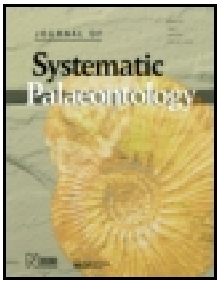

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Unionidae (Bivalvia; Palaeoheterodonta) from the Palaeogene of northern Vietnam: exploring the origins of the modern East Asian freshwater bivalve fauna

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Unionidae (Bivalvia; Palaeoheterodonta) from the Palaeogene of northern Vietnam: exploring the origins of the modern East Asian freshwater bivalve fauna

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Eocene/Oligocene sediments deposited in two Cenozoic pull-apart basins in northern Vietnam, i.e. the Na Duong and Cao Bang basins, yield several rich and well-preserved assemblages of unionid bivalves. This study outlines the taxonomy of the Unionidae from these communities, and all taxa are described and illustrated in detail. As far as we are aware, this is the first comprehensive treatment of Cenozoic Unionidae from South-East Asia. Eight of the nine taxa are described as new to science. Four species – *Cuneopsis quangi* sp. nov., *Cristaria mothanica* sp. nov., *Cristaria falcatocostata* sp. nov. and *Lamprotula hungi* sp. nov. – can be confidently assigned to modern genera. The generic position of the remaining species is equivocal (?*Nodularia cunhatia* sp. nov., ?*Cuneopsis* sp., ?*Lanceolaria* sp., ?*Lamprotula* sp.) or remains tentative (Anodontini sp.). The phyletic relationships of the fossil taxa to modern species are discussed and interpreted in light of the Cenozoic tectonic history of South-East Asia and the intimately associated evolution of drainage systems. The results confirm a close relationship of the fossil unionids to the modern mussel fauna of the Yangtze, Pearl and Red River catchment areas. Moreover, the fossils from Cao Bang and Na Duong are among the earliest confirmed records of all genera identified, and thus document an important, early stage in the development of the modern East and South-East Asian bivalve faunas.

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Keywords: freshwater mussels; East Asia; Eocene–Oligocene; Red River; Yangtze

Introduction

With around 700 extant species, the Unionoidea represent one of the most diverse modern bivalve superfamilies (Graf & Cummings 2007; Huber 2010). Approximately 150 of these species are indigenous to the Indochina (South-East Asia) and Yangtze-Huang areas (Graf & Cummings 2007). In spite of this remarkable diversity, knowledge about these taxa is scarce and mostly restricted to shell morphology. Data on anatomical characters, ecology and reproductive biology are available for a few unionid species from China (e.g. Gong *et al*. 2003; Hu *et al*. 2007; Liu & Wang 2008). For most genera, however, especially those from South-East Asia, these features are largely unknown. Moreover, the evolution and phylogeny of many taxa are still unresolved (e.g. Huang *et al*. 2002; Graf & Cummings 2007; Zhou *et al*. 2007). Likewise, very little has been reported on the origins, exact distribution and radiation patterns of these bivalve genera, and fossil evidence of most taxa is meagre (e.g. Leroy 1940; Yen 1943; Gou *et al*. 1976) or wanting. The discovery of Eocene/Oligocene unionid fossils in lake sediments from northern Vietnam may thus add important information, especially since northern Vietnam lies in the boundary region between the Indochina and Yangtze-Huang bio-provinces.

The occurrence of unionids at Na Duong and Cao Bang, northern Vietnam (Fig. 1) has been known since at least the 1960s, and the fossils were the subject of the PhD thesis of Yuri Tsceltzov in 1967. However, only a short abstract that lists 10 different genus names (*Nodularia*, *Contradens*, *Discomya*, *Oxynaia*, *Pseudodon*, *Cuneopsis*, *Chamberlainia*, *Paresia* [sic], *Lamprotula* and *Sinanodonta*) is available (Tsceltzov 1968); the main body of results from this PhD study have never been published. The material Tsceltzov's studies were based on has to be considered lost as it could not be found at the Paleontological Institute at Moscow. In the Mollusca volume of the *Palaeontological Atlas of Vietnam*, Khuc (1991) described and figured *Unio* sp. and *Anodonta* sp. from Na Duong, Cao Bang and Tieu Giao, and additionally reported the occurrence of

