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The oldest known cyclophoroidean land snails (Caenogastropoda) from Asia

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The earliest Miocene (Aquitanian, 23–21 Ma) Hang Mon Formation at Hang Mon in Northern Vietnam has yielded a rich assemblage of terrestrial gastropods. Four species from this assemblage belong to the land caenogastropod superfamily Cyclophoroidea. Three of these are assigned to genera with Recent representatives in Southeast Asia and are described as new species: *Cyclophorus hangmonensis* Raheem & Schneider sp. nov. (Cyclophoridae: Cyclophorini), *Alycaeus sonlaensis* Raheem & Schneider sp. nov. (Cyclophoridae: Alycaeinae) and *Tortulosa naggsi* Raheem & Schneider sp. nov (Pupinidae: Pupinellinae). These fossil species represent the earliest records for their genera and are thus of great value for calibrating molecular phylogenies of the Cyclophoroidea. The fourth species is represented only by poorly preserved fragments and is retained in open nomenclature in the Cyclophoridae. While extant Cyclophoroidea have their greatest diversity in Tropical Asia, the oldest fossils described to date from the region are from the Late Pleistocene. The fossils from Hang Mon predate these by more than 20 million years and are also globally among the earliest cyclophoroideans recorded from the area of the present-day forested Tropics. Cyclophoroidea older than the Miocene are only known from Europe. Given that Recent Cyclophoridae and Pupinidae are typically associated with tropical forests, it seems likely that the Hang Mon fossils were also tropical forest taxa and that suitable habitat was present in the general vicinity of Hang Mon in the earliest Miocene.

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Keywords: *Cyclophorus*; *Alycaeus*; *Tortulosa*; early Miocene; Vietnam; palaeobiogeography

Introduction

Land snails of the superfamily Cyclophoroidea (*sensu* Bouchet & Rocroi 2005) are a characteristic and widespread component of the modern terrestrial fauna of the forested tropics (Kobelt 1902; Wenz 1938–1939; Stanisic 1998) (Fig. 1A). The superfamily comprises nine families (Bouchet & Rocroi 2005). Eight are extant (Cyclophoridae Gray, 1847; Aciculidae Gray, 1850; Craspedopomatidae Kobelt & Möllendorff, 1898; Diplommatinidae Pfeiffer, 1856; Maizaniidae Tielecke, 1940; Megalomastomatidae Blanford, 1864; Neocyclotidae Kobelt & Möllendorff, 1897a and Pupinidae Pfeiffer, 1853) and one is extinct (Ferussinidae Wenz, 1923). While recent decades have seen revisionary taxonomic studies of a number of genera and the description of many new species (e.g. Girardi 1978; Emberton 2002, 2003; Marshall & Barker 2007; Nantarat *et al.* 2014b; Yamazaki *et al.* 2015), the taxonomy and systematics of the superfamily as a whole have been neglected for much of the last century. The last major monographic treatment of the Cyclophoroidea, both extinct and extant, was by Kobelt (1902), and the last classification of the group (including a comprehensive list of extant and fossil genera and their type species) was by Wenz (1938–1939). Taxonomic reviews of the Cyclophoroidea at regional or continental scales (e.g. Gude (1921) for South Asia; Torre *et al.* (1942) for the Neotropical taxa) have also been few and far between, as have studies of individual families (e.g. Aciculidae, Boeters *et al.* 1989; Diplommatinidae, Webster *et al.* 2012).

The fossil record contains a number of extinct cyclophoroidean taxa and fossil representatives of Recent European cyclophoroidean genera from the Late Jurassic to Miocene of Europe (Wenz 1938–1939; Hrubesch 1965; Bandel 1991; Stworzewicz 1995). Comparable data are scarce for the forested tropics (but see, for example,

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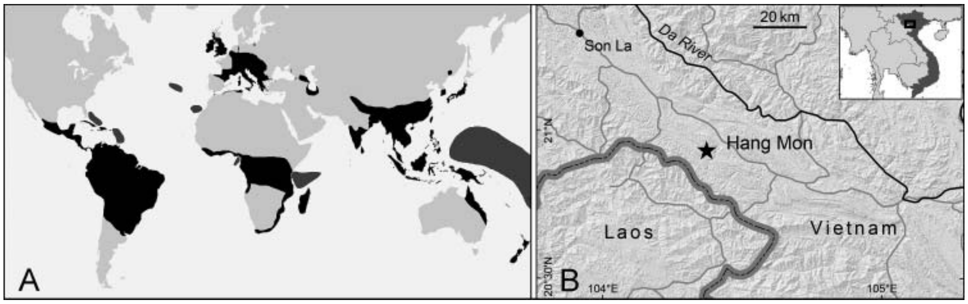

Figure 1. **A,** global distribution of Recent Cyclophoroidea (dark shading), including occurrence on island groups (data sources: Kobelt 1902; Gude 1921; Van Bruggen 1982; Boeters *et al.* 1989; Gascoigne 1994; Emberton 2002; Kantor *et al.* 2010; Thompson 2011); **B,** the location of Hang Mon, Sơn La Province, Northern Vietnam.

Pickford 1995), and although tropical Asia is the major centre of extant generic and species richness (Kobelt 1902; Wenz 1938–1939), the earliest known Asian cyclophoroideans are from the Late Pleistocene to Mid Holocene of South and South-east Asia (Deraniyagala 1956; Gorman 1971; Rabett *et al.* 2009, 2011; Conrad *et al.* 2013; Kulatilake *et al.* 2014). We report here on the fossils of four cyclophoroidean genera, the cyclophorids *Cyclophorus* Montfort, 1810 and *Alycaeus* Baird, 1850, the pupinid *Tortulosa* Gray, 1847, and a species of uncertain generic status, from the early Miocene of Northern Vietnam (23–21 Ma). We describe the fossils in detail, comparing them with extant congeneric representatives, discuss their significance in the context of the cyclophoroidean fossil record, and speculate on the palaeobiogeography and palaeoecology of cyclophorids and pupinids.

Material and methods

The fossil gastropods described here were collected from the stratotype of the 90–116 m thick Hang Mon Formation, at the abandoned Hang Mon coal mine in Yên Châu District, Sơn La Province, Northern Vietnam (20.93583°N, 104.37033°E; Fig. 1B; locality Hang Mon 1 of Prieto *et al.* in press). The Hang Mon Formation infills the Cenozoic Hang Mon Basin, resting unconformably on Middle Triassic limestones (Thanh & Khuc 2006). Structurally, the Hang Mon Basin is a pull-apart basin associated with the wider Red River Shear Zone. This major sinistral strike-slip fault zone forms the boundary between the South China and Indochina blocks and was active from the late Eocene to early Miocene (e.g. Gilley *et al.* 2003; Guo *et al.* 2016). Biostratigraphy of the Hang Mon Formation is based on mammals, and this clearly supports an earliest Miocene (23–21 Ma), Aquitanian age (Prieto *et al.* in press).

Today the mine at Hang Mon is filled by a groundwater lake, leaving only the uppermost sediments (∼10 m thick) exposed (see Prieto *et al.* in press, fig. 1). The gastropods were obtained from the lowermost part of this exposure, which consists of a 3 m thick succession of marly siltstones with thin intercalations of lignitic clays (see Böhme *et al.* 2011, fig. 11).

The Cyclophoroidea described here are part of a taxonomically diverse terrestrial gastropod assemblage, which also includes various Pulmonata *sensu* Bouchet & Rocroi (2005) that have not been studied in detail so far. The gastropods evidently form an allochthonous assemblage; they occur in what are most likely fluvial sediments (Böhme *et al.* 2011) where they accumulated in shallow water under low-energy hydrodynamic conditions. They may thus have been part of different terrestrial communities, but are unlikely to have been transported any great distance and probably lived in close vicinity to the water body.

All shells are preserved in their original aragonite as can be seen from the retention of crossed-lamellar shell microstructure in *Cyclophorus* and *Tortulosa* (see descriptions below). Most specimens, however, were fragmented and distorted during sediment compaction. The periostracum most likely was lost before or during deposition, and the shells show traces of the corrosion typical of dead gastropod shells that have been exposed to a tropical climate for a prolonged period.

