian rainforest during the Mid-Miocene Climatic Optimum (MMCO) can be looked at.

Herein we present four new records of gastropod species from the Zhangpu amber, including ?Tinnyea sp., Cyclophoridae gen. et sp. indet., and two new species: Metalycaeus fossilis n. sp. and Tortaxis zhangpuensis n. sp. Those taxa belong to the freshwater Pachychilidae (Caenogastropoda) and the terrestrial Achatinidae (Stylommatophora), Cyclophoridae, and Alycaeidae (Caenogastropoda). These unique fossils not only increase the distribution record of these gastropod genera in Miocene deposits, but also provide insights into the evolution of ancient gastropod fauna and the palaeoecology of Miocene amber forests.

https://doi.org/10.1016/j.palwor.2022.07.004
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Please cite this article as: T.T. Yu, B. Páll-Gergely and R.B. Salvador, Caenogastropoda and Stylommatophora (Gastropoda) from the mid-Miocene Zhangpu amber of East Asia, Palaeoworld, https://doi.org/10.1016/j.palwor.2022.07.004
2. Geological setting

The Miocene Zhangpu amber was collected from the Fotan Group at Qianting Town (24°16′03″N, 117°59′01″E), Zhangpu County, Fujian Province, southeastern China. The Fotan Group hosts abundant amber and plant fossils and occurs widely throughout eastern and western Fujian. It consists primarily of three basaltic layers and three sedimentary layers. The sedimentary layers are composed of arenaceous conglomerates, sandstones, sandy mudstones, mudstones, lignite and diatomite, with interbedded three layers of basaltic rocks derived from several episodes of volcanic activity during the Neogene (Zheng and Wang, 1994). Both plant compression/impres- sion fossils and amber are preserved in two mudstone units, (i.e., the length of R2 usually corresponds with the length of the sutural tube, see Pál-Gergely et al., 2016); and Region 3 (R3), ranging from the constriction up to the peristome.

4. Systematic palaeontology

Class Gastropoda Cuvier, 1795
Subclass Caenogastropoda Cox, 1960
Superfamily Cerithioidea Fleming, 1822
Family Pachychilidae Fischer and Crosse, 1892

Genus Tinnyea Hantken, 1887

Type species: Tinnyea vasarhelyii Hantken, 1887, by monotypy.

Material analyzed: NIGP180008.

Description: Sinistral adult, incomplete, with embryonic whorls and aperture missing. The residual middle whorls indicate a probable turreted shape, consisting of three teleoconch whorls; last whorl slightly allometric and broader. Strong opisthocline and slightly curved axial ribs are present on first whorls, forming small spines where they interlace with spiral cords. The last two whorls are characterized by marked spiral cords, numbering 10–12; more widely spaced spiral cords appear on the abapical-to-umbilical region, which obliquely intersects with the spiral cords on body whorl.

Measurements (in mm): NIGP180008: H = 10.54, D = 5.91. The Miocene Zhangpu amber is most similar to Tinnyea lauraea (Matheron, 1842), known from the Oligocene to the
Fig. 1. (A–D) ?Tinnyea sp., NIGP180008; (A) optical microscope photograph; (B–D) micro-CT reconstruction. (E–H) Tortaxis zhangpuensis n. sp., NIGP180009, holotype; (E) optical microscope photograph; (F–H) micro-CT reconstruction, apertural, dorsal, and apical views respectively. (I–L) Cyclophoridae gen. et sp. indet., NIGP180010; (I) optical microscope photograph, apertural view; (J–L) micro-CT reconstruction, apertural, dorsal, and umbilical views respectively; the arrow to indicate the protoconch/teleoconch boundary. Scale bar = 1 mm.
Pliocene of Central Europe (and particularly abundant during the Miocene; Kadolsky, 1995; Harzhauser et al., 2001) due to the turreted shell and characteristic teleoconch sculpture (very strong opisthoclone and slightly curved axial ribs on first whorls and both axial ribs and spiral cords on remaining whorls). However, ?Tinyea sp. has more marked spiral cords, numbering 10–12 on the last two whorls preserved on the specimen.

Superfamily Cyclophoroidea Gray, 1847
Family Cyclophoridae

Material analyzed: NIGP180010 (juvenile).