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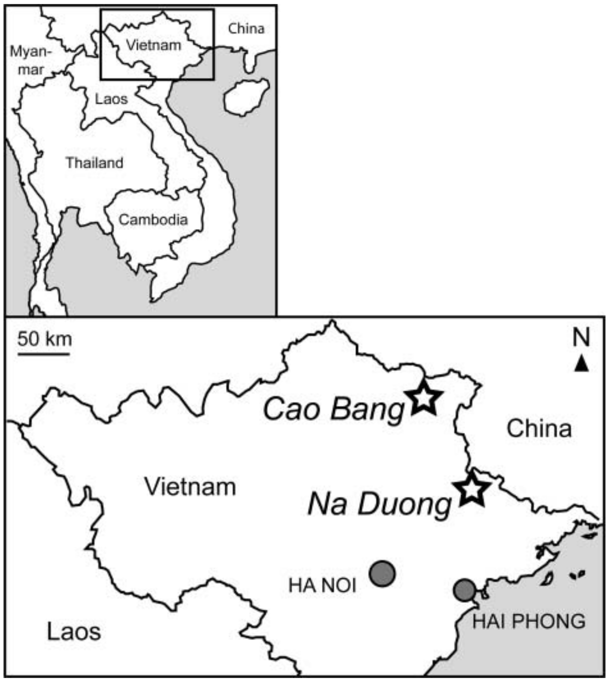

Figure 1. Geographical overview of northern Vietnam. The localities of Na Duong and Cao Bang are indicated by asterisks.

Oxynaia in Neogene sediments. The explanatory notes to the respective geological maps of Lang Son and Chinh Si–Long Tan also mention the occurrence of unionids, but list only *Acuticosta caobangensis*, *Oxynaia* sp., *Unio* sp. and *Anodonta* sp. (Long 2001; Thuy 2001). A more extensive list of unionid taxa was given by Dzanh (1996), who mentioned "*Oxynaia jourdyi* Morelet, *Cuneopsis* sp., *Chamberlainia* sp., *Schistodesmus* aff. *campreyianus* Baird. et Adams. [sic], *Pseudobaphia* cf. *biessiana* Hende [sic], *Discomya* aff. *radulosa* Dronet et Chaper [sic], *Unio* (*Nodularia*) cf. *continentalis* Haas, *Unio* cf. *baicalensis* Rammel, *Cristaria* sp., *Pilsbrioconcha* sp. [sic], *Microdontia ovata* Haas… and *Acuticosta caobangensis* Mod.". However, none of these species is figured and the determinations cannot be scrutinized. Furthermore, most of the names, although often misspelt, belong to extant species, some of them living in remote areas such as Lake Baikal or the Indonesian Archipelago. Consequently, these determinations surely result from misidentification. The Geological Museum at Hanoi houses only those (poorly preserved) specimens figured by Khuc (1991), and thus no material is available for comparison.

Knowledge of fossil unionids from South-East Asia (i.e. Myanmar, Laos, Cambodia, Vietnam, Thailand and the Indonesian archipelago) is scarce. The internal mould of *Pseudodon*? sp. from the Neogene of Thailand figured by Oyama (1978) is just barely distinguishable as a bivalve, but does not provide characters for generic or specific assignment. Udomkan *et al.* (2003), applying stable isotope chemistry to ?Eocene freshwater molluscs from Thailand, listed '*Mya arenaria*' from lacustrine deposits without, however, illustrating the specimens. Since *Mya arenaria* Linnaeus, 1758 is a Pleistocene to extant invasive marine bivalve species of northern hemisphere distribution (WoRMS 2010) that displays a roughly unionid shape, it seems likely that the specimens from Thailand were misidentified and are in fact unionids. As far as we are aware, the present study thus provides the first comprehensive description of Cenozoic Unionoidea from South-East Asia.

Speciation and particular radiations in the Unionoidea are usually confined to the evolution of large fluvial systems (Graf & Cummings 2007), and Cenozoic tectonic activity has progressively led to significant changes in drainage patterns in the study area (see below). We attempt to reconsider these processes herein based on dispersal data of fossil and extant unionids.

Geological setting

The material described in this study comes from two onshore Cenozoic pull-apart basins situated in northern Vietnam adjacent to the Chinese border, i.e. the Na Duong and Cao Bang basins. Both basins are associated with the Cao Bang–Tien Yen Fault, a left-lateral shearing, NW–SE trending strike-slip fault (Pubellier *et al.* 2003) that parallels the Red River Fault Zone, which represents the main fault system of the area (e.g. Leloup *et al.* 1995; Morley 2002; Searle 2006; Hoang *et al.* 2009). There is an ongoing debate on the exact timing of the start (presumably Eocene; Clift & Sun 2006), progress (Oligocene–Miocene, cumulative estimates 34–15.5 Ma; Gilley *et al.* 2003; Zhen *et al.* 2006; Zhu *et al.* 2009) and extent of these tectonic movements. As a result, conflicting opinions exist with regard to the age of the sedimentary infill of both basins (for a summary see Böhme *et al.* 2011).