The gastropods were collected during two field excursions in 2009 and 2011. The fossiliferous siltstones were broken up in the field and screened for gastropods, which were usually partly enclosed by matrix. Larger, more fragile specimens were fixed with liquid glue in the field; they were later cleaned with water and a needle, and then dried and impregnated with Paraloid resin. Some specimens were too brittle for adequate cleaning. Small specimens were extracted by processing sediment with diluted hydrogen peroxide and screen-washing (0.3 mm mesh width); fossils were picked from dried residues.

Taxonomic study of the fossil material was carried out in the Mollusca Section of the Natural History Museum, London, UK (**NHM**), and involved comparative study of the fossils with material in the museum's type and general collections. Additional comparisons were made with land-snail material and/or images of such material from two other institutions: Senckenberg Forschungsinstitut und Naturmuseum, Frankfurt am Main, Germany (**SMF**), and the University Museum of Zoology, Cambridge, UK (**UMZC**). All fossil material from Hang Mon is currently deposited at the Paläontologische Sammlung der Universität Tübingen, Germany (**GPIT**); see systematic palaeontology section and Supplemental Table 1 for registration numbers.

Systematic palaeontology

Remarks. The systematic arrangement above genus level largely follows Bouchet & Rocroi (2005), but see also Kobelt (1902) and Raheem *et al.* (2014); at genus level we follow Kobelt (1902). Shell morphological terminology follows Cox (1960a) and whorl counts are based on the approach of Kerney & Cameron (1979). Unless stated otherwise we have used the term 'shell sculpture' to refer to the sculpture of the teleoconch.

Clade **Caenogastropoda** Cox, 1960b
Superfamily **Cyclophoroidea** Gray, 1847
Family **Cyclophoridae** Gray, 1847
Subfamily **Cyclophorini** Gray, 1847
Genus ***Cyclophorus*** Montfort, 1810

Type species. *Helix volvulus* O. F. Müller, 1774; by original designation.

Remarks. The only confirmed occurrences of this genus in the fossil record are from the Late Pleistocene to Mid Holocene of South and South-east Asia (Deraniyagala 1956; Gorman 1971; Rabett *et al.* 2009, 2011; Conrad *et al.* 2013; Kulatilake *et al.* 2014). Fabre-Taxy (1959) reported five supposed species of *Cyclophorus* from the latest Cretaceous to early Paleocene of France, but the taxonomic status of these fossils is uncertain (see Discussion). The extant diversity of *Cyclophorus* is high (*c.* 180 nominal species) and the genus ranges across most of South and South-east Asia (Nantarat *et al.* 2014a). Several subgenera were recognized by Kobelt (1902) on the basis of shell shape and shell sculptural features, but the limits of these groups are not well understood. Shell sculpture is an important subgeneric character, typically consisting of fine striae which in some taxa are combined with spiral linear elevations in the form of lirae and/or cords.

Cyclophorus hangmonensis Raheem & Schneider sp. nov.
(Fig. 2A–I)

2011 *Lagochilus* sp.; Böhme *et al.*: 683.

Diagnosis. Small (shell width < 20 mm), turbinate, narrowly umbilicate *Cyclophorus* with raised spire, rounded body whorl and continuous, expanded lip. Shell surface lacks sculpture.

Etymology. Named after the type locality, Hang Mon.

Material. Holotype: GPIT/GA/05086, largely intact adult shell (Fig. 2A–D). Paratypes: GPIT/GA/05083, largely intact adult shell (Fig. 2E–G); GPIT/GA/05077, 05079, 05085, adult shells with the spire and parts of the body whorl intact (Fig. 2H, I). Other material: GPIT/GA/05078, 05080–05082, 05084, 05087, six adult or sub-adult shell fragments; GPIT/GA/05099, three fragmentary specimens with only some of the earlier whorls intact.

Type locality. Hang Mon coal mine, Yên Châu District, Sơn La Province, Northern Vietnam.

Type stratum and age. Hang Mon Formation; early Miocene, Aquitanian.

Description. Adult shell small (holotype: width = 18.7 mm, height = 15.5 mm; paratype: width = 18.5 mm, height = 13.6 mm), with approximately 4.5–4.75 whorls; solid, turbinate, narrowly umbilicate, spire raised with apex inflated and whorls well rounded in profile; body whorl disproportionately large, periphery rounded; lip continuous, expanded, thickened. Shell surface lacking sculpture, eroded in places to reveal underlying axial crossed-lamellar microstructure, which is similar to that observed in Recent *Cyclophorus* species and *Tortulosa naggsi* sp. nov. (see below).

Remarks. *Cyclophorus hangmonensis* sp. nov. falls within the current range in shell shape for *Cyclophorus* and is at the lower end of the size spectrum (e.g. Kobelt 1902; Nantarat *et al.* 2014a, b). In shell size it agrees closely with Recent species such as *C. loloensis* Heude, 1886 and *C. ngankingensis* Heude, 1882 from China, the Northern Vietnamese species *C. tornatus* Morlet, 1892, and an undescribed Northern Vietnamese species with the manuscript name '*Cyclophorus stenopholis* Möllendorff' (Fig. 2J–N; NHMUK 1901.12.23.46, 1902.03.22.63-64, 'Central-Tonkin, Chiem-Hoa'). While all of these species have turbinate shells, the periphery of the body whorl is rounded in *C. loloensis*, *C. ngankingensis* and *C. hangmonensis* sp. nov. but distinctly sub-angulate in the two Vietnamese species (Fig. 2J, K, N).

Cyclophorus hangmonensis sp. nov. is unique among known *Cyclophorus* in lacking all traces of shell sculpture, which makes its subgeneric classification uncertain. The sculpture of all four of the extant taxa listed above consists solely of fine striae, the shell surface having a smooth, silky sheen with no traces of spiral cords or lirae (Fig. 2J–N; compare with the extant Indian species *C. altivagus* Benson, 1854 and *C. nilagiricus* (Benson, 1852) (Fig. 2O, P), which have the shell surface spirally corded). This type of smooth, finely striated shell surface is characteristic of Kobelt's (1902) sub-genus *Cyclophorus* (Kobelt