Description: Shell minute, juvenile, lowly turbinate in shape, consisting of 2–3 convex whorls. Spire low conical, apex blunt, protoconch consisting of about 1.5 smooth whorls; onset of teleoconch indicated by formation of dense growth lines that gradually become stronger. Body whorl inflated and convex, occupying nearly 2/3 of shell height. Suture distinct and deeply impressed. Umbilicus narrow and deep. Aperture large, circular; outer lip thin and fragile. Shell surface with fine growth lines and thick growth ribs near the aperture region, with spiral cordlets on the periphery of the whorls; surface of body whorl covered with densely spaced, thin periostracal hairs that emerge on growth line margins.

Measurements (in mm): NIGP180010: H = 1.10, D = 1.20, h = 0.69, d = 0.58.

Remarks: Hairy land snails have been reported from mid-Cretaceous Burmese amber, being *Hirsuticyclus* the first one reported (Hirano et al., 2019; Neubauer et al., 2019; Yu, 2021). The distinctive morphology of *Hirsuticyclus*, with large periostracal hairs along growth lines, trochoid shell shape, and spiral striation is typical for some species of tropical-forest land snails in the family Cyclophoridae. The present specimen from mid-Miocene Zhangpu amber is a juvenile snail and cannot be confidently assigned to a genus. Therefore, it is classified here provisionally as Cyclophoridae gen. et sp. indet. The lowly gyroscopic shell with a large circular aperture, as well as the surface of body whorl covered with thin periostracal hairs, differ from *Hirsuticyclus electrum* Neubauer, Xing and Jochum, 2019 with its trochoid shell ornamented with distinctly longer periostracal hairs. Cyclophoridae gen. et sp. indet. also differs from *Hirsuticyclus canaliculatus* Yu, 2021, which shows a low turbinate to nearly discoidal shell with deeply incised spiral keels and a broadly elliptical aperture interrupted by two canals. Cyclophoridae gen. et sp. indet. has a similar trochiform and globose shell with thin periostracal hairs to *Lagocheilus cretaspira* Asato and Hirano in Hirano et al., 2019, but differs in having blunt apex and convex whorls.

Family Alycaeidae Blanford, 1864

Genus *Metalycaeus* Pilsbry, 1900

Type species: *Alycaeus* (*Metalycaeus*) *melanopoma* Pilsbry, 1900 (synonym of *Chamalycaeus nipponensis* Reinhardt, 1877, see Minato, 1988), by subsequent designation (Thiele, 1929).

*Metalycaeus* fossilis* n. sp.
(Fig. 2)


Etymology: From Latin, meaning “dug up” and indicating the fossil nature of this species.

Type material: NIGP180011, holotype.

Type locality and stratum: Qianting Town, Zhangpu County, Fujian Province, China (24°16′03″N, 117°59′01″E); Fotan Group, Zhangpu amber (Miocene).

Diagnosis: A *Metalycaeus* species with strong, widely spaced R1 ribs (ca. 18 on the last half whorl of R1), short R2, and a combined length of R2+R3 slightly exceeding a quarter whorl.

Description: Shell outline oval from dorsal view; spire elevated, body whorl rounded; protoconch elevated, consisting of ca. 1.5 whors, spiral striation visible on its last whorl and on its ventral surface (inside umbilicus); last half whorl of R1 with regular, strong, widely-spaced ribs, sculpture of preceding ribs not clearly visible; spiral striation clearly visible on R1; transition between R1 and R2 clearly visible due to change in rib density; R2 and R3 slightly more than a quarter whorl length combined, R3 more than 2 times longer than R2; ribbing on R2 about 3 times as dense as in R1; R2 ribs rather blunt; transition between R2 and R3 sudden, indicated with a slight constriction; R3 with some rather strong ribs reminiscent in shape and density of those on R1; aperture shape not clearly visible; peristome not fringed; outer peristome strongly expanded; umbilicus less than one third of shell width.

Measurements (in mm): NIGP180011: H = 2.24, D = 3.02, h = 1.33, d = 1.49.

