



FIRST RECORDS OF FRESHWATER RISSOOIDEAN GASTROPODS FROM THE PALAEOGENE OF SOUTHEAST ASIA

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ABSTRACT

This paper provides the first records of freshwater rissooidean gastropods from the Palaeogene (uppermost Eocene to Lower Oligocene) of northern Vietnam (Cao Bang Basin). The most abundant element of the assemblage is the new genus *Bacbotricula* (Pomatiopsidae: Triculinae²), comprising numerous well-preserved specimens belonging to two new species, *B. nhamaygachensis* and *B. dongbangensis*. The assemblage also contains poorly preserved specimens of two other species, one of which is tentatively assigned to the Bithyniidae. The Cao Bang assemblage is among the earliest Cenozoic freshwater gastropod faunas described from Southeast Asia and *Bacbotricula* is the only pomatiopsid that has been recorded for the Palaeogene. The occurrence of *Bacbotricula* in northern Vietnam during this period of time suggests that the palaeo-Red River may have served as an early dispersal corridor for the Triculinae. The gastropods likely lived on deltaic plains in Lake Cao Bang and were preyed upon by cyprinid fishes.

INTRODUCTION

The extant freshwater rissooidean gastropods of Southeast Asia and adjacent southern China are relatively well documented in a series of monographs starting in the second half of the nineteenth century (e.g. Pfeiffer, 1862; Crosse & Fischer, 1863, 1876; Morelet, 1875; Deshayes & Jullien, 1876; Poirier, 1881; Heude, 1882–1890; Morlet, 1886, 1889; Watebled, 1886; Möllendorff, 1888; Fischer, 1891; Neumayr, 1898; Rao, 1928; Temcharoen, 1971). These monographs include surveys of the molluscan faunas of Thailand (Brandt, 1974) and Vietnam (Dang, Thái & Phum, 1980). More recent studies have investigated the anatomy and phylogeny of regional representatives of several rissooidean families, including the Stenothyridae (Davis & Hoagland, 1979; Davis *et al.*, 1986b, 1988) and Amnicolidae (Davis & Kang, 1995; Davis & Rao, 1997; Wilke *et al.*, 2000). The regionally diverse Pomatiopsidae has been a focus of taxonomic, evolutionary and (palaeo-)biogeographic studies, in part because certain members of this family are potential intermediate hosts of the trematodes that cause human schistosomiasis (e.g. Brandt & Temcharoen, 1971; Davis, 1979, 1980, 1992; Davis *et al.*, 1999; Wilke *et al.*, 2000; Attwood *et al.*, 2003).

On the other hand, there is little published evidence on the Cenozoic freshwater gastropods of continental East Asia.

Gastropods have been described from Lower Oligocene to Pleistocene deposits of China (e.g. Mansuy, 1918; Odhner, 1930; Yen, 1935) and detailed inventories of the fossil freshwater molluscs of China (Yen, 1943) and East Asia (including Japan; Suzuki, 1949) have been compiled. The variation of Eocene *Pachymelania* from Myanmar has been studied (Kotaka & Uozumi, 1962) and a Pleistocene lacustrine gastropod fauna from that country has been described (Annandale, 1919). Eocene and Miocene freshwater gastropods (*Viviparus*, *Melanoides*) from southern Thailand have been used in stable isotope studies (Udomkan *et al.*, 2003; Ratanasthien, Takashima & Matsubaya, 2008) and several assemblages dominated by viviparids have been reported from the Miocene of northern Thailand (Oyama, 1973; Songtham *et al.*, 2005; Ugai, Ratanasthien & Silaratana, 2006).

Gastropods have also been documented from the Palaeogene of northern Vietnam. Three species of viviparids from the Early Oligocene (?) Rinh Chua Formation of the Na Duong Basin (Lang Son Province, North Vietnam) were illustrated by Khuc (1991) and listed by Dzanh (1995, 1996, 1998) and Thuy (2001). Dzanh (1996) also reported a species of *Brotia* from the same stratum. The viviparids from the Rinh Chua Formation are indeterminate at genus and species level because of poor preservation. Furthermore, the species

erroneously assigned to the North American genus *Tulotoma* (Khuc, 1991) may in fact represent a thiarid (? *Tarebia*; S.S., personal observation). These taxa were also found during the course of our excavations at Na Duong Coalmine and most of them have been figured by Böhme *et al.* (2011). Viviparids and ? *Brotia* were also recorded for the underlying Na Duong Formation. However, none of the Gastropoda from the Na Duong Basin are preserved sufficiently well to be distinguished at species level.