The Na Duong Basin, named after the village of Na Duong situated ~20 km SE of Lang Son, the capital of Lang Son Province, has an extent of approximately 45 km^2. It is filled by an up to 570 m thick succession of partially coal-bearing sandstones, siltstones and marls that rest unconformably on Mesozoic siliciclastics (for details, including sections, see Wysocka 2009 and Böhme *et al.* 2011). The lower part of the succession, comprising the Na Duong Formation (Thuy 2001), is composed of alternating coal seams and marls. In the upper portion of the succession, coal seams retreated, and an entirely silty to marly series, termed the Rinh Chua Formation (Thuy 2001), was deposited. Both formations are best exposed in the Na Duong coalmine (21°42.2 N, 106°58.6 E), where the upper ~130 m of the Na Duong Formation and ~40 m of the Rinh Chua Formation are accessible. The type section of the Rinh Chua Formation, which is located next to Rinh

Chua village on the banks of the Ky Cung River (Wysocka 2009), was also visited for the present study but only strongly weathered samples were available. Palynological data widely confirm an Oligocene age for the Na Duong and Rinh Chua formations (Dy *et al*. 1996; Trung *et al*. 2000; Böhme *et al*. 2011). However, preliminary results from the study of several recently unearthed specimens of Anthracotheriidae (Mammalia; unpublished data from fieldwork in 2011) rather indicate an older, Late Eocene to Early Oligocene age.

In part, both the coal layers and the silty to marly sediments are rich in fossils. While the main coal seam has yielded numerous turtle shells, as well as crocodiles, mammals and fish remains, carbonate hard parts have been essentially dissolved in these sediments during diagenesis. In contrast, mollusc remains occur in high abundances in several silt and marl layers of the Na Duong and Rinh Chua formations. Usually, shells are entirely or partly preserved in specimens from the Na Duong Formation, while they are largely or entirely dissolved in specimens from the more severely weathered Rinh Chua Formation. Generally, bivalves are preserved with contiguous or slightly gaping valves (75%), but occasionally also in butterfly position (4%) or disarticulated (21%), indicating autochthonous deposition. While most specimens are undistorted, some are slightly deformed by synsedimentary compression. Several gastropod taxa co-occur with the bivalves. Large shells of viviparid gastropods are common, both in the Na Duong and Rinh Chua formations, and may form coquina-like accumulations in the latter. In contrast, a gastropod species that closely resembles the thiarid genus *Tarebia* occurs exclusively in the Rinh Chua Formation, where it is relatively abundant. Two moulds with remnants of shell that resemble the pachychilid genus *Brotia* were discovered from the Na Duong Formation. Frequently, plant remains, especially of lotus flowers (*Nelumbo* sp.), co-occur with the molluscs in the Na Duong Formation. Additionally, a few different seeds and relatively abundant fish remains have been found in the same layers (Böhme *et al*. 2011).

The Cao Bang Basin is slightly larger than the Na Duong Basin (~65 km^2; see Wysocka (2009) and Böhme *et al*. (2011) for details). The Cenozoic sediments that fill the basin rest on Palaeozoic and Mesozoic rocks and are exposed in road cuts, building sites, and brickyards in and around the city of Cao Bang, which is the capital of Cao Bang Province. The lower, fluvial-terrestrial part of these sediments is assigned to the Cao Bang Formation. Based on comparisons with the Na Duong Basin, the upper sediment portion that comprises lacustrine and lacustrine-deltaic deposits is attributed to the Na Duong Formation (Thanh & Khuc 2006). Whether this is a sensible decision is open to discussion, as the strata at Cao Bang contain a fauna distinctly different from that of Na Duong (Böhme *et al*. 2011; see also discussion section below). Moreover, it seems problematic to assign the same lithostratigraphic terms to the sediments of two large, independent lake systems. However, these issues are beyond the scope of the present study, and assignment of the sediments to the Na Duong Formation is thus retained herein. To date, no palynological data are available from the Cao Bang basin, but a similar age is assumed for the Na Duong Formation from both localities based on the conjoint tectonic evolution of the basins (Khuc *et al*. 2005; Thanh & Khuc 2006).