Remarks: *Metalycaeus fossilis* n. sp. has a spirally striated protoconch as the key diagnostic character of the genus (Päll-Gergely et al., 2017, 2020). Among the *Metalycaeus* species inhabiting mainland China and Taiwan (Hsieh et al., 2006, Päll-Gergely et al., 2017), only *M. latecostatus* (Möllendorff, 1882) possesses similarly strong, widely-spaced ribs, although its body whorl is slightly angled, and has denser R1 ribs (ca. 25 ribs/last half whorl of R1 versus ca. 18 in the new species). *Metalycaeus fossilis* n. sp. also differs from *Alycaeus sonlaensis* Raheem and Schneider in Raheem et al., 2018 from the earliest Miocene (Aquitanian, 23–21 Ma) of Northern Vietnam, which has a fringed aperture and a denser R1 ribbing and has no signs of spiral striae (Raheem et al., 2018).
Fig. 2. *Metalycaeus* fossilis n. sp., NIGP180011, holotype. (A, B) Optical microscope photograph. (C–F) micro-CT reconstruction; (C, F) dorsal view; (D) apical view; (E) apertural view. Scale bar = 0.5 mm.
Subclass Heterobranchia Burmeister, 1837
Order Stylommatophora Schmidt, 1855
Superfamily Achatinoidea Swainson, 1840
Family Achatinidae Swainson, 1840

Genus Tortaxis Pilsbry, 1906
Type species: Achatina erecta Benson, 1842, by original designation.

*Tortaxis zhangpuensis* n. sp. (Fig. 1E–H)

ZooBank reg. nr.: urn:lsid:zoobank.org:act:97ECBD3A-066-4195-AC01-22AD0A5E1FC

**Etymology:** Alluding to the locality, Zhangpu, which also gives name to the fossil amber biota as a whole.

**Type material:** NIGP180009, holotype (juvenile).

**Type locality and stratum:** Qianting Town, Zhangpu County, Fujian Province, China (24°16′03″N, 117°59′01″E); Fotan Group, Zhangpu amber (Miocene).

**Diagnosis:** Whorls taller and more convex in comparison to congeners. More slender and delicate-looking spire. From around 3.75th whorl onwards, the sub-sutural area of whorls displays a crenulated pattern.

**Description:** The specimen is a juvenile (~5.5 whorls). Shell dextral, cylindrical, thin, with a high turreted spire. Protoconch rounded, smooth; ca. apparently of 1.5 whorls, but transition to teleoconch is unclear (seemingly marked by a slight reduction in shell height and width). Shell surface smooth, except for sparse growth lines and, from around the 3.75th whorl onwards, by a crenulated pattern on sub-sutural area of whorls. Whorl profile lightly convex, with somewhat bulging appearance. Spire apex obtuse (slightly angled in relation to columellar axis), rounded, weakly bulbous. Suture deeply impressed. Aperture small, ovate, apically elongated. Peristome simple. Umbilicus closed.

**Measurements (in mm):** NIGP180009: H = 5.22, D = 1.96, h = 1.57, d = 1.18.

**Remarks:** The present juvenile turreted shell with rounded apex, angled spire, and weakly convex whorls can be assigned to the genus *Tortaxis* (Zilch, 1959; Schileyko, 1999). The angled spire (or obtuse apex) is the key diagnostic feature for generic allocation (*Zilch, 1959; Schileyko, 1999*). As a juvenile specimen, the light columellar fold that can be observed in adults is not yet developed. Despite being a juvenile shell, its morphological features, supported by the temporal isolation, allows the allocation and description of a new species. The only other fossil known is an unconfirmed and unfigured *Tortaxis* sp. from the early Miocene of Vietnam cited by Böhme et al., 2011.

*Tortaxis zhangpuensis* n. sp. has a more slender and delicate-looking shell in comparison to *T. erectus, T. mandarinus* (Pfeiffer, 1856) and *T. matudai* Kuroda, 1941 (the latter endemic to Taiwan). *T. mandarinus* also has a strongly-marked axial sculpture on the teleoconch. The spire and whorl profiles of *T. zhangpuensis* n. sp. are more akin to those of *T. mirus* (Gredler, 1884) from southeastern China.

5. Discussion

The Alycaeidae are members of the operculate land snail superfamily Cyclophoroidea. The 7 genera and nearly 400 species of the Alycaeidae inhabit Asia from western India eastward through the Himalaya to Japan in the east, Korea in the north and Indonesia in the south (Benthem Jutting, 1948, 1959; Minato, 1988; Päll-Gergely et al., 2020, 2021). In contrast to their present diversity and wide geographical distribution in the region, the fossil record of this family is relatively sparse, with only one known species, *Alycaeus sonlaensis* from the earliest Miocene of Vietnam (Raheem et al., 2018). In China, the extant Alycaeidae *Metalycaeus* spp. are distributed in Guangxi, Hunan, Yunnan, Anhui, Hubei, Sichuan and Chongqing in southeastern and southwestern China (Päll-Gergely et al., 2017). *Metalycaeus fosilis* n. sp., found in Fujian Province, is within the known present distribution of the genus in southeastern China. Furthermore, *M. fossilis* n. sp. is the earliest representative of this genus.