One of the newly described fossil gastropod species from the Na Duong Formation of the Cao Bang Basin has previously been figured by Böhme *et al.* (2011: fig. 10A: Hydrobiidae indet.). The present study provides formal taxonomic descriptions of these gastropods. The systematic relationships of the snails are discussed and evaluated with regard to the early Cenozoic dispersal routes of East Asian freshwater Rissooidea. Moreover, the gastropods provide valuable data for the palaeoecological interpretation of the Cao Bang fossil assemblage.

GEOLOGICAL SETTING

The Cao Bang Basin is a Cenozoic pull-apart basin in northern Vietnam close to the Chinese border (Fig. 1). The basin is situated at the Cao Bang–Tien Yen Fault, a left-lateral shearing, NW–SE trending strike-slip fault (Pubellier *et al.*, 2003) that parallels the major fault system of the area, i.e. the Red River Fault Zone (e.g. Leloup *et al.*, 1995; Morley, 2002; Searle, 2006; Hoang *et al.*, 2009). The precise timing of the initiation (Eocene–Oligocene; Clift & Sun, 2006; Aitchison, Ali & Davis, 2007) and duration (Oligocene–Miocene, cumulative estimates 34–15.5 Ma; Gilley *et al.*, 2003; Zhen *et al.*, 2006; Zhu, Graham & McHargue, 2009) of the tectonic movements along the Red River Fault Zone are still debated. Furthermore, there are conflicting opinions regarding the age of the sedimentary infill of Cao Bang Basin (for a summary, see Böhme *et al.*, 2011), which is today drained by the Bang River and is part of the upper Pearl River catchment.

The Cao Bang Basin extends for *c.* 65 km² (Wysocka, 2009; Böhme *et al.*, 2011) and its base and margins are composed of Palaeozoic and Mesozoic rocks. The basin infill consists of Cenozoic sediments which are exposed in road cuts, construction sites and brickyards in and around the city of Cao Bang. The lower, fluvial–terrestrial portion of these sediments is assigned to the Cao Bang Formation, while the upper portion, composed of lacustrine and lacustrine-deltaic deposits, is assigned to the Na Duong Formation (Thanh & Khuc, 2006). These assignments are entirely based on a comparison with the Na Duong Basin, which is structured by the same fault zone and located about 120 km SSE of Cao Bang. The type locality of the Na Duong Formation is relatively well dated as Oligocene by palynology (Dy, Trung & An, 1996; Trung *et al.*, 2000; Böhme *et al.*, 2011). Several recently collected specimens of fossil Anthracotheriidae (Mammalia) from these deposits indicate a Late Eocene to Early Oligocene age (unpublished data from fieldwork in 2011). Unfortunately, there are no reliable stratigraphical data from the Cao Bang Basin.

Currently the most productive fossiliferous outcrop within the basin is an active brickyard in Cao Bang (N 22°40.72, E 106°15.23). The Na Duong Formation at this locality contains an autochthonous to parautochthonous assemblage of unionid bivalves (Schneider, Böhme & Prieto, *in press*), disarticulated skeletal remains of a remarkably rich fish fauna and the rissooidean gastropods described in this study. The two species of *Bacbotricula* n. gen. occur in great density in several of the horizons (Fig. 2; Böhme *et al.*, 2011).

MATERIAL AND METHODS

The material described in this paper was obtained from rock samples collected at the Cao Bang brickyard in 2008 and 2009. The clay and marl samples were dissolved in diluted hydrogen peroxide and wet-sieved down to a mesh width of 0.3 mm. The gastropods were picked from the resulting dried residues. Two gastropod species were sufficiently well preserved and abundant (>50 specimens each) to be described in detail. Several specimens of two other gastropods were also found.

Voucher material is deposited in the palaeontological collections of the Eberhard-Karls-Universität Tübingen, Institute for Geoscience, under accession numbers GPIT/GA/5013–5032 and GPIT/BI/5575.