With regard to palaeontology, the currently most productive outcrop of the basin is an active brickyard within the municipal area of Cao Bang (N 22°40.72, E 106°15.23). Several sediment layers of the Na Duong Formation exposed at this locality yield unionid bivalves in abundance. Large wing-shaped *Cristaria* mussels are generally strongly compressed and exclusively preserved with contiguous valves. Most shells of other genera are also still articulated, either with contiguous valves or in butterfly position. In certain horizons, however, shells are enriched by depositional processes and often occur as single valves, but none show signs of abrasion or erosion. In conclusion, the shells may represent an autochthonous to para-autochthonous community. Besides unionids, the sediments contain a remarkably rich and diverse fish fauna, preserved as disarticulated bones and teeth, and two small-sized hydrobioid gastropod species that are highly abundant in particular horizons (Böhme *et al*. 2011).

Material and methods

Approximately 100 bivalve specimens each were collected from the sediments exposed at Na Duong coalmine and at Cao Bang brickyard. The shells were carefully cleaned with needles, brushes and water. Those from Cao Bang were subsequently soaked in liquid glue to stabilize the shell matrix. Measurements were taken using a calliper with an accuracy of 0.5 mm. For photographs, most of the specimens were coated with ammonium chloride.

Holotypes and some of the paratypes are deposited at the Senckenberg Center for Human Evolution and Paleoecology (**HEP**), Eberhard-Karls-Universität Tübingen, Institute for Geoscience, under accession numbers GPIT/BI/5558 to 5578. Additional paratypes and figured specimens are deposited at the Bayerische Staatssammlung für Paläontologie und Geologie (**BSPG**), Munich, Germany under accession number BSPG 2011 XXI 1 to 14. Matching plaster casts of those type specimens stored at the other institution complement the material in each repository. Supplementary material is deposited at the Geology Museum, Hanoi, Vietnam. For comparative purposes, several shells of extant mussels are figured, which have been photographed at the Muséum National d'Histoire Naturelle, Paris (**MNHN**) and the Senckenberg Forschungsinstitut und Naturmuseum, Frankfurt (**SMF**).

Systematic palaeontology

(by Simon Schneider)

The systematic concepts used in this section follow Bieler *et al*. (2010).

Class **Bivalvia** Linnaeus, 1758
Superorder **Heteroconchia** Gray, 1854
Clade **Palaeoheterodonta** Newell, 1965
Order **Unionida** Gray, 1854
Superfamily **Unionoidea** Rafinesque, 1820
Family **Unionidae** Rafinesque, 1820
Subfamiliy **Unioninae** Rafinesque, 1820
Tribe **Unionini** Rafinesque, 1820
Genus ?***Nodularia*** Conrad, 1853

Type species. *Unio douglasiae* Griffith & Pidgeon, 1834.

Remarks. Several scholars have regarded *Nodularia* as a junior synonym of *Unio* (e.g. Haas 1969; Gou *et al*. 1976). I follow the concept of Graf & Cummings (2007), and regard *Nodularia* as an independent genus with at least four extant species. Fossil representatives clearly assignable to *Nodularia* are known from Pleistocene strata of Hebei, Henan and Guanxi provinces in China (Leroy 1940; Gou *et al*. 1976; Huang 1981; Huang & Guo 1982), and Taiwan (Suzuki 1949).

?***Nodularia cunhatia*** sp. nov.
(Fig. 2B–G)

pp. 1991 *Unio* sp.; Khuc: 78, pl. 43, fig. 5 only.

Diagnosis. Small, oval species of ?*Nodularia* with almost central umbones ornamented with low and narrow, wavy, undulating ridges.

Derivation of name. From the Vietnamese words ‘Cũn hất’, meaning ‘the oldest’.

Material. Na Duong Formation: 41 specimens with contiguous or slightly gaping valves, 3 specimens in butterfly position, 3 left valves, 5 right valves.

Type specimens. Holotype: GPIT/BI/5558). Paratypes: GPIT/BI/5559, GPIT/BI/5560, BSPG 2011 XXI 12, BSPG 2011 XXI 13, BSPG 2011 XXI 14.

Dimensions. L = 30–54 mm, H = 18–32.5 mm, T = 16–23 mm.

Type locality and occurrence. Na Duong coalmine, Lang Son Province, northern Vietnam.

Type stratum. Na Duong Formation, Palaeogene.