*Tortaxis* contains thirteen extant species, distributed in Asia along subtropical and tropical areas from China to Laos and Vietnam (Schileyko, 1999), including one species (*T. xiazyayensis*) that lives at altitudes of 1800–2700 m in southern Tibet (Chen and Zhang, 2001). Extant representatives of *Tortaxis* usually inhabit wet environments under fallen leaves or rocks, or in rock crevices (Chen and Zhang, 2001). *Tortaxis zhangpuensis* n. sp. from mid-Miocene Zhangpu amber is potentially the oldest representative of this genus, given that the only other record remains unconfirmed (*?Tortaxis* sp. from the early Miocene of Vietnam; Böhme et al., 2011).

The thiariid *Timmyea* is an extinct freshwater genus, common in the Oligocene-Neogene lake systems of Mediterranean and Paratethys areas (Harzhauser and Mandic, 2008), being the species *T. lauraea* (*T. escheri* in older literature) particularly widespread in central Europe (e.g., Harzhauser et al., 2001, 2011; Salvador and Rasser, 2016). The ubiquitous *Timmyea* seems to have been a strictly freshwater-bound form, with a preference for swift fluvial environments (Harzhauser et al., 2002). The present report of *?Timmyea* sp. from mid-Miocene Zhangpu amber would be the first record of the genus in lake systems of East Asia, outside of Mediterranean and Paratethys areas, if the generic allocation is proven to be correct by future fossil finds.

Preserved periostraca have been reported in several fossil representatives of cyclophorids from mid-Cretaceous Kachin amber. Two *Hirsuticyclus* spp., in particular, display a similarly low turbinate to nearly discoidal shell
shape and a sculpture consisting of spiral striation observed in the present Cyclophoroidea indet. from Zhangpu amber. *Hirsuticyclus electrum* shows dense, regularly-spaced periostral hairs on the apical area and whorl flank and in having a cancellate sculpture pattern, whereas *H. canaliculatus* lacks periostral hairs around the periphery, and is sculptured with only incised spiral keels. A further cyclophoroid, *Lagocheilus cretaspira* shows a small, thin, trochiform and globose shell characterized by convex shell whorls with an angulation on its lower portion, ornamented by fine and prominent plica-like collabral lirae and furnished with several periostral hairs (Hirano et al., 2019; Neubauer et al., 2019; Yu, 2021).

The Zhangpu amber is the second amber biota where cyclophoroids with thin periostral hairs have been found. Hairs and periostral flanges have been observed in land snails inhabiting humid forest and meadows and are suggested to increase adhesion to wet surfaces during foraging (Pfenninger et al., 2005). However, a later study showed that hairs are not unambiguously beneficial in humid environment as a hairy snail has to carry much more weight when being wet compared to snails with hairless shells (Shvydka et al., 2020). Furthermore, hairy shell has been also developed in arid environments (Cuezzo et al., 2018). Even if during the middle Miocene, the Zhangpu amber biota was located in megathermal seasonal rainforests that reach at least 24.2°N (modern-day latitude), north of the Tropic of Cancer (23.5°N) (Wang et al., 2021), the hairs of Zhangpu amber snails cannot be directly explained as an adaptation for humid environment.

**Acknowledgements**

We are very grateful to two anonymous reviewer and editors for the helpful comments and suggestions. This work was supported by the National Natural Science Foundation of China (Nos. 41972018 and 41730317). This study was also funded by the Strategic Priority Pre-Research Program (B) of the Chinese Academy of Sciences (XDB26000000) and the Geological Survey of China (No. DD20221645). This study was supported by the Bolyai Research Scholarship of the Hungarian Academy of Sciences, and the Hungarian Research Fund (OTKA FK 135262) to B. P.-G.

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Please cite this article as: T. T. Yu, B. Pall-Gergely and R. B. Salvador, Caenogastropoda and Stylopharamatophora (Gastropoda) from the middle Miocene Zhangpu amber of East Asia, Palaeoworld, https://doi.org/10.1016/j.palwor.2022.07.004
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