SYSTEMATIC DESCRIPTIONS

The systematic arrangement follows Bouchet & Rocroi (2005).

Superfamily Rissooidea Gray, 1847

Family POMATIOPSIDAE Stimpson, 1865

Subfamily TRICULINAE Annandale, 1924

Remarks: The systematic placement of the new fossil genus described below is tentative because family and genus group definitions of freshwater Rissooidea are predominantly delineated by soft-part anatomy and/or molecular data (e.g. Davis, 1979; Davis *et al.*, 1994; Wilke *et al.*, 2001).

Genus *Bacbotricula* Neubauer & Schneider new genus

Type species: *Bacbotricula nhamayachensis* Neubauer & Schneider n. sp.

Etymology: The genus name is a combination of the Vietnamese denomination of northern Vietnam, 'Bắc Bộ', and the type genus of the Triculinae, *Tricula* Benson, 1843.

Diagnosis: Protoconch low-trochiform; no ornamentation discernable; diameter of initial whorl *c.* 350 µm. Shell conical, with apical angle of *c.* 40° and weakly incised sutures, comprising five to six whorls in total. Height of last whorl *c.* 60% of total shell height. Teleoconch whorls ornamented with one or two distinct, cord-like keels emerging from second to third whorl. Keel(s) and suture subparallel (resulting from allometric growth), producing slightly increasing offset of (lower) keel and lower suture. Aperture broadly ovate, with distinct, blunt angulation between columellar and palatal margins. Umbilicus closed.

Remarks: The diameter of the initial shell whorl of *Bacbotricula* (350 µm) falls within the dimensions known for other triculines (e.g. *Tricula bollingi*, 350 µm; *T. bamboensis*, 375 µm; *T. hudi-quanensis*, 360 µm; *T. gregoriana*, 340 µm; *Neotricula jinghongensis*, 400 µm; *Kunmingia kunmingensis*, 400 µm; Davis *et al.*, 1984, 1986a; Davis, Rao & Hoagland, 1986c).

Several triculine genera, i.e. *Paraprososthenia* Annandale, 1919 (Pleistocene, Myanmar), *Karelainia* Davis, 1979 (extant, Mekong basin, Thailand and Laos) and *Neoprososthenia* Davis & Kuo in Davis *et al.*, 1984 (extant, Mekong basin, Thailand) closely resemble *Bacbotricula* in also having turreted shells with spiral sculpture. However, these genera differ from *Bacbotricula* in having nodes, spines, serrations or axial ornamentation elements and lacking a distinct angulation between the columellar and palatal margins (Davis, 1979; Davis *et al.*, 1984). Moreover, the protoconchs of *Karelainia* and several species of *Neoprososthenia* (Davis *et al.*, 1984) have spiral sculpture whereas the protoconchs of *Bacbotricula* are