Description. Shell almost oval, with faintly indicated dorsal corners, relatively thin, moderately inflated. Posterior end of fully grown specimens slightly tapering; positioned at about mid height. Umbones slightly prosogyrous; positioned almost central with regard to shell length. Shell surface covered with distinct, slightly irregular growth lines. Umbones ornamented with narrow, moderately elevated, wavy, undulating folds or ridges; ornamentation usually restricted to juvenile shell portion (<10 mm in height; Fig. 2B, E); occasionally extending on adult shell (Fig. 2C).

Remarks. Although more than 50 specimens of ?*Nodularia cunhatia* have been collected, it is impossible to observe the hinge area and interior shell characters of this species. The entire sediment at Na Duong is enriched with finely dispersed pyrite, which has also replaced the organic material of the bivalve shells. As frequently seen in modern unionids from soft-water environments, the umbones are usually corroded in the mussel specimens from Na Duong (Fig. 2B, C, F). As a result, the shell around the hinge is much thinner than would be expected in uncorroded specimens, and oxidation of the pyrite starts from these worn-out regions. It is therefore impossible to prepare the hinge region of the shells, and the specimens cannot be assigned to *Nodularia* with confidence. Nevertheless, the outside of the fossil shells is very similar to that seen in extant representatives of this genus, especially with regard to ornamentation (Fig. 2A). This species can be distinguished from modern representatives of *Nodularia* by its less elongate, more oval shell, and almost centrally positioned umbones.

Genus ***Cuneopsis*** Simpson, 1900

Type species. *Unio celtiformis* Heude, 1874.

Remarks. When Simpson (1900) established the genus *Cuneopsis*, he assigned five extant species – *C. capitatus*, *C. celtiformis*, *C. heudei*, *C. pisciculus* and *C. rufescens* – all originally described by Heude (1874). Today, a sixth species, *C. demangei*, is included that was erected by Haas (1929). Several fossil species of *Cuneopsis* have been proposed from Miocene to Pleistocene strata of China (e.g. Leroy 1940; Gou *et al*. 1976; Huang 1981, 1983; Huang & Guo 1982; Xie 1999) and Japan (e.g. Mizuno 1966; Matsuoka 1988).

In addition, *Cuneopsis* has been used as a wastebasket taxon for numerous, usually poorly preserved Mesozoic unionoid bivalves of more or less *Cuneopsis*-like shape, which do not belong to this genus. The hinge characters seen in the poorly preserved material of *C. globulosus* Mongin, 1963a and *C. johannisboehmi* (Frech, 1911) from the Cretaceous of Niger do not match with any of the extant species assigned to this genus (Mongin 1963b). The type specimen of *Cuneopsis giganteus* Mongin, 1963a, described from the same stratum, has contiguous valves (Mongin 1963b). It