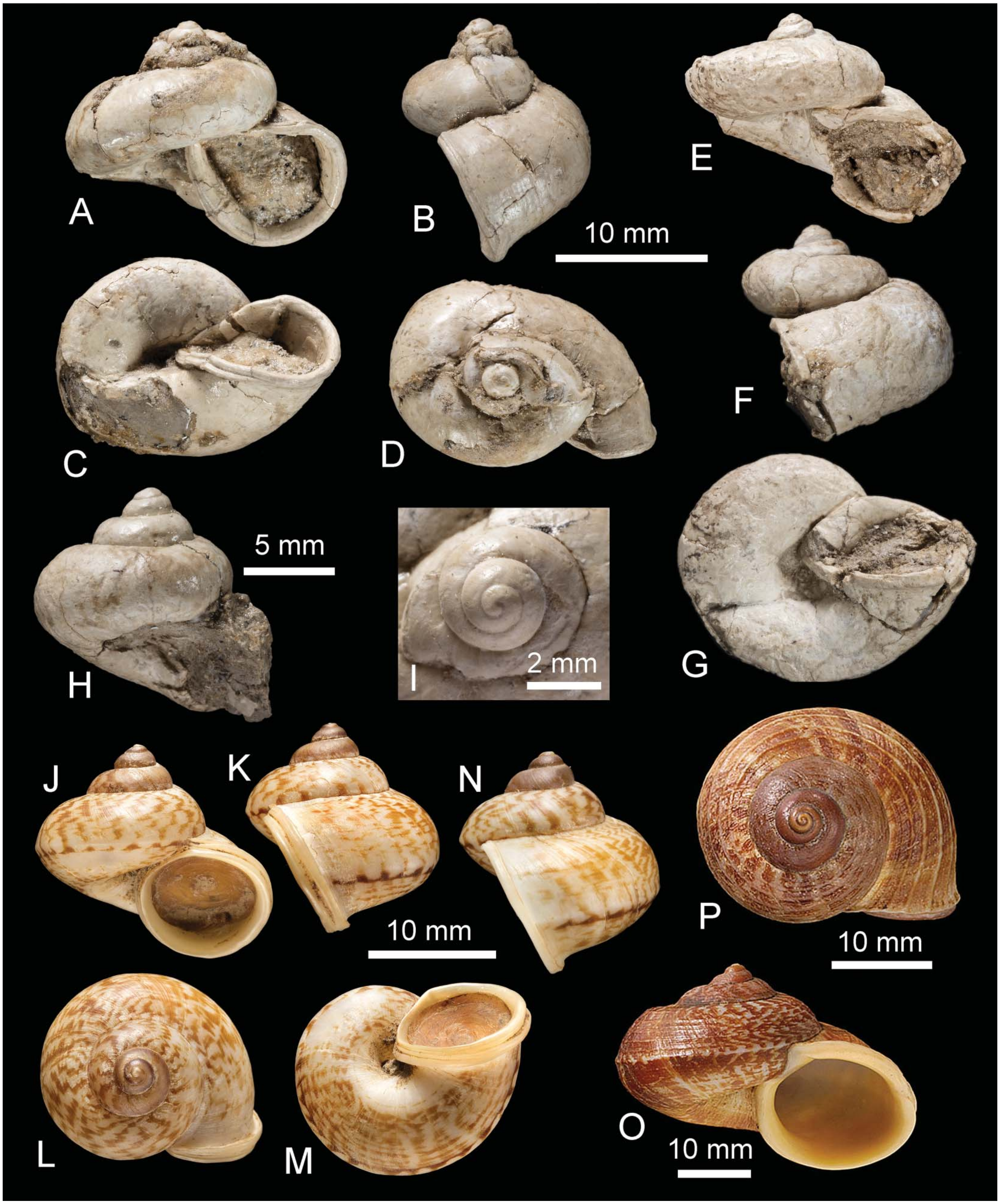

Figure 2. **A–I,** *Cyclophorus hangmonensis* sp. nov., whole shells: **A–D,** holotype, GPIT/GA/05086; **E–G,** paratype, GPIT/GA/05083; **H**, paratype, GPIT/GA/05077, with uncompressed spire; **I**, paratype, GPIT/GA/05085, with less damaged earlier whorls. **J–N**, two examples of the Recent species with the manuscript name '*Cyclophorus stenopholis* Möllendorff', note the difference in the thickness of the lip: **J–M,** NHMUK 1902.03.22.63; **N,** 1902.03.22.64. **O, P,** extant *Cyclophorus* species with a spirally corded dorsal shell surface: **O,** *C. nilagiricus* (Benson, 1852), lectotype, UMZC I.103890.A, with fine, less distinct raised spiral elevations; **P,** *C. altivagus* Benson, 1854, neotype, UMZC I.103835.A, with bold, widely spaced spiral cords.

included *C. loloensis*, *C. ngankingensis* and *C. tornatus* in this group along with a number of other Recent Northern Vietnamese and Chinese species). As far as is currently known, all of the extant species occurring in Northern and Central Vietnam have a smooth, finely striated shell surface (K. and P. von Oheimb, unpubl. data).

A possible explanation for the absence of shell sculpture in the fossil material we examined is that the outer shell surface is missing, the periostracum and outermost layer of the ostracum having been lost by natural processes of shell weathering/decomposition (cf. Cadée 1999; Pearce 2008; Říhová *et al.* 2014) prior to the fossilization of the specimens. Study of shell material from two extant, forest-living Northern Vietnamese species (NHMUK 20170132, 20170133, Cuc Phuong National Park, May 2007) supports this view. These shells were found on the forest floor and are at various stages of decay (Fig. 3). The most extensively decomposed examples (Fig. 3D) are strikingly similar to the fossils from Hang Mon: the periostracum is absent; the outermost layer of the ostracum is missing, along with all traces of pigmentation and sculpture; and the underlying axial crossed-lamellar microstructure is clearly evident in places.

Only a few, poorly preserved, fragmented shells of *Cyclophorus hangmonensis* sp. nov. were available for Böhme *et al.*'s (2011) preliminary assessment of the fossil gastropod fauna of Hang Mon. These were erroneously assigned to *Lagocheilus* Blanford, 1864 (*Lagochilus* Kobelt & Möllendorff, 1897b is an unjustified emendation under ICZN 1999, Article 33), which is superficially similar to smaller species of *Cyclophorus* in shell shape and size.

Subfamily **Alycaeinae** Blanford, 1864
Genus ***Alycaeus*** Baird, 1850

Type species. *Alycaeus eydouxi* Venmans, 1956 (replacement name for *Cyclostoma gibbum* Eydoux, 1838 [Férussac MS], non *Cyclostoma gibbum* Draparnaud, 1805); type by subsequent designation (Nevill 1878).

Remarks. No published data are available on the fossil record of *Alycaeus* or any other Alycaeinae. Shell shape in Recent *Alycaeus* varies from conoid to depressedly turbinate (Kobelt 1902; Wenz 1938; Kuroda 1943, 1951). The genus contains several subgenera (Kobelt 1902; Wenz 1938) that are characterized by depressedly turbinate shells; the limits of these groups are poorly understood.

Alycaeus sonlaensis Raheem & Schneider sp. nov.
(Fig. 4A–J)

Diagnosis. Very small (shell width approximately 4 mm), depressedly turbinate and widely umbilicate species of *Alycaeus* with slightly swollen apex. Constriction of body whorl short and close to lip. Teleoconch collabrally lirate, the lirae widely spaced, apart from a densely lirated zone, which is immediately behind the constriction of the body whorl and is equivalent to one-quarter the length of the body whorl. Presence of sutural tube uncertain in the material described here; most likely present in the species and lost during taphonomy.

Etymology. The name is derived from Sơn La Province, Northern Vietnam.

Material. Holotype: GPIT/GA/05092, almost entire, adult shell (Fig. 4A–F). Paratypes: GPIT/GA/05093, fragmented adult individual (Fig. 4I); GPIT/GA/05094, fragmented specimen with only the earlier whorls intact (Fig. 4G, H); GPIT/GA/05095, 05096, two adult individuals with the earlier whorls and part of the body whorl intact (Fig. 4J); GPIT/GA/05097, fragment with only the terminal part of a body whorl intact. Other material: GPIT/GA/05098, 30 shell fragments.

Type locality. Hang Mon coal mine, Yên Châu District, Sơn La Province, Northern Vietnam.

Type stratum and age. Hang Mon Formation; Early Miocene, Aquitanian.

Description. Shell very small (width = approximately 4 mm, height = approximately 2 mm), consisting of about 3.5–3.75 whorls; depressedly turbinate, widely umbilicate, collabrally lirate; apex slightly swollen; body whorl a short distance behind lip constricted in width, constriction short relative to length of body whorl; lip continuous, widely expanded, heavily thickened. Sutural tube absent in most fragments with dorsal shell surface intact, but a possible trace of it on the holotype (Fig. 4F). Initial 0.75 of earliest whorl smooth; thereafter, shell collabrally lirate (Fig. 4I, J), lirae widely spaced, apart from closely lirate zone located a short distance behind constriction of body whorl (Fig. 4D–H); this zone constitutes 20–25% of body whorl length.