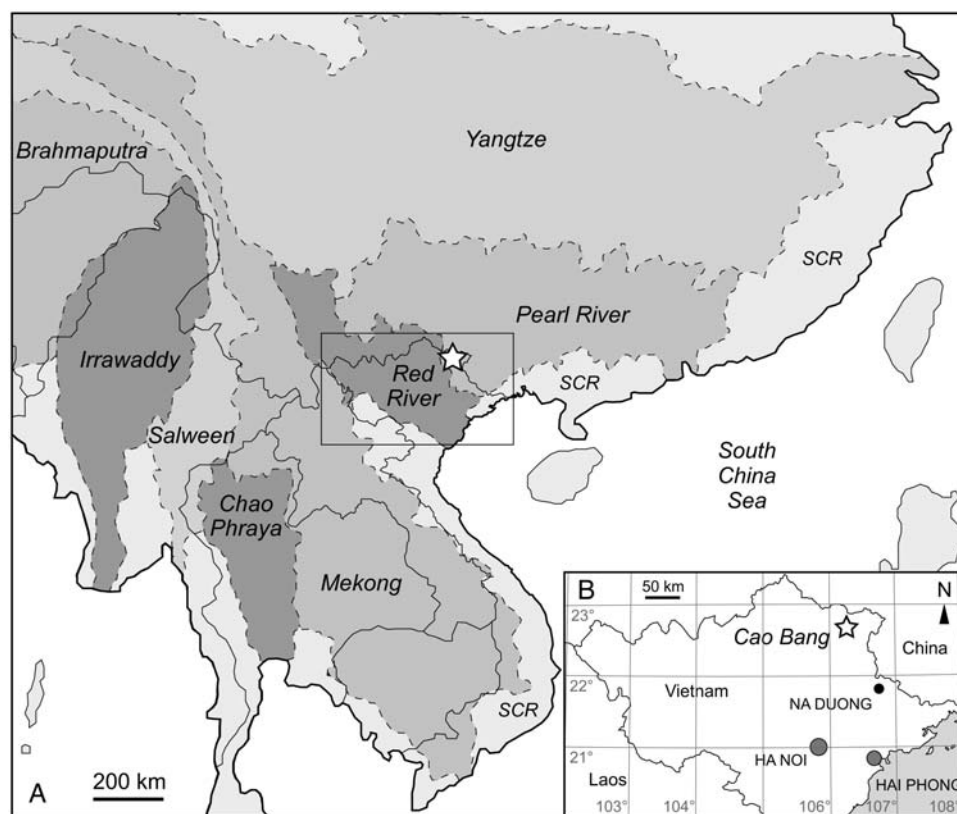


Figure 1. **A.** Geographic overview of SE Asia showing catchment areas of major rivers. Abbreviation: SCR, small coastal rivers. **B.** Detailed map providing overview of the study region. The locality of Cao Bang is marked by a star.

smooth. The protoconch of *Paraprososthenia* remains unknown. *Bacbotricula* is also geographically separated from these other taxa, which are/were distributed in the Irrawaddy/Salween and Mekong River (*Karelainia*, *Neoprososthenia*) basins, respectively (see Fig. 1A and Discussion section below).

Two species are included in the new genus, *B. nhamaygachensis* and *B. donghangensis*.

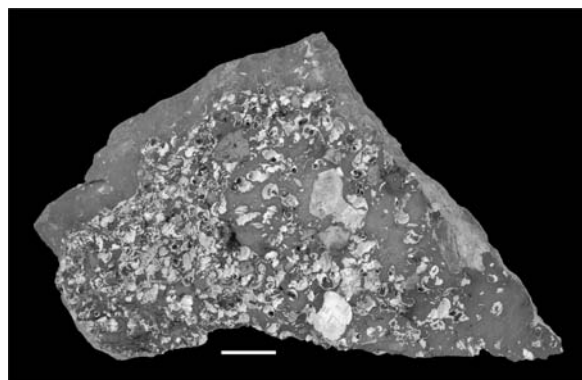


Figure 2. Limonitic concretion showing mass accumulation of *Bacbotricula nhamaygachensis*. Cao Bang brickyard section; uppermost Eocene to Lower Oligocene (GPIT/GA/5013). Scale bar = 1 cm.

***Bacbotricula nhamaygachensis* Neubauer & Schneider
new species**

(Fig. 3A, B, E–G, I)

Hydrobiidae indet.—Böhme *et al.*, 2011: fig. 10A; tab. 1.

Types: Holotype: GPIT/GA/5014 (Fig. 3A; 5.7 × 2.9 mm); paratype 1: GPIT/BI/5575 (Fig. 3B; 6.5 × 4.0 mm); paratype 2: GPIT/GA/5015 (Fig. 3E); paratype 3: GPIT/GA/5016 (Fig. 3F); paratype 4: GPIT/GA/5017 (Fig. 3G); paratype 5: GPIT/GA/5018 (Fig. 3I). Type locality: Cao Bang brickyard section, eastern Cao Bang Basin, Vietnam (N 22°40.72, E 106°15.23); lacustrine layers of the Na Duong Formation [Latest Eocene to Early Oligocene (?)].

Etymology: From the Vietnamese expression for ‘brickworks’, ‘nhà máy gạch’.

Material examined: 51 shells, mostly spire fragments.

Diagnosis: *Bacbotricula* having two spiral keels, one central and one at base of whorl. Both keels originate on the third shell whorl.