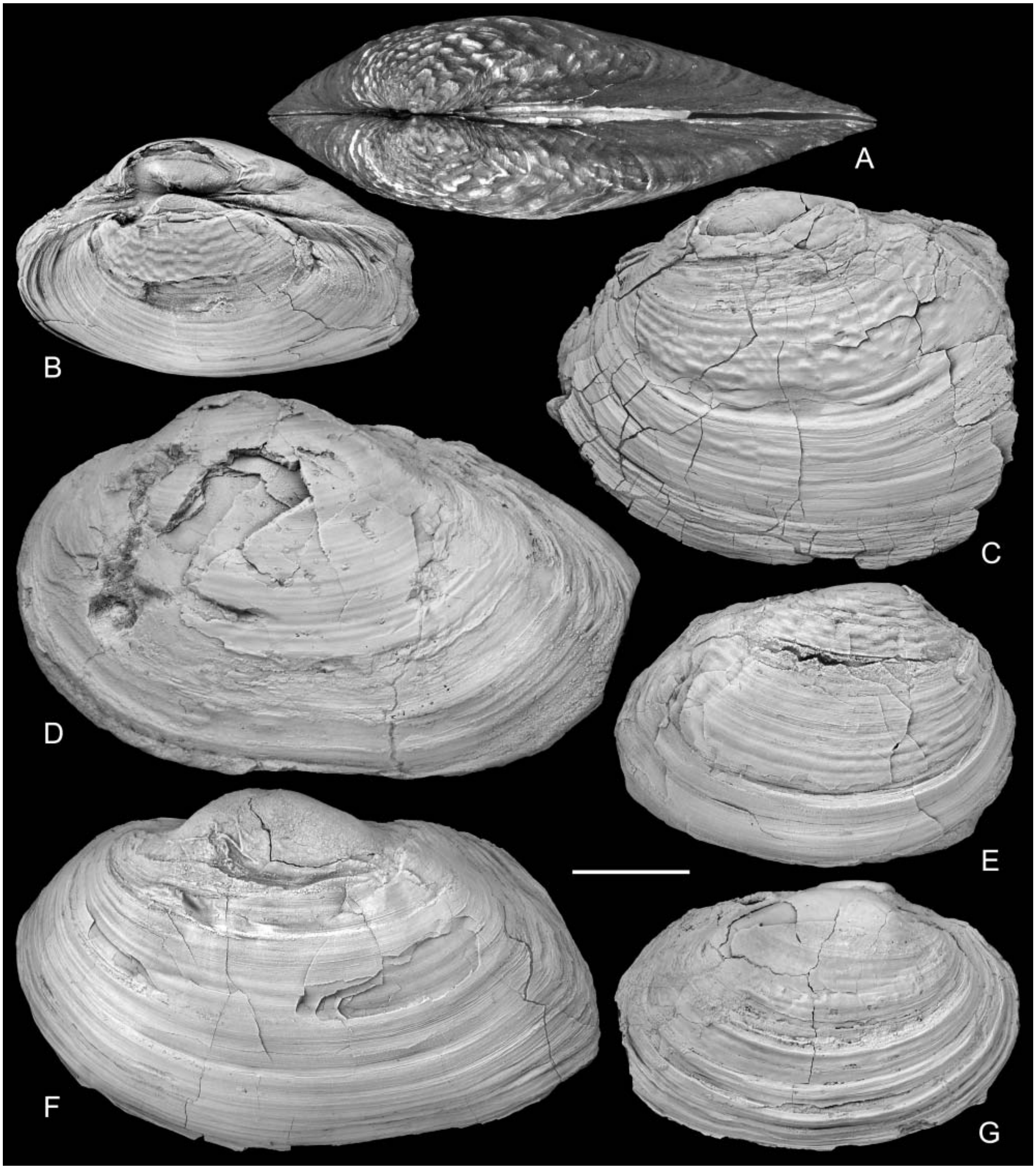

Figure 2. **A**, *Nodularia douglasiae* (Griffith & Pidgeon, 1834), dorsal view, showing strong ornamentation of undulating rugae on juvenile shell portion; Recent, Petchily, China; Syntype of *Unio sculptus* Deshayes, 1874, MNHN MP 0108). **B–G**, ?*Nodularia cunhatia* sp. nov., Na Duong Formation, Palaeogene, Na Duong coalmine; **B**, small articulated specimen, oblique-dorsal view, showing ornamentation of undulating rugae and markedly corroded umbones; paratype, GPIT/BI/5559; **C**, large, slightly fragmented articulated specimen, left valve view, showing ornamentation of undulating rugae, extending on more than half of shell flank; paratype, BSPG 2011 XXI 12; **D**, large articulated specimen with smooth shell surface, left valve view; holotype, GPIT/BI/5558; **E**, small, short articulated specimen ornamented with rugae, right valve view; paratype, GPIT/BI/5560; **F**, large articulated specimen with corroded umbones, left valve view; paratype, BSPG 2011 XXI 13; **G**, small articulated specimen with smooth shell surface and prominent growth lines, right valve view; paratype, BSPG 2011 XXI 14. Scale bar = 10 mm.

neither resembles extant *Cuneopsis* in shape, nor can it be assigned to any genus with confidence, as no details of its hinge morphology are available. In the author's opinion, the fossils from Niger definitely do not belong to *Cuneopsis*, and any phylogenetic relationships with this exclusively East Asian genus are out of the question.