Remarks. Recent Alycaeinae have a disjunct range, with distinct genera occurring in Madagascar and in South and South-east Asia (Kobelt 1902; Gude 1921; Wenz 1938; Kuroda 1943; Emberton 2002; Balashov & Griffiths 2015). The Asian Alycaeinae are represented by *c.* 350 species (Páll-Gergely *et al.* 2016) and need taxonomic revision. The extant Asian genus *Alycaeus* Baird, 1850 comprises several subgenera (e.g. Kobelt 1902; Wenz 1938; Kuroda 1943, 1951). Although broadly speaking these vary in shell shape from high-spired, conoid shells to low-spired, depressedly turbinate shells, the subgeneric limits are very poorly defined (B. Páll-Gergely, unpubl. data). The fossil species falls within the current range in shell morphology and size of the genus (see taxa listed in Kobelt 1902). The extant Northern Vietnamese snail fauna includes several species (e.g. *Alycaeus cristatus*

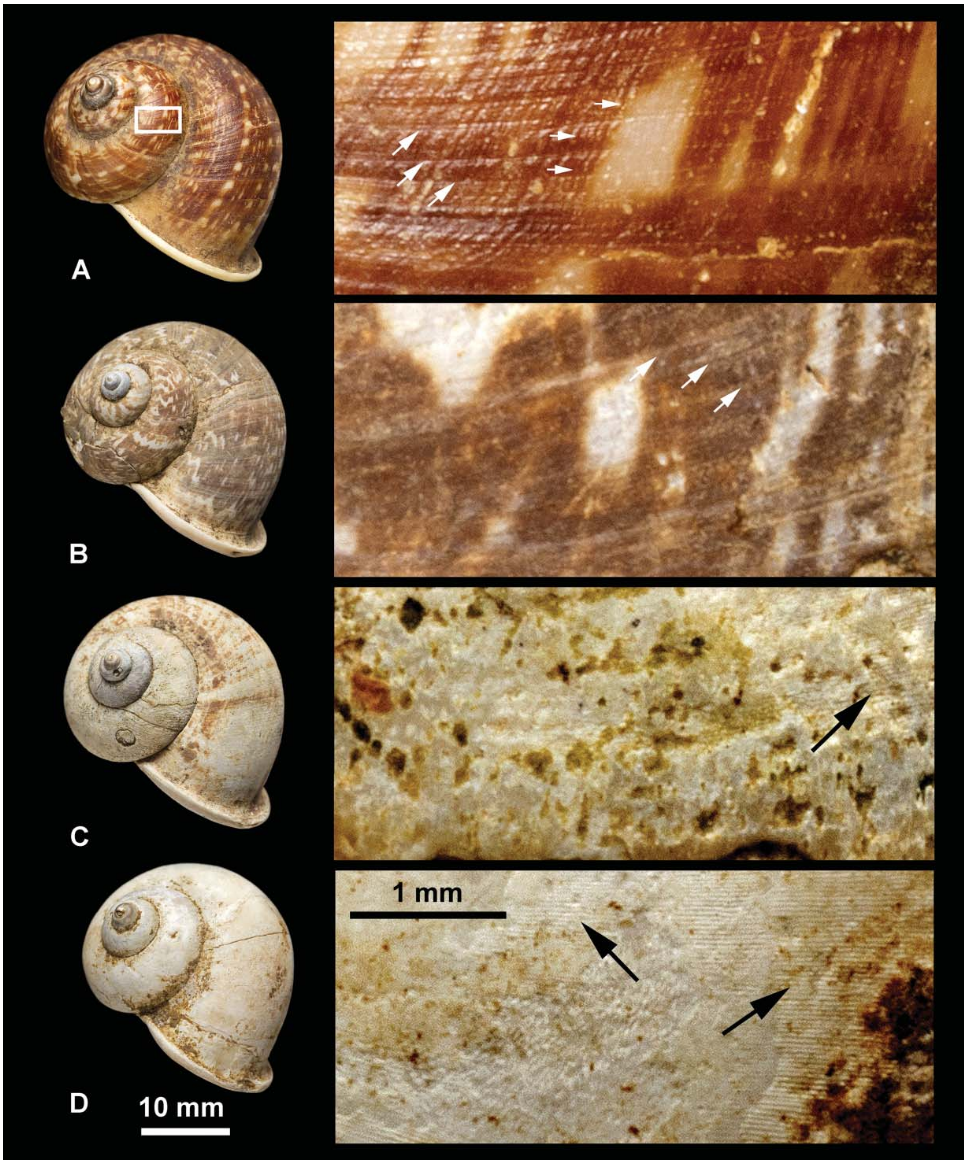

Figure 3. Stages in the natural weathering of the shell surface as seen in a series of four shells of a Recent Vietnamese *Cyclophorus* species collected from Cuc Phuong National Park, north Vietnam, in May 2007 (the lot comprises 10 shells in total, NHMUK 20170132). Each shell is illustrated with a view of its dorsal surface, and a close-up view (corresponding approximately in area to the white box in the dorsal view of **A**). **A,** NHMUK 20170132/1 with periostracum fully intact and outer shell surface irregularly ornamented with a combination of close spiral (horizontal white arrows) and more distant collabral (oblique white arrows) striae, giving the shell a silky lustre. This type of smooth, finely striated shell surface is characteristic of extant Northern and Central Vietnamese *Cyclophorus*. **B,** NHMUK 20170132/2, with the periostracum completely worn away, the collabral striae (oblique white arrows) barely evident and the spiral striae largely absent. The very close collabral lines seem to correspond with the underlying axial crossed-lamellar shell microstructure (compare with **C** and **D**). **C,** NHMUK 20170132/3, substantially weathered shell in which the outer surface of the ostracum has been irregularly eroded away in places to show the underlying axial crossed-lamellar structure (black arrow); note the traces of pigmentation. **D,** NHMUK 20170132/4, heavily weathered shell in which the outer surface of the ostracum has been largely stripped away, along with all traces of pigmentation, and the underlying axial crossed-lamellar microstructure is clearly evident (black arrows; the dark coloured patches along the suture and near the lip are accumulations of dirt).

Möllendorff, 1886a, *A. depressus* Bavay & Dautzenberg, 1912, *A. fraterculus* Bavay & Dautzenberg, 1900; Fig. 4L–N), which, in common with *A. sonlaensis* sp. nov., exhibit a depressedly turbinate shell, a smooth protoconch and a teleoconch free of spiral ornamentation (B. Páll-Gergely, unpubl. data). These species were classified in the Recent subgenus *Dicharax* Kobelt & Möllendorff, 1900 by Kobelt (1902) and some other early workers (e.g. Bavay & Dautzenberg 1900, 1912). However, given that there are other extant Asian subgenera (e.g.

Figure 4. **A–J,** *Alycaeus sonlaensis* sp. nov.: **A–F**, holotype, GPIT/GA/05092, the closely lirated zone of the body whorl and the supposed trace of the sutural tube are indicated by white and black arrows, respectively; **G, H,** paratype, GPIT/GA/05094; **I,** paratype, GPIT/GA/05093, early whorls; **J,** paratype, GPIT/GA/05095, early whorls showing that only the first 0.75 of the earliest whorl is free of the strong collabral lirae characteristic of this species. **K,** the extant species *A. parvulus* Möllendorff, 1886b, paratype, NHMUK 1891.03.17.799, black arrow indicates sutural tube. **L–N,** the Recent *A. cristatus* Möllendorff, 1886a, lectotype, SMF 39231, black arrow indicates sutural tube.

Chamalycaeus Kobelt & Möllendorff, 1897a, *Metalycaeus* Pilsbry, 1900) broadly similar in shell shape to *Dicharax* and that some species of *Chamalycaeus* lack spiral ornamentation (see Kobelt 1902), the subgeneric classification of the fossil is uncertain.

As in the fossil species, extant Asian Alycaeinae possess a very closely (and/or strongly) collabrally lirate zone on the body whorl. In Recent taxa this zone bears the sutural tube, which is usually tubular in form (e.g. *A. cristatus* Möllendorff, 1886a) (Fig. 4L–N) and is used in gas exchange (Páll-Gergely *et al*. 2016). The sutural tube is fragile and easily damaged (e.g. Raheem *et al.* 2014, fig. 25D) and may have been lost from the fossil specimens during taphonomy. It is also possible that the fossil species lacks a sutural tube. While this has not been reported for any extant taxa, in some species (e.g. *A. microconus* Möllendorff, 1886b, *A. microdiscus* Möllendorff, 1886b, *A. parvulus* Möllendorff, 1886b), the sutural tube is reduced to a small hemispherical bump (Fig. 4K).

