



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

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## Abstract

Four gastropod species including two new species (*?Tinmyea* 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, *?Tinmyea* 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 3.75<sup>th</sup> 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.

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**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 Diptero-carpaceae, 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 *?Tinmyea* 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 Alycaidae (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.

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## 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, south-eastern 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/impression fossils and amber are preserved in two mudstone units, and some amber pieces and fossilized wood also occur within coal seams. The  $^{40}\text{Ar}$ - $^{39}\text{Ar}$  dating of the basaltic rocks in the middle part of the Fotan Group indicates an age of 14.7–14.9 Ma (Ho et al., 2003), belonging to the Langhian Stage (middle Miocene).

The Zhangpu amber is preserved in blue-grey sandy mudstone, or sometimes in situ in lignified fossil wood. It is yellow, brown to brownish red in color, and pieces of amber can be large but they are extremely fragile. Zhangpu amber is characterized by amyirin- and amyrone-based triterpenoids and cadalene-based sesquiterpenoids (Shi et al., 2014a). It is considered to be derived from the tropical angiosperm family Dipterocarpaceae, based on the above-mentioned compounds as well as the co-occurring fossil winged fruits typical of that family in the Zhangpu deposits (Shi et al., 2014b; Wang et al., 2021).

## 3. Material and methods

The amber pieces containing gastropods are housed in the collection of the NIGPAS (Nanjing Institute of Geology and Palaeontology, China). They were photographed using a Zeiss Stereo Discovery V16 microscope system at the NIGPAS. The final images were obtained by using digitally stacked photomicrographic composites of approximately 40 individual focal planes using the image-editing software Helicon Focus 6 (Helicon Soft, Kharkiv, Ukraine).

We scanned NIGPAS specimens NIGP180008–NIGP180011 in the micro-CT lab of NIGPAS using a 3D X-ray microscope (3D-XRM), Zeiss Xradia 520 versa for additional detail. Unlike conventional micro-CT, which relies on maximum geometric magnification and a flat panel detector to achieve high resolution, the 3D-XRM uses CCD-based objectives to get higher spatial resolution. A CCD-based 0.4x objective was used, providing isotropic voxel sizes from 0.5 mm with the help of geometric magnification. During the scan, the running voltage for the X-ray source was set at 40 kV (NIGP180011), 50 kV (NIGP180010), 60 kV (NIGP180009) and 90 kV (NIGP180008), and a thin filter (LE2) was used to avoid beam-hardening artefacts. To get a high signal-to-noise

ratio, 2001 projections over 360° were collected and the exposure time for each projection was set at 1.5s (NIGP180008), 3s (for NIGP180009), 4s (for NIGP180011) and 4.5s (for NIGP180010). Volume data processing was performed using the software Vgstudio Max (v.3.0, Volume Graphics, Heidelberg, Germany).

Shell measurements include: shell height (H), greatest width of shell perpendicular to height (D), aperture height parallel to shell height (h), and aperture width perpendicular to aperture height (d).

We follow Páll-Gergely et al. (2017) regarding the terminology of the three regions of the teleoconch of *Metalycaeus* Pilsbry, 1900: Region 1 (R1), ranging from the beginning of the teleoconch to the beginning of the differently ribbed region where the sutural tube lies; Region 2 (R2), extending from the end of R1 to the constriction (i.e., the length of R2 usually corresponds with the length of the sutural tube, see Páll-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.

?*Tinnyea* sp.  
 (Fig. 1A–D)

**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.

**Remarks:** The species can be tentatively assigned to *Tinnyea* by its turreted shell and characteristic teleoconch sculpture (very strong opisthocline and slightly curved axial ribs on first whorls and both axial ribs and spiral cords on remaining whorls). ?*Tinnyea* sp. from the mid-Miocene Zhangpu amber is most similar to *Tinnyea lauraea* (Matheron, 1842), known from the Oligocene to the

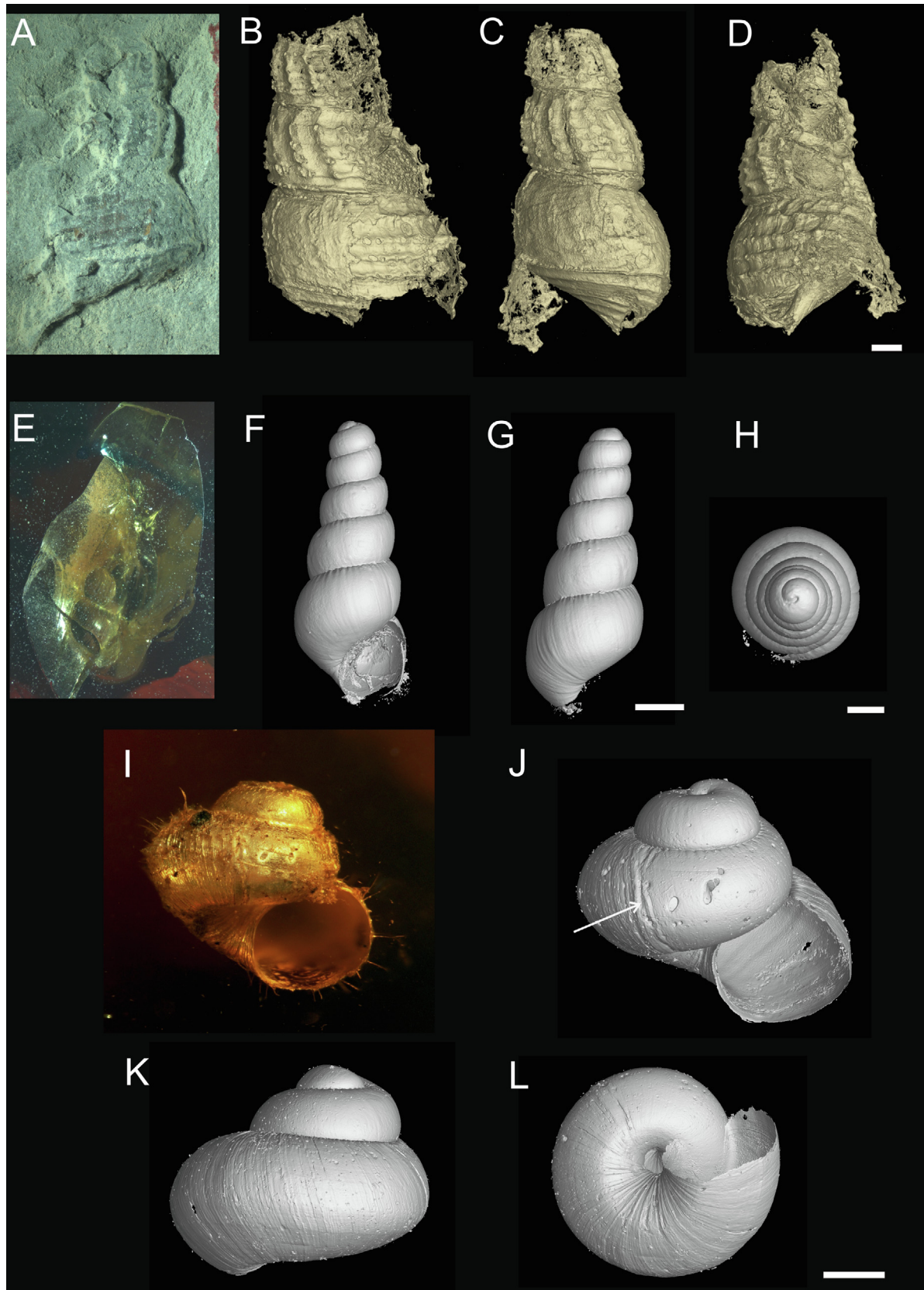


Fig. 1. (A–D) *Tinnyea* sp., NIGP180008; (A) optical microscope photograph; (B–D) micro-CT reconstruction. (E–H) *Tortaxis zhangpuensis* n. sp., NIGP180009, holotype; (E) optical microscope photograph; (F–H) micro-CT reconstruction, apertural, dorsal, and apical views respectively. (I–L) Cyclophoridae 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 opisthocline and slightly curved axial ribs on first whorls and both axial ribs and spiral cords on remaining whorls). However, ?*Tinnyea* sp. has more marked spiral cords, numbering 10–12 on the last two whorls preserved on the specimen.

Superfamily Cyclophoroidea Gray, 1847  
Family Cyclophoridae

Cyclophoridae gen. et sp. indet.  
(Fig. 1I–L)

**Material analyzed:** NIGP180010 (juvenile).

**Description:** Shell minute, juvenile, lowly turbinat 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:** Haired 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 turbinat 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 Alycaecidae 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)

**ZooBank reg. nr.:** urn:lsid:zoobank.org:act:615C841B-6F97-47C7-B1D0-5073EDFD5C98.

**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 whorls, 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 (Páll-Gergely et al., 2017, 2020). Among the *Metalycaeus* species inhabiting mainland China and Taiwan (Hsieh et al., 2006, Páll-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 (Aquitainian, 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).

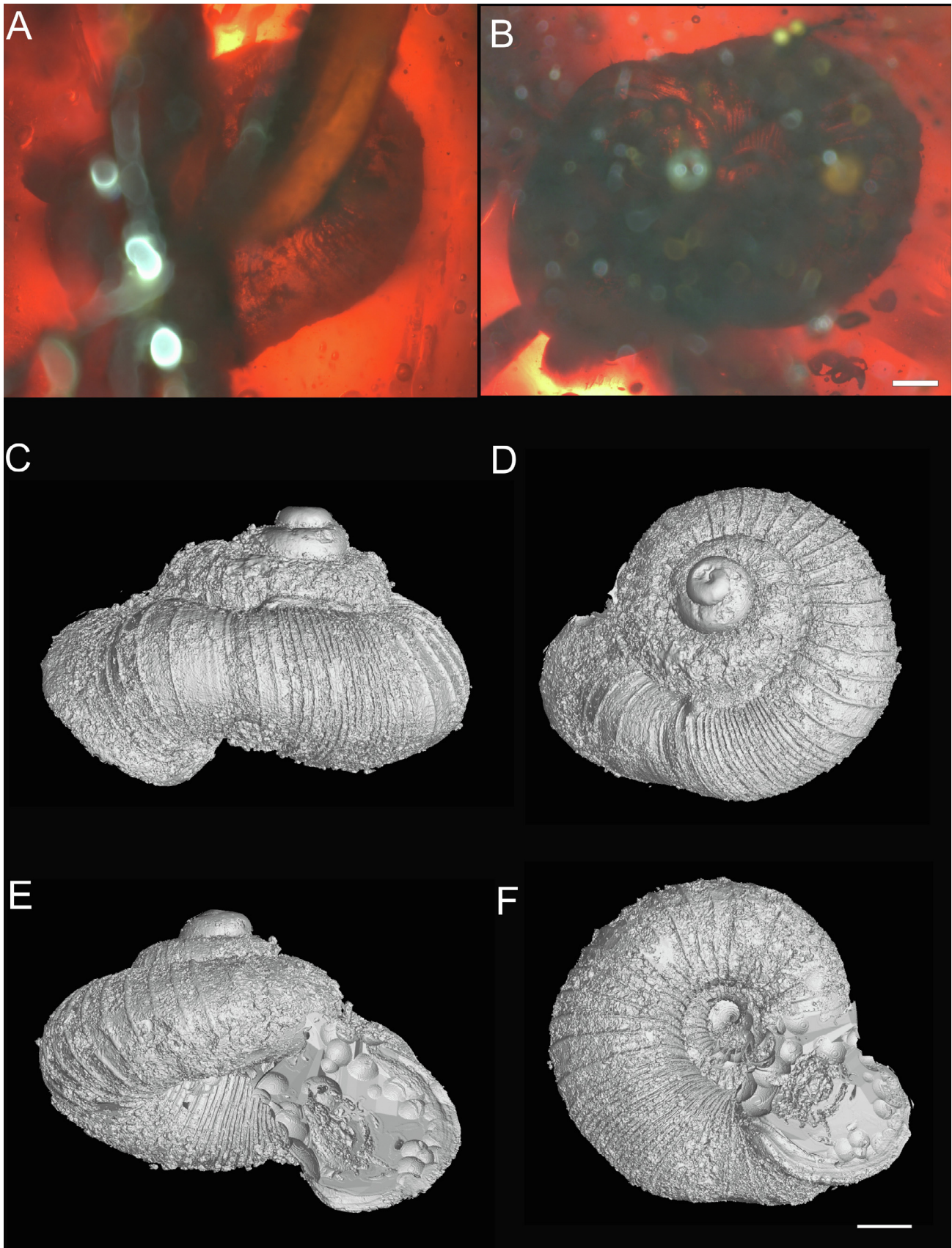


Fig. 2. *Metalycaeus fossilis* n. sp., NIGP180011, holotype. (A, B) Optical microscope photograph. (C–F) micro-CT reconstruction; (C, F) dorsal view; (D) apical view; (E) apertural view. Scale bar = 0.5 mm.

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:97ECBDDA-0662-4195-AC01-22AD0A5EC1FC.

**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 3.75<sup>th</sup> 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 3.75<sup>th</sup> 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 more convex whorls than recent Chinese *Tortaxis* spp. Furthermore, it has a crenulated subsutural pattern on the whorls, which is lacking in *T. xiazayuensis* [Chen and Zhang, 2001](#) from Tibet. It

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 ([Bentham Jutting, 1948, 1959](#); [Minato, 1988](#); [Páll-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 south-western China ([Páll-Gergely et al., 2017](#)). *Metalycaeus fossilis* 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. xiazayuensis*) 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 thiarid *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 cyclophoroids 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 periostracal hairs on the apical area and whorl flank and in having a cancellate sculpture pattern, whereas *H. canaliculatus* lacks periostracal 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 periostracal hairs (Hirano et al., 2019; Neubauer et al., 2019; Yu, 2021).

The Zhangpu amber is the second amber biota where cyclophoroids with thin periostracal hairs have been found. Hairs and periostracal 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 reached 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.

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