Whether the numerous Mesozoic unionids from China that have historically been assigned to *Cuneopsis* really belong to this genus is more difficult to assess. Recently, Pan & Sha (2009) studied the morphologic variability of *C. johannisboehmi* (Frech, 1911) from the Middle Jurassic of southern China and synonymized almost 20 fossil species. However, the rather poorly preserved material used for their study does not display hinge characters, and thus assignment to *Cuneopsis* is arbitrary. Based on comparison of numerous fossils mainly from China and Japan, Suzuki (1949) stated that no direct generic relationships exist between the Mesozoic and Cenozoic unionids from East Asia. Strong evidence for the distinction of Jurassic and Cenozoic forms also comes from a study of shell mineralogy by Chen (1983, 1987), who compared Jurassic and extant material. All tested shells showed a simple prismatic outer layer, lenticular nacreous middle layer, and sheeted nacreous inner layer. However, in Jurassic shells, including '*Cuneopsis*' and '*Lamprotula*', the prisms of the outer layer are unbranched, while they produce three or four branches in adult extant unionids. In Jurassic taxa, the prism axes meet the shell surface at angles of 83–90°, while they meet at 50–75° in extant taxa. The width/length ratio of these prisms is 25–33% in Jurassic and 12–17% in extant unionids. The inner shell layer is thinner than the middle layer in fossil, and thicker than the middle layer in extant unionids. Considering these striking differences, Chen (1983, 1987) proposed a new family, Qiyangiidae Chen, 1983, for Jurassic taxa, and recommended that names of extant genera be used for the Jurassic unionids only in quotation marks. The present author is not aware of any Mesozoic unionid showing typical *Cuneopsis*- or *Lamprotula*-type hinge dentition, and hence shares the opinion of Chen (1987).

Cuneopsis quangi sp. nov.
(Fig. 3A, D–I)

Diagnosis. Elongate, sub-rectangular, markedly inflated *Cuneopsis* with strongly prosogyrous umbones and slightly truncated posterior end.

Derivation of name. Named in honour of Đỗ Đúc Quang, curator at the Geology Museum, Hanoi, Vietnam.

Material. 16 specimens with contiguous valves, 5 specimens in butterfly position, 23 left valves, 20 right valves.

Type specimens. Holotype: GPIT/BI/5561a, b. Paratypes: BSPG 2011 XXI 9a, b, BSPG 2011 XXI 10, BSPG 2011 XXI 11, GPIT/BI/5562, GPIT/BI/5563, GPIT/BI/5564.

Dimensions. L = 24–88 mm, H = ~9–41 mm, T = ? to ~30 mm.

Type locality and occurrence. Cao Bang brickyard section, Cao Bang, northern Vietnam.

Type stratum. Na Duong Formation, Palaeogene.

Description. Shell thick, elongate, undistorted shells twice as long as high (L:H = 2.1); overall outline shape elongate rounded-rectangular. Anterior shell margin bluntly rounded to truncate, passing into well-rounded anteroventral shell margin; ventral margin slightly rounded to almost straight, curving upward towards posterior end. Anterior portion of dorsal margin almost straight; posterior part sloping down toward posterior end. Posterior tip bluntly angled. Posterior margin slightly oblique; bluntly truncated. Anterodorsal part of shell lunule-like incurved. Shell markedly inflated, with slightly protruding, strongly prosogyrous umbones, positioned next to anterior end of shell. Outside of shell ornamented with smooth, but distinct growth lines. No ridges or undulations discernible in early growth stages.

Hinge of left valve with a massive, elevated, elongate-triangular pseudocardinal tooth, emerging from broad hinge plane that rests on a strong pillar. Trapezoidal socket with deeply engraved vertical furrows positioned directly in front of the pseudocardinal tooth. Strong, elongate, lower posterior lateral tooth emerging directly behind pseudocardinal, stretching parallel to shell margin up to approximately two-thirds of total shell length. Upper posterior lateral tooth much weaker; gradually emerging from inner shell margin and paralleling lower posterior lateral. Hinge of right valve with massive trapezoidal pseudocardinal tooth with deep vertical engravings, resting on strong pillar. No hinge plate present behind pseudocardinal tooth. Single posterior lateral tooth emerging from internal shell margin behind gap for pseudocardinal tooth of left valve. Anterior adductor muscle scars deep, almost rectangular; framed by anterior shell margin and hinge plate pillar. Pallial line distinct, continuous.

Remarks. The fossil *Cuneopsis quangi* closely resembles the extant *C. celtiformis* (Heude, 1874), both with regard to shell shape and hinge dentition (Fig. 3B, C). However, *C. celtiformis* is slightly more elongate and its posterior end not truncated, but tapering. Its umbones are positioned less closely to the anterior end and are ornamented with two radial rows of knobs. Finally, the hinge plate of the right valve extends to the dorsal inner shell margin behind the pseudocardinal tooth, while there is a gap in *C. quangi*. This character clearly distinguishes *C. quangi* from all other fossil and extant species of *Cuneopsis*. Nevertheless, the similarity of *C. celtiformis* and *C. quangi* is astonishing and seems to be much closer than between the five extant species of *Cuneopsis*.