Cyclophoridae subfam. indet.
(Fig. 5A–D)

2011 *Ptychopoma* sp.; Böhme *et al.*: 683.

Material. GPIT/GA/05090 (Fig. 5A–D), eight fragmented specimens including one large adult or sub-adult shell with the earlier whorls intact; GPIT/GA/05091, seven smaller individuals with only the earliest whorls intact.

Locality. Hang Mon coal mine, Yên Châu District, Sơn La Province, Northern Vietnam.

Stratum and age. Hang Mon Formation; Early Miocene, Aquitanian.

Description. Shell small, with the largest specimen (width = approximately 9 mm, height = approximately 4 mm) comprising just under four whorls; depressedly turbinate, low spired with apex slightly swollen; widely umbilicate; whorls increasing rapidly in width and rounded in profile; shell surface lacks sculpture.

Remarks. In shape and size, this species is similar to Recent tropical Asian cyclophorid genera such as *Cyclotus* Guilding in Swainson, 1840 *sensu lato*, *Pterocyclos* Benson, 1832, *Ptychopoma* Möllendorff, 1885, *Rhiostoma* Benson, 1860 and *Scabrina* Blanford, 1863. All of these genera are extant in Northern Vietnam (see Kobelt 1902; Do *et al*. 2015). The generic classification of the fossil species is uncertain because none of the specimens have the body whorl and lip largely or wholly intact. Nonetheless, this species is readily distinguishable from *Cyclophorus hangmonensis* sp. nov., which has a more elevated profile and whorls that increase more rapidly in width.

Family **Pupinidae** Pfeiffer, 1853
Subfamily **Pupinellinae** Kobelt, 1902
Genus ***Tortulosa*** Gray, 1847 (= *Perlisia* Tomlin, 1948)

Type species. *Turbo tortuosus*, an unavailable Chemnitz name, made available as *Helix* (*Cochlodina*) *tortuosa* Férussac, 1821; by original designation.

Remarks. No data have been published on the fossil record of *Tortulosa*. The name *Tortulosa* Gray, 1847 was published as a junior synonym of *Brachypus* Guilding, 1828 (see Gray, 1847, p. 177) and is an available name (see ICZN, 1999, Article 11.6.1). The type species of *Tortulosa* Gray, 1847 by original designation is *Turbo tortuosus* (see ICZN, 1999, Articles 67.12, 12.2.1 and 12.2.5), a name published by Chemnitz (1795, p. 158, pl. 195A, figs 1882, 1883) and made available by Férussac (1821, p. 61) *as Helix* (*Cochlodina*) *tortuosa*. Although Chemnitz's name was published before Férussac's, it is unavailable

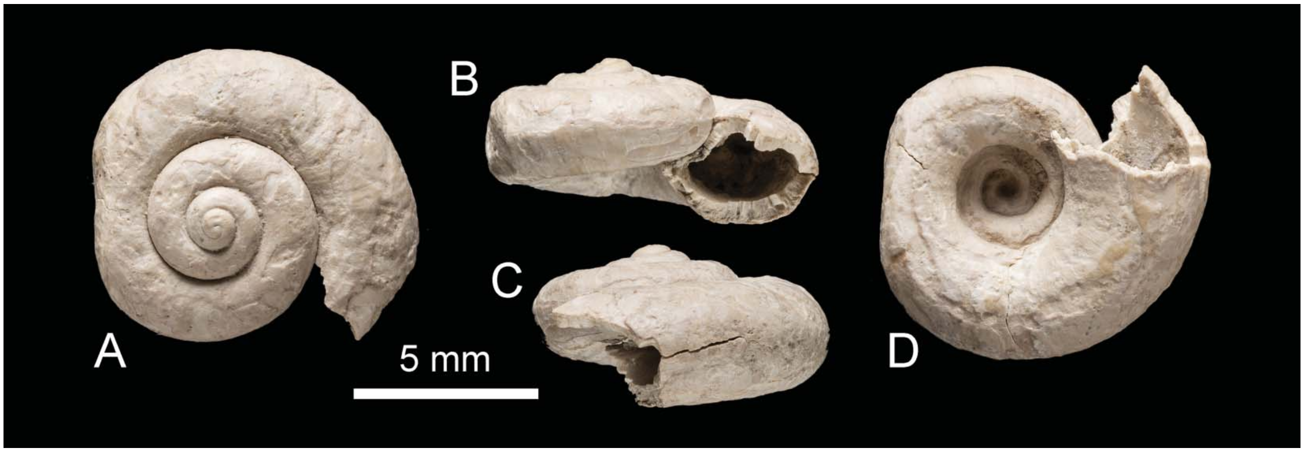

Figure 5. **A–D**, Cyclophoridae indet., large, adult or sub-adult shell, GPIT/GA/05090.

because specific names introduced by Martini and Chemnitz from 1769 to 1795 have been ruled unavailable by the International Commission on Zoological Nomenclature (ICZN 1944, Opinion 184; 1954, Direction 1).

Férussac's (1821, p. 61) description of *Helix* (*Cochlodina*) *tortuosa* consists simply of an indication to the two figures published by Chemnitz of *Turbo tortuosus* ("Turbo Tortuosus, Chemnitz, XI, tab. 195A, fig. 1882, 1883", these figures were reproduced by Raheem *et al.* 2014, fig. 9E), and a reference to the locality, which was wrongly given as the 'Antilles'. Férussac made no mention of the description that accompanied Chemnitz's figures (see Chemnitz 1795, p. 158). This description was quite detailed for its time, and in it Chemnitz gave the locality as the Nicobar Islands and indicated that the material seen by him (i.e. several specimens) was from Spengler. The Spengler material figured by Chemnitz is thus the type material of *Tortulosa tortuosa*, but no examples could be traced in the Spengler collection at the Zoological Museum, Natural History Museum of Denmark, University of Copenhagen (pers. comm. T. Schiøtte).

While Chemnitz's figures (either two separate shells or two views of a single shell) do not show the distinctive basal keel of *Tortulosa*, in all other respects they agree closely with his description. All subsequent published descriptions and illustrations of the shell of this species (for a full list see Gude 1921, p. 190) also correspond with Chemnitz's description. Thus, the identity of *Tortulosa tortuosa* has been consistently understood since Chemnitz's time and this makes the designation of a neotype inappropriate (see ICZN 1999, Article 75.2). Neither Chemnitz nor Férussac provided any shell measurements, but the length (18–19 mm) and 'width' (i.e. not the measurement referred to elsewhere in this paper, but the width at the approximate mid-point of the shell's vertical axis, 6.5 mm) of Chemnitz's figures broadly agree with the corresponding measurements subsequently published by Pfeiffer (1849, p. 166; 1852, p. 136) for material from the Cuming Collection. The NHM has two shells from Cuming (NHMUK 20100643; see Raheem *et al.* 2014, fig. 30B, C) and the larger of these broadly corresponds with the size of Chemnitz's figures and Pfeiffer's measurements.

Note that while most authors have given the Nicobars as the locality of *Tortulosa tortuosa*, first Férussac and later Beck (1837, p. 83) wrongly gave it as the 'Antilles'. Later authors, notably Mörch (1872, p. 339), Theobald (1876, p. 41) and Blanford (1869a, pp. 138–139; 1880, p. 216), have questioned the accuracy of the Nicobars as the locality of *T. tortuosa*. Blanford (1880) went so far as to say that he thought the species was most likely South Indian and its occurrence in the Nicobars was 'highly improbable'. However, given that there are several land-caenogastropod taxa, which range from South Asia through the Andaman/Nicobar Islands to South-east Asia (e.g. *Lagocheilus* Blanford, 1864, *Cyathopoma* Blanford & Blanford, 1861, *Acmella* Blanford, 1869b; see Gude 1921), and that the snail fauna of these islands is poorly known, it is possible that *Tortulosa* does indeed occur in the Nicobars. We note here that there are at least two recent published references to the occurrence of *T. tortuosa* in the Malay Peninsula (southern Thailand: Hemmen & Hemmen 2001, p. 40; northern peninsular Malaysia: van Benthem Jutting 1960, p. 12; Maassen 2001, p. 44). Both these records, we would argue, are misidentifications of the Recent species *T. tweedei* (see below for further details); van Benthem Jutting (1960) in fact stated that her material was from the type locality of *T. tweedei*.

Perlisia tweedei Tomlin, 1948 is the type species by original designation of the extant monotypic genus *Perlisia* Tomlin, 1948 (the type locality is Kaki Bukit, Perlis, Malaysia). The NHM type collection contains a single syntype of this species (NHMUK 1948.10.2.6). This shell agrees with Tomlin's description and is here designated the lectotype; images are available at the website 'Malay Peninsular Terrestrial Molluscs' (http://malaypeninsularsnail.myspecies.info). On the basis of available published data and a comparison of the lectotype of *P. tweedei* with Chemnitz's (1795) figures and description of *Turbo tortuosus* and all available material of *T. tortuosa* from the Nicobars in the NHM collections (the two shells from the Cuming Collection, and an additional single shell, NHMUK 20170305), we consider that the name *Perlisia* is a junior synonym of *Tortulosa*. Both *P. tweedei* and *T. tortuosa* in their adult state are characterized by a pupiform shell with the terminal part of the body whorl detached from the penultimate whorl; the body whorl is fully attached to the rest of the shell in all other known species of *Tortulosa*. Tomlin (1948, p. 225) stated that *Perlisia* could be distinguished from *Tortulosa* because the basal keel of the former lacked the prominently perforated opening on the lip, which he indicated "characterizes all *Tortulosa* (*sensu lato*), the peristome being entire." The latter assertion is, however, inaccurate. The opening of the basal keel in *P. tweedei* is certainly shallower and less spherical than in other species of *Tortulosa*, but it nevertheless clearly interrupts the otherwise circular shape of the inner margin of the lip (see the figure accompanying Tomlin's description: pl. 11, fig. 6). This is a subtle distinction and does not in our opinion justify the erection of a separate genus (e.g. the size and shape of the opening of the basal keel can be quite variable in some species of Sri Lankan *Tortulosa*). Only a small number of shells were available to us for examination: the three shells of *T. tortuosa* detailed above; the lectotype of *P. tweedei*; and three shells of *P. tweedei* from Phnom Mountain, Krabi Province, southern Thailand (NHMUK 20060334). On the basis of this material, the two species only differ in the following characters. The shell of *T. tortuosa* is white, whereas that of *P. tweedei* is dull yellow or yellowish pink. *Perlisia tweedei* (height = 20.1–24.1 mm, width = 8.5–9.6 mm, whorls = 6.25–7.7) is larger than *T. tortuosa* (height = 15.2–18 mm, width = 6.6–7.3 mm, whorls = 6.8–7.5). In *P. tweedei* the opening of the basal carina on the lip is a little wider and shallower, and, as was noted by Tomlin (1948), the length of the detached part of the body whorl relative to the height of the shell is greater than in *T. tortuosa*. In our view this variation falls within the interspecific range in shell morphology of the genus *Tortulosa*, and *Perlisia* is best treated as a junior synonym of *Tortulosa*. However, we would not go so far as Maassen (2001, p. 44), who treated *P. tweedei* as a junior synonym of *Tortulosa tortuosa*. Until further field and molecular systematic studies are carried out, we consider that these two taxa should be treated as distinct species.

Tortulosa naggsi Raheem & Schneider sp. nov.
(Fig. 6A–I)

Diagnosis. *Tortulosa* with body whorl fully attached to penultimate whorl. Prominent, internally grooved basal keel on body whorl, widening at its junction with lip and forming hemispherical opening well to left and above lowest point of lip. A hemispherical notch on inner margin of lower palatal lip.

Derivation of name. Named in honour of Fred Naggs in recognition of his major contribution to the study of the South and South-east Asian land-snail fauna.

Material. Holotype: GPIT/GA/05088 (Fig. 6A–E), an adult shell (width = 4.7 mm, height = 9.4 mm) with only the two terminal whorls and the lip intact. Paratypes: GPIT/GA/05089 (Fig. 6F–I), an adult/sub-adult shell fragment (width = 5.1 mm, height = 6.6 mm) with only the five apical whorls intact; and GPIT/GA/05100, a juvenile shell (width = 3.4 mm, height = 3.3 mm, 3.75 whorls) with only the earlier whorls intact.

Type locality. Hang Mon coal mine, Yên Châu District, Sơn La Province, Northern Vietnam.

Stratum and age. Hang Mon Formation; early Miocene, Aquitanian.

Description. Holotype pupiform, narrowly umbilicate; body whorl fully attached to penultimate whorl and bearing prominent hollow (tubular) basal keel; lip continuous, thickened, duplicate, with inner lip narrower, slightly produced, and outer lip expanded, slightly reflected. Basal keel corresponds to a groove within aperture; keel widens at junction with lip, forming a hemispherical opening, located well to the left and above lowest point of lip (Fig. 6A, C, E). Prominent hemispherical notch on inner margin of lower palatal lip (Fig. 6A). Both paratypes show traces of the strong collabral striae characteristic of extant *Tortulosa* (Fig. 6H–J). Shell surface of holotype and two paratypes eroded in places to reveal traces of underlying axial crossed-lamellar microstructure. Holotype also shows traces on surface of lip of underlying crossed-lamellar microstructure consisting of fine, close lines that run across the thickened surface and at right angles to the inner and outer margins of the lip.

Remarks. The current distribution of *Tortulosa* is disjunct: 29 species are restricted to Sri Lanka or the Western Ghats of India, one species (*T. tortuosa* (Férussac, 1821)) occurs in the Nicobars, and another (*T. tweedei* (Tomlin, 1948)) on the Malay Peninsula (Gude 1921; Tomlin 1928, 1948; van Benthem Jutting 1960; Hemmen & Hemmen 2001; Maassen 2001; Raheem *et al.* 2014). *Tortulosa naggsi* sp. nov. falls within the range in shell morphology and size of extant *Tortulosa*. As in the South Asian species (subgenus *Eucataulus* Kobelt, 1902; Fig. 6K–N), the terminal part of the body whorl is fully attached to the penultimate whorl, whereas in *T. tortuosa* and *T. tweedei* it is detached (subgenus *Tortulosa*; see Kobelt 1902, and Fig. 6O–Q). The position of the opening of the basal keel in *T. naggsi* sp. nov. is similar to that in the Indian species *T. albescens* (Blanford, 1880), *T. costulatus* (Blanford, 1880) and *T. recurvata* (Pfeiffer, 1862) (Fig. 6N). In other extant species of *Tortulosa* the basal keel opens at or just slightly left of the centre of the basal lip (Fig. 6K, M). The only character unique to *T. naggsi* sp. nov. is the notch on the lower palatal lip (Fig. 6A). Two extant Sri Lankan species, *T. greeni* (Sykes, 1899) and *T. eurytrema* (Pfeiffer, 1854), also have a notch on the palatal edge of the lip, but this is on the upper palatal side (Fig. 6K, M). A similarly positioned but less obvious notch is found in *T. tortuosa* (Férussac, 1821) and *T. tweedei* (Tomlin, 1948) (Fig. 6Q). Hang Mon lies well to the north-east of the current range of *Tortulosa*, but within the current range of other extant pupinids, most notably *Schistoloma* Kobelt, 1902, which ranges from North-east India into South-east Asia (Kobelt 1902; Tumpeesuwan & Panha 2008). The shell of *Schistoloma* is very similar to *Tortulosa* but lacks the internally grooved basal keel.

Discussion

Globally, the earliest putative records of Cyclophoroidea are from the European Mesozoic (e.g. Late Cretaceous: Hrubesch 1965; Late Jurassic–Early Cretaceous*:* Bandel 1991). Extinct genera that are recognizably similar in adult shell morphology to Recent tropical cyclophoroideans are known from the European Late Cretaceous, Paleocene and Eocene (Wenz 1938–1939; Fabre-Taxy 1959). These include five supposed species of *Cyclophorus* from the latest Cretaceous to early Paleocene of

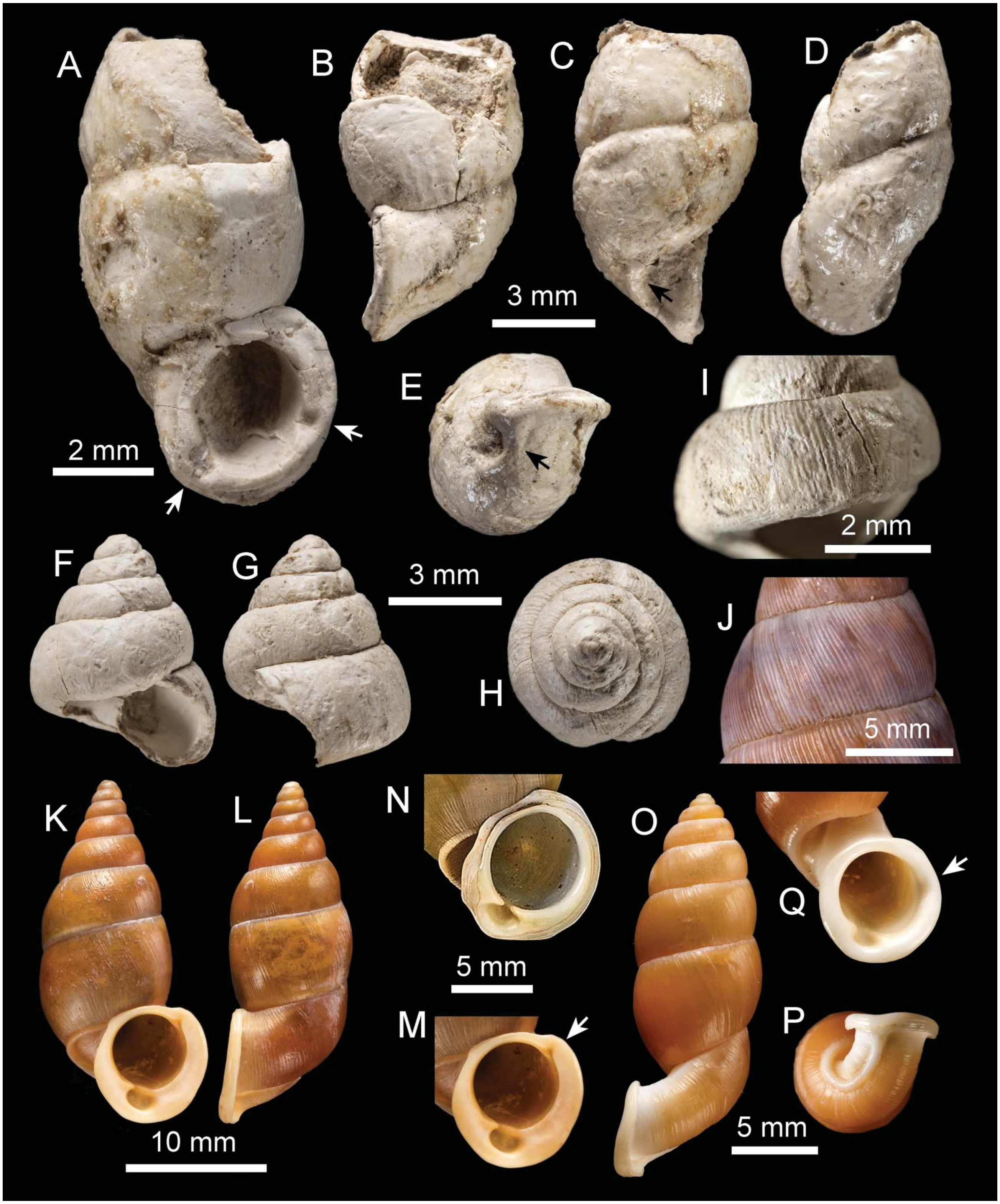

Figure 6. **A–I,** *Tortulosa naggsi* sp. nov.: **A–E,** holotype, GPIT/GA/05088, with the opening of the basal keel and lower palatal notch indicated by white arrows and the basal keel by black arrows; **F–I,** paratype, GPIT/GA/05089, showing traces of the strong collabral striae (**H, I**). **J,** collabral striae of the extant Sri Lankan species *T. austeniana* (Benson, 1853), possible syntype, NHMUK 1912.08.16.312. **K–M,** the Recent species *T. eurytrema* (Pfeiffer, 1854), NHMUK 1906.05.05.42/1, a species characterized by a notch on the upper palatal lip (shown by a white arrow) and a slightly off-centre opening to the basal keel. **N,** the extant species *T. recurvata* (Pfeiffer, 1862), NHMUK 1906.05.05.47/1, with the opening of the basal keel in a similar position to that of *T. naggsi* sp. nov. **O–Q,** the Recent species *T. tweedei* (Tomlin, 1948), NHMUK 20060334/1, note the detached terminal part of the last whorl (**O**, compare with **L**), the ventral surface of the shell with the prominent basal keel (**P**) and the faint notch on the upper palatal lip (shown by the white arrow in **Q**).

France (Fabre-Taxy 1959). On the basis of the figures provided by Fabre-Taxy, three of these, *C. heliciformis* (Matheron, 1832), *C. luneli* (Matheron, 1842) and *C. galloprovincialis* (Matheron, 1842), appear to be broadly similar to Recent *Cyclophorus*, but critical study of the fossil material is needed. The occurrence of tropical land snails in Europe up to the terminal Eocene corresponds with the prevalence of greenhouse conditions across Europe during much of the Late Cretaceous, Paleocene and Eocene (e.g. Huyghe *et al.* 2015). The substantial drop in temperature recorded for the Eocene–Oligocene boundary (Hren *et al.* 2013; Huyghe *et al.* 2015) culminated in the development of a large-scale Antarctic ice sheet (e.g. Lear *et al.* 2008). This change is considered to have caused major extinctions of terrestrial plants and animals in Europe (e.g. Prothero 1994) and may have driven most of the European cyclophoroidean lineages to extinction. In this respect, it is noteworthy that the extant European cyclophoridean fauna is composed of primarily European, warm- to cool-temperate genera. These appear in the fossil record for the first time in the Eocene (*Platyla* Moquin-Tandon, 1856; Kadolsky 2008), Oligocene (*Acicula* Hartmann, 1821; Kadolsky 2008) or Miocene (*Caspicyclotus* Forcart, 1935; Stworzewicz 1995).

In comparison to the European fossil record, the earliest known occurrences of Cyclophoroidea in South and South-east Asia date from the Late Pleistocene to Mid Holocene (< 0.2 Ma) (Deraniyagala 1956; Gorman 1971; Rabett *et al.* 2009, 2011; Conrad *et al*. 2013; Kulatilake *et al.* 2014). These records are mainly of *Cyclophorus*, but a few other cyclophoroidean genera, all extant, have also been reported, e.g. the cyclophorids *Cyclotus*, *Scabrina* and *Rhiostoma*, and the pupinid *Pupina* Vignard, 1829 (Gorman 1971; Rabett *et al.* 2011; Conrad *et al.* 2013). In this context, the data we present here on fossil cyclophoroideans from the early Miocene (23–21 Ma) of Northern Vietnam are of major importance. South and South-east Asia is the centre of extant cyclophoroidean diversity, and these fossils are the earliest cyclophoroideans currently known from the region. Moreover, the Hang Mon fossils are among the earliest cyclophoroideans known from the tropics as a whole. Despite the widespread distribution of Recent Cyclophoroidea across the forested tropics, the tropical fossil record for the group is sparse prior to the Pleistocene (but see Pickford 1995 on the Neogene fossil record of East Africa). The only reliable record of comparable age to the Hang Mong fossils is the early Miocene record of the extant genus *Maizania* Bourguignat, 1889 (Family Maizaniidae) from Meswa Bridge, Kenya (22.5–19.5 Ma, Pickford 1995).

There are a handful of other published records of tropical fossil cyclophoroideans of a similar age (Woodring *et al*. 1924; Torre *et al*. 1942; Yen 1952; Parodiz 1969; Goodfriend 1993). However, the taxonomic status of Parodiz's (1969) record of *Poteria* Baird, 1850 *sensu lato* (Family Neocyclotidae) from the early Miocene of Ecuador is uncertain, and *Pseudarinia* Yen, 1952 from the Late Cretaceous of Wyoming is not a cyclophoroidean (it has recently been classified as a member of the pulmonate Family Subulinidae; see Isaji 2010). *Incerticyclus bakeri* Simpson, 1895 and the other Jamaican fossil neocyclotids treated by Torre *et al.* (1942) as being Miocene in age are now considered to be Pliocene or younger (Goodfriend 1993; G. Rosenberg, pers. comm.). The Miocene fossil *Crocidopoma* Shuttleworth, 1857 (Family Neocyclotidae) reported from Haiti (Woodring *et al.* 1924) has not been described or figured and thus cannot be evaluated.

The Hang Mon fossils of *Cyclophorus*, *Alycaeus* and *Tortulosa* extend the stratigraphical range of these genera by more than 20 million years. These fossils are of potentially great value for calibrating molecular phylogenies of the Cyclophoroidea; interest in the molecular systematics of cyclophorideans has been growing in recent years (e.g. Webster *et al.* 2012; Nantarat *et al.* 2014a). If used in combination with other well-dated fossils (e.g. fossils of extant European genera) and molecular and/or palaeogeographical calibration methods (Kumar & Hedges 2016; Landis 2016), the Hang Mon fossils could substantially advance understanding of the palaeobiogeography and diversification of this major pan-tropical group of land snails.

The current distribution of the Alycaeinae contrasts with that of the Cyclophorini and Pupinidae. Apart from a handful of species in the Western Ghats of India and the Andaman and Nicobar islands, the Alycaeinae are confined to Madagascar, North-east India and South-east Asia (Kobelt 1902; Gude 1921; Wenz 1938; Kuroda 1943; Emberton 2002; Balashov & Griffiths 2015). The most likely interpretation of this pattern is that the Alycaeinae are Gondwanan in origin and dispersed into South-east Asia after India accreted to South-east Asia, as has been inferred for some plant and other animal taxa (Conti *et al.* 2002; Gower *et al.* 2002; Klaus *et al.* 2010; Li *et al.* 2013). A Laurasian origin followed by long-distance dispersal to Madagascar (as inferred for some plant groups; Buerki *et al.* 2013; Federman *et al.* 2015) seems less plausible (but see Gittenberger *et al*. 2006). The current distribution of the Cyclophorini extends from the Afrotropics (including Madagascar and other islands of the Western Indian Ocean) through Eurasia into Oceania (Kobelt 1902; Wenz 1938; Stanisic 1998). Diversity is concentrated in South and South-east Asia, with just two temperate zone Eurasian genera: the troglodytic *Pholeoteras* Sturany, 1904 (two species) of southern Europe, and the forest-living *Caspicyclotus* (one species) that ranges from eastern Georgia to northern Iran (Kobelt 1902; Wenz 1938; Štamol *et al.* 1999; Stworzewicz 1995). The Pupinidae have a more restricted distribution, ranging across tropical Asia and Oceania as far as New Zealand (Kobelt 1902; Wenz 1938; Stanisic 1998; Barker 2005). With putative fossil representatives from the Late Cretaceous to early Paleocene of Europe (Wenz 1938; Fabre-Taxy 1959; Hrubesch 1965), Recent Cyclophorini and Pupinidae may belong to clades that have a Laurasian rather than Gondwanan origin, with a history dating back to at least the Mesozoic.

Extant Cyclophoridae and Pupinidae typically inhabit tropical forests (tropical rainforests and monsoon forests), but apart from a few recent studies (e.g. Emberton & Pearce 1999; Raheem *et al.* 2009; Liew *et al.* 2010; Vermeulen *et al.* 2015), detailed data on the geographical distributions and habitat and bioclimatic ranges of individual taxa are scarce. Assuming that the fossil taxa were broadly similar in their ecology to extant cyclophorids and pupinids, tropical forest should have occurred in the vicinity of Hang Mon in the early Miocene. This inference is consistent with available palaeoclimatic data: a warm-temperate climate was prevalent during the late Oligocene and earliest Miocene across Northern Vietnam and other parts of northern Indochina, with a shift to a wetter, warmer tropical monsoonal climate regime from the beginning of the Miocene (Morley 2000, 2012). Note also that while none of the mammals documented from the earliest Miocene of Hang Mon represent extant genera (Prieto *et al.* in press), they belong to families (Rhinocerotidae, Tragulidae, Suidae with three, two and one fossil species, respectively) with living representatives in tropical South-east Asia (e.g. Wilson & Reeder 2005). It is tempting to speculate that the faunistic similarities between the earliest Miocene of Hang Mon and the present day are indicative of the sustained presence of tropical forest since the earliest Miocene, and that in this part of South-east Asia, biome stability has led to the constant accumulation of biodiversity over time (Stebbins 1974).

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Supplemental data

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Table 1. List of fossil material examined with relevant registration numbers and other details. All fossil material is currently deposited at the Paläontologische Sammlung der Universität Tübingen, Germany.

Taxon	Type status and specimen number	Registration number	Physical state and likely growth stage	Number of shells/fragments
Cyclophorus hangmonensis	Holotype	GPIT/GA/05086	Largely intact (adult)	1
	Paratype 1	GPIT/GA/05083	Largely intact (adult)	1
	Paratype 2	GPIT/GA/05077	Spire and part of body whorl intact; apex worn (adult/sub-adult)	1
	Paratype 3	GPIT/GA/05079	Spire and part of body whorl intact; apex worn (adult/sub-adult)	1
	Paratype 4	GPIT/GA/05085	Spire and part of body whorl intact; apex not worn (adult/sub-adult)	1
	-	GPIT/GA/05078	Spire and most of body whorl intact (adult/sub-adult)	1
	-	GPIT/GA/05080	Largely Intact, apart from apex (adult)	1
	-	GPIT/GA/05081	Part of spire and body whorl (adult/sub-adult)	1
	-	GPIT/GA/05082	Largely Intact, apart from apex (adult)	1
	-	GPIT/GA/05084	Largely intact (adult)	1
	-	GPIT/GA/05087	Spire and most of body whorl intact (adult/sub-adult)	1
	-	GPIT/GA/05099	Earlier whorls of three separate shells	3
Alycaeus sonlaensis	Holotype	GPIT/GA/05092	Largely entire shell (adult)	1
	Paratype 1	GPIT/GA/05093	Shell fragment (adult)	1
	Paratype 2	GPIT/GA/05094	Earlier whorls	1
	Paratype 3	GPIT/GA/05095	Earlier whorls and large part of body whorl (adult/sub-adult)	1
	Paratype 4	GPIT/GA/05096	Earlier whorls and part of body whorl	1
	Paratype 5	GPIT/GA/05097	Terminal part of body whorl (adult)	1
	-	GPIT/GA/05098	Various shell fragments	30
Tortulosa naggsi	Holotype	GPIT/GA/05088	Only basal part of shell intact (adult)	1
	Paratype 1	GPIT/GA/05089	Apical whorls only (adult/sub-adult)	1
	Paratype 2	GPIT/GA/05100	Intact shell (juvenile)	1
Cyclophoroidea sp.	Specimen 1	GPIT/GA/05090	Earlier whorls (adult/sub-adult)	1
	Specimens 2-8	GPIT/GA/05091	Earlier whorls of seven separate shells	7