Description: Height: 4.5–6.5 mm; width: 2–4 mm; apical angle: 30–45°. (Since the specimens are usually fragmented and often also deformed, these are only approximate size ranges.) Protoconch without discernable ornamentation, low-trochiform; transition to teleoconch obscured by poor preservation; diameter of initial whorl *c.* 350 µm. Shell slender conical

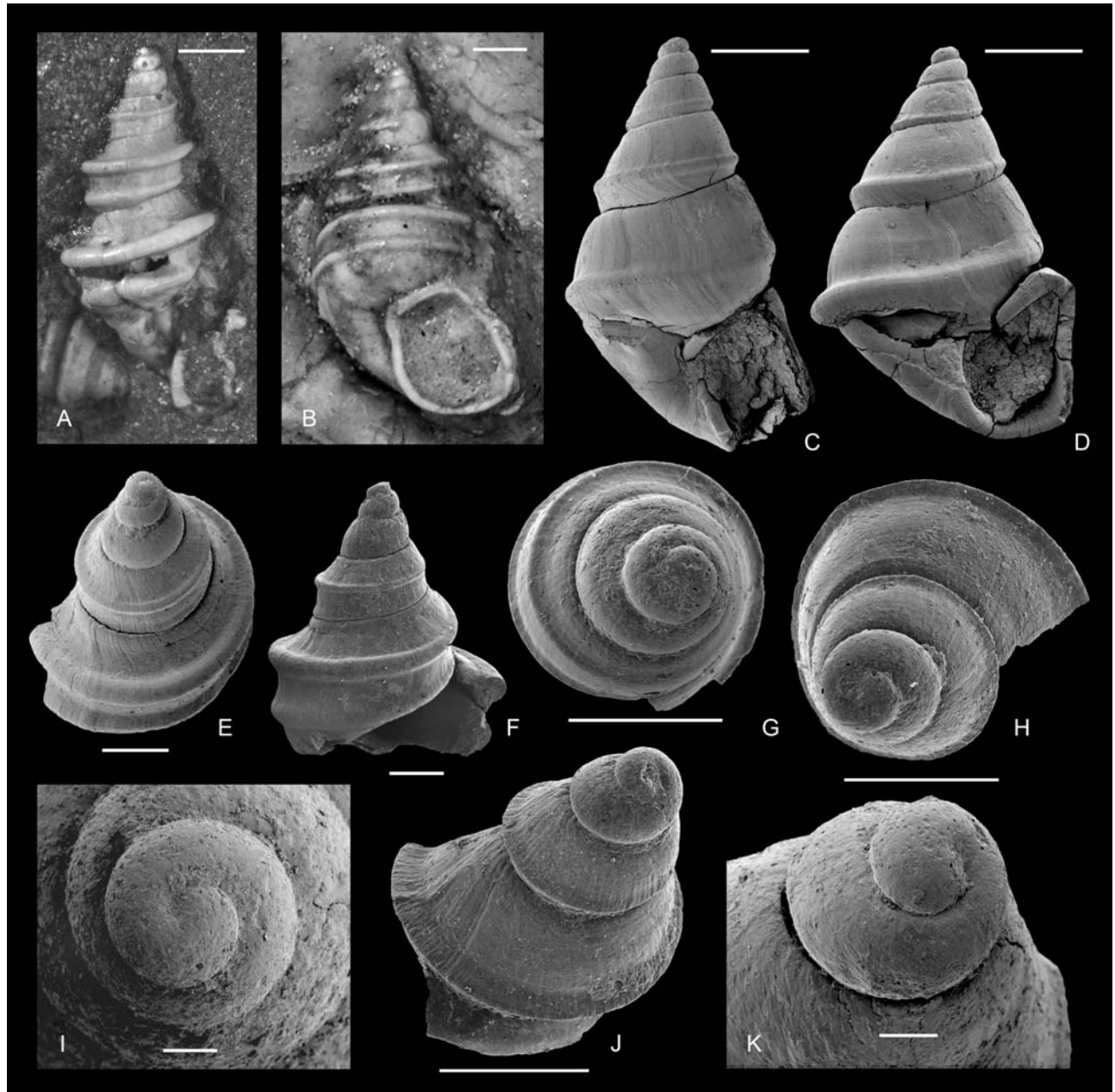


Figure 3. *Bacbotricula* n. gen. Cao Bang brickyard section; uppermost Eocene to Lower Oligocene. **A.** *B. nhamaygachensis* n. sp., holotype (GPIT/GA/5014). **B.** *B. nhamaygachensis*, paratype 1 (GPIT/BI/5575), with entire aperture preserved. **C.** *B. dongbangensis* n. sp., holotype (GPIT/GA/5019). **D.** *B. dongbangensis*, paratype 1 (GPIT/GA/5020). **E.** *B. nhamaygachensis*, paratype 2 (GPIT/GA/5015). **F.** *B. nhamaygachensis*, paratype 3 (GPIT/GA/5016). **G.** *B. nhamaygachensis*, paratype 4 (GPIT/GA/5017). **H.** *B. dongbangensis*, paratype 2 (GPIT/GA/5021). **I.** *B. nhamaygachensis*, paratype 5 (GPIT/GA/5018). **J.** *B. dongbangensis*, paratype 3 (GPIT/GA/5022). **K.** *B. dongbangensis*, paratype 4 (GPIT/GA/5023). Scale bars = 1 mm (**A–D**), 0.5 mm (**E–H, J**), 0.1 mm (**I, K**).

(apical angle *c.* 40°), comprising 5–6 whorls; height of last whorl *c.* 60% of total shell height. Early whorls moderately convex, smooth. Adult shells with slightly emergent band at top of whorl; adapical portion of whorl forming straight to slightly concave ramp, inclined *c.* 45° towards prominent, blunt keel at mid-height of whorl. Broad, shallow furrow below central keel transitioning smoothly into less pronounced but still distinct basal keel. Both keels originating on third whorl. Central keel originating as narrow, well rounded, closely adjoined cord, becoming gradually more prominent; adapical demarcation of keel flattened to slightly concave. Basal keel gradually emerging from lower suture, not appearing as distinct keel until fourth or fifth whorl. Growth rate of interkeel

distance slightly less than growth rate of whorl height (allometric growth), resulting in increasing distance between basal keel and suture. Keels broad and well rounded in adult shells. Sutures weakly incised. Growth lines distinct, faintly opisthocyrt. Aperture broadly ovate. Columellar and palatal margins forming distinct, blunt angle. Palatal and parietal margins forming faint, acute angle. Basal margin slightly swollen. Umbilicus closed.

Remarks: *Bacbotricula nhamaygachensis* is readily distinguished from *B. dongbangensis* (described below) by having two prominent keels. Moreover, the two keels in *B. nhamaygachensis* emerge from the third whorl, while the single keel in *B.*

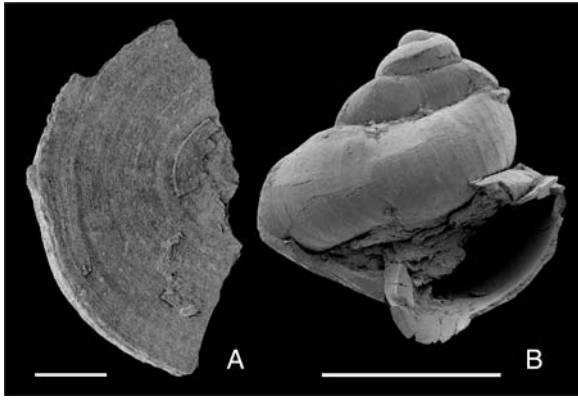


Figure 4. Bithyniidae sp. indet. Cao Bang brickyard section; uppermost Eocene to Lower Oligocene. **A.** Fragment of an operculum (GPIT/GA/5024). **B.** Deformed specimen (GPIT/GA/5025). Scale bars = 1 mm.

dongbangensis originates on the second whorl and is conspicuously more acute during early growth. No transitional forms were found.

***Bacbotricula dongbangensis* Neubauer & Schneider
new species**

(Fig. 3C, D, H, J, K)

Types: Holotype: GPIT/GA/5019 (Fig. 3C; 4.3 × 2.8 mm); paratype 1: GPIT/GA/5020 (Fig. 3D; 4.0 × 2.7 mm); paratype 2: GPIT/GA/5021 (Fig. 3H); paratype 3: GPIT/GA/5022 (Fig. 3J); paratype 4: GPIT/GA/5023 (Fig. 3K). Type locality: Cao Bang brickyard section, eastern Cao Bang Basin (N 22°40.72, E 106°15.23); lacustrine layers of the Na Duong Formation [Latest Eocene to Early Oligocene (?)].

Etymology: From the Vietnamese word for ‘delta’, ‘Đòng bằng’.

Material examined: 138 shells, mostly spire fragments.

Diagnosis: A species of *Bacbotricula* having a single keel positioned in lower third of whorl. Keel originating on second whorl.

Description: Height: 4–5 mm; width: 1.5–3 mm; apical angle: 30–40°. (As for *B. nhamayachensis*, these data represent only approximate size ranges.) Protoconch without discernable ornamentation, low-trochiform, with strongly convex whorls; transition to teleoconch obscured by poor preservation; diameter of initial whorl *c.* 350 µm. Adult shell conical (apical angle *c.* 35°) comprising 5–5.5 whorls; height of last whorl *c.* 60% of total shell height. Adapical portion of whorls (70–80% of whorl height) almost straight, steeply sloping towards single, prominent, but rather blunt keel; abapical portion of whorl almost straight, constricted near lower suture (outline frustate *sensu* Marwick, 1971). Keel gradually originating on second to third whorl; initially forming a narrow, relatively sharp crest; subsequently changing into a broad, rounded, cord-like bulge; marked by flatly rounded concavity at adapical side. Keel subparallel to suture; ratio of upper to lower whorl portion decreasing during ontogeny. Sutures weakly incised. Growth lines distinct; opisthocyrt adapically, prosocline below keel, resulting in slightly irregular sigmoidal curve. Aperture broadly ovoid. Columellar and palatal margins meeting at a distinct, blunt angle. Palatal and parietal margins meeting at a faint, acute

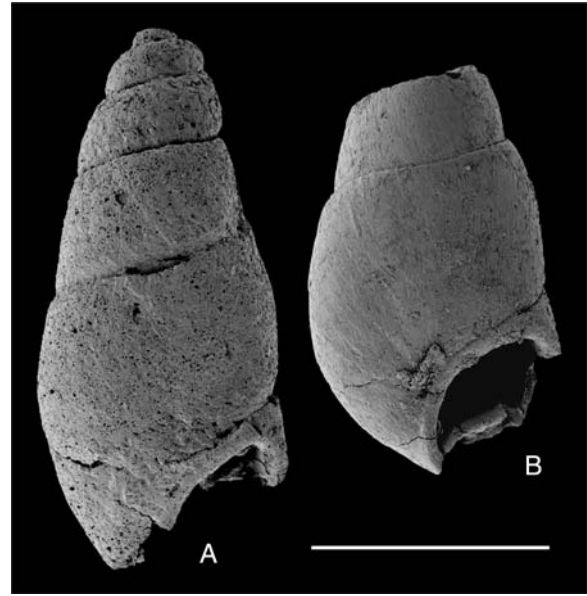


Figure 5. Rissooidea sp. indet. Cao Bang brickyard section; uppermost Eocene to Lower Oligocene. **A.** GPIT/GA/5026. **B.** GPIT/GA/5027. Scale bar = 1 mm.

angle. Entire margin of peristome slightly and constantly swollen. Umbilicus closed.

Family BITHYNIIDAE Gray, 1857

***Bithyniidae* sp. indet.**

(Fig. 4A, B)

Material examined: A single shell comprising four whorls and a fragment of an operculum.

Description: Protoconch low-trochiform; surface poorly preserved; transition to teleoconch indistinct. Shell broadly conical (apical angle *c.* 75°); strongly compressed; consisting of four moderately convex whorls. Sutures moderately incised. Aperture broken, with small anterior portion preserved; peristome sharp, slightly everted. Growth lines faint, prosocyr. Fragment of calcitic operculum showing distinct, concentric growth lines.

Remarks: These two specimens are classified within the Bithyniidae based on the presence of a calcified operculum and the gross shape of the shell fragment. The poor preservation of the specimens precludes better taxonomic resolution.

Family unknown

***Rissooidea* sp. indet.**

(Fig. 5A, B)

Material examined: Two shell fragments.

Description: Shell small (2–2.5 mm in height), ovoid, with obtuse apex. One specimen having apical portion preserved, but shell surface corroded. Early whorls strongly convex, becoming increasingly straight-sided with growth. Sutures weakly incised. Height of last whorl more than half of total shell height; whorl weakly angled at midpoint; base slightly convex. Aperture broken in both specimens; obliquely pyriform; umbilicus absent. Apertural lip blunt, but not thickened. Growth lines absent, presumably due to surface erosion.

Remarks: The size and shape of these shells suggest that they belong to the Rissoidae.

DISCUSSION

The two species of *Bacbotricula* described in this paper appear to be the earliest Cenozoic Pomatiopsidae yet recorded from East Asia. It is interesting to note that there is virtually no fossil record of the Pomatiopsidae from the Palaeocene to Pliocene, although older (Cretaceous) fossils have been reported from southern Africa and India (Davis, 1979). The Pomatiopsidae are thought to have originated on the former Gondwana supercontinent, where they split into the subfamilies Pomatiopsinae and Triculinae during the Mesozoic (Davis, 1979). The Triculinae were presumably introduced to Asia following the Indian-Asian collision (Davis, 1979) after the epicontinental seaway between India and Asia was finally closed, which likely occurred around the Eocene–Oligocene boundary (Aitchison *et al.*, 2007). Subsequent radiations within the Pomatiopsidae were mostly confined to long-lived lakes, springs and streams in the catchment areas of the large rivers of Southeast Asia (e.g. Annandale, 1919; Davis, 1979; Davis *et al.*, 1986a,c, 1992; Strong *et al.*, 2008). During the Palaeogene, large areas of southern China, Laos and northern Vietnam were drained by the palaeo-Red River that originated from the South Tibet Plateau (Clift *et al.*, 2008; Hoang *et al.*, 2009) and thus from an area very close to the Indian-Asian suture zone, where the triculine snails likely entered Asia. Since the Cao Bang Basin is situated in the lower reaches of the palaeo-Red River, the latter may have acted as an early vector of dispersal for the Triculinae.

Davis (1979) suggested that the Triculinae lineage diverged into distinct tribes during the Miocene, perhaps right after a major phase of tectonic activity that resulted in the establishment of the present day Yangtze and Mekong drainages (Clift *et al.*, 2008; Hoang *et al.*, 2009). The effective separation of the mollusc faunas of these rivers during the Cenozoic is consistent with the independent radiations of the Triculinae in the Yangtze and Mekong river catchment areas (Davis, 1979; Davis *et al.*, 1986a, c, 1992; Strong *et al.*, 2008).

Although molecular and anatomical studies are indispensable in resolving the phylogeny of pomatiopsids because of the extensive convergence of shell morphology in this family, fossil data are also important and the sparse fossil record of the Pomatiopsidae has constrained interpretations of the biogeographic history of this group (Davis, 1979). This is emphasized by the occurrence of the new genus *Bacbotricula* in the Palaeogene of northern Vietnam, which supports previous concepts of Triculinae evolution (Davis, 1979) and identifies the palaeo-Red River as a route of early triculine dispersal.

Bacbotricula likely formed dense populations on the muddy shoals and deltaic planes in Lake Cao Bang, as suggested by the local enrichment of the fossil shells (Fig. 2). Layering of the sediments is largely obscured, likely by bioturbation caused by unionid mussels (Schneider *et al.*, in press), and by small-scale tectonic displacements. We are unable to determine whether *B. nhamaygachensis* and *B. dongbangensis* occurred in separate layers, although this seems reasonable, because modern Triculinae species also inhabit distinct microhabitats (Davis, 1979). Fossil evidence of malacophagous cyprinids, documented by numerous teeth in the assemblage from Cao Bang, suggests that the *Bacbotricula* snails were intensely preyed upon by these fishes (Böhme *et al.*, 2011). The development of prominent keels on the shell surface of *Bacbotricula* may thus result

from an arms race of the gastropods and their shell-crushing predators. No extant representative of the genus *Bacbotricula* has been documented from northern Vietnam (Dang *et al.*, 1980).

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