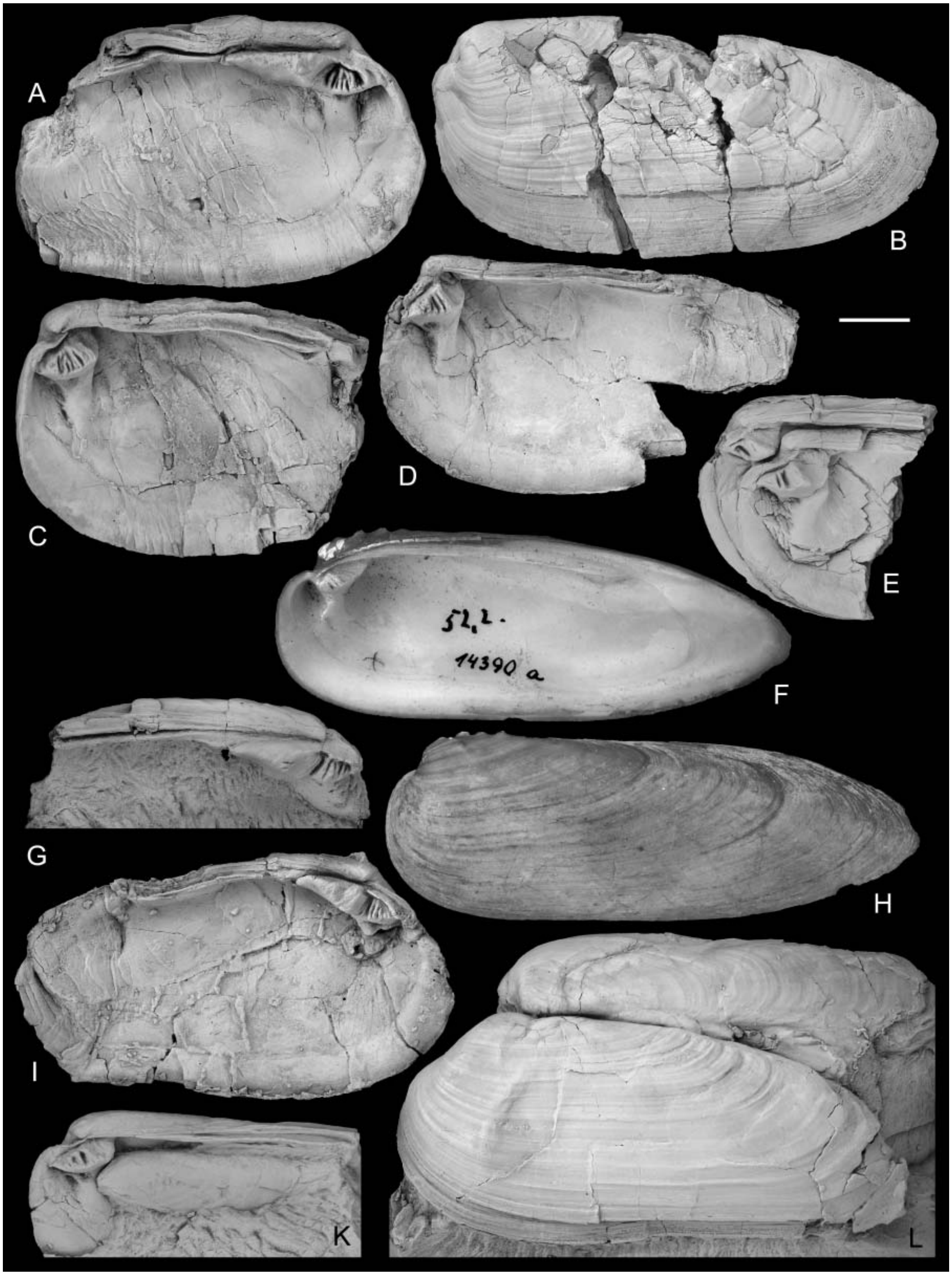

Figure 3. **A–E, G, I–L**, *Cuneopsis quangi* sp. nov., Na Duong Formation, Palaeogene, Cao Bang brickyard; **A**, inside view of left valve; holotype, GPIT/BI/5561a; **B**, specimen with contiguous valves, left valve view; paratype, BSPG 2011 XXI 10; **C**, inside view of right valve; holotype, GPIT/BI/5561b; **D**, inside view of slightly distorