The oldest known cyclophoroidean land snails (Caenogastropoda) from Asia

Dinarzarde C. Raheem a, Simon Schneider b,*, Madelaine Böhme c, Davit Vasilian d,e and Jérôme Prietto f,g

aLife Sciences Department, The Natural History Museum, London SW7 5BD, UK; bCASP, 181A Huntingdon Road, Cambridge CB3 0DH, UK; cSenckenberg Center for Human Evolution and Paleoecology, University of Tübingen, Institute for Geoscience, Sigwartstraße 10, 72076 Tübingen, Germany; dDepartment of Geosciences, University of Fribourg, Chemin du musée 6, 1700 Fribourg, Switzerland; eJURASSICA Museum, Route de Fontenais 21, 2900 Porrentruy, Switzerland; fBayerische Staatssammlung für Paläontologie und Geologie; gDepartment of Earth and Environmental Sciences, Palaeontology & Geobiology, Ludwig-Maximilians-University Munich, Richard-Wagner-Strasse 10, 80333 München, Germany

(Received 4 April 2017; accepted 26 July 2017; published online 28 December 2017)

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.

http://zoobank.org/urn:lsid:zoobank.org:pub:B0C2C715-1184-4930-BD94-21ED1E9281B4

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; Megalomatimatidae 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,
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 cyclo-
phoroideans are from the Late Pleistocene to Mid Hol-
cene of South and South-east Asia (Deraniyagala 1956;
2013; Kulatilake et al. 2014). We report here on the fos-
sils of four cyclophoroidean genera, the cyclophorids
Cyclophorus Montfort, 1810 and Alycaeus Baird, 1850,
the pupinid Tortulosa Gray, 1847, and a species of uncer-
tain 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 cyclophor-
oid fossil record, and speculate on the palaeobiogeog-
raphy 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
Basin, resting unconformably on Middle Trias-
sic 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
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 taxo-
nomically diverse terrestrial gastropod assemblage, which
also includes various Pulmonata sensu Bouchet & Rocroi
(2005) that have not been studied in detail so far. The gas-
tropods 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 descrip-
tions below). Most specimens, however, were fragmented
and distorted during sediment compaction. The periostrac-
um most likely was lost before or during deposition, and
the shells show traces of the corrosion typical of dead gas-
tropod shells that have been exposed to a tropical climate
for a prolonged period.

The gastropods were collected during two field excur-
sions in 2009 and 2011. The fossilerous siltstones were
broken up in the field and screened for gastropods, which
were usually partly enclosed by matrix. Larger, more frag-
ile 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 hydro-
gen 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 Paliontologische 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)


**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, Son 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 naggasi* 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 stenophilus* Möllendorf’ (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. ngakingensis* 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 stenophilus* 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. nilagricus* (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 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; Rihová 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 cross-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 Lagochilus 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 Alyceaus Baird, 1850

Type species. Alyceaus 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 Alyceaus or any other Alycaeinae. Shell shape in Recent Alyceaus 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.

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

Diagnosis. Very small (shell width approximately 4 mm), depressedly turbinate and widely umbilicate species of Alyceaus 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 Son 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, Son 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 (Pall-Gergely et al. 2016) and need taxonomic revision. The extant Asian genus Alyceaus 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. Pall-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. Alyceaus cristatus
Mollendorff, 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 & Mollendorff, 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 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).
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 whors; J, paratype, GPIT/GA/05095, early whors 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* M"ollendorff, 1886b, paratype, NHMUK 1891.03.17.799, black arrow indicates sutural tube. L–N, the Recent *A. cristatus* M"ollendorff, 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)


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 Cyclopus 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 Féroussac, 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 Féroussac (1821, p. 61) as Helix (Cochlodina) tortuosa. Although Chemnitz’s name was published before Féroussac’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).

Férrussac’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’. Férrussac 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 description. All subsequent 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 pugiform 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 Chău 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. albecens* (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 cyclophoroids are known from the European Late Cretaceous, Paleocene and Eocene (Wenz 1938–1939; Fabre-Taxi 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. galloprensis (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 cyclophoroidean 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 (Acula Hartmann, 1821; Kadolsky 2008) or Miocene (Cascicyclus 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 (c. 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 Rhistoma, 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 cyclophoroideans has been growing in recent years (e.g. Webster et al. 2012; Nantarath 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 Alycaenidae 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 Alycaenidae 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 Alycaenidae 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 troglobytic 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; Stamol 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 Pupiniidae 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 Pupiniidae 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; 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).

Acknowledgements

We would like to thank the following people: N. V. Hung, D. D. Quang and P. D. Pha for support in Vietnam; H. Taylor for imaging the fossils; M. Biszczyzuk for preparing the map of Hang Mon; B. Pål-Gergely for generously sharing his work on the taxonomy of the Vietnamese Alytidae, and providing images; K. and P. von Oheimb for sharing his work on the taxonomy of the Vietnamese Alytidae, Suidae, 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).

Deutsche Forschungsgemeinschaft grant numbers BO 1550/11-1 & 2. This paper contributes to CNRS project GDRI 0849 PalBioDivASE.

Funding

Deutsche Forschungsgemeinschaft [BO 1550/11-1 & 2].

Supplemental data

Supplemental material can be accessed online at: https://doi.org/10.1080/14772019.2017.1388298

References


Bianford, W. T. 1863. Contributions to Indian malacology. No. IV. Descriptions of land shells from Ava, and other parts of


Kantor, Y. I., Vinarski, M. V., Schleyko, A. A. & Sysoev, A. V. 2010. On-line catalogue of continental (fresh-, brackish-


Oldest known cyclophoroidean land snails from Asia


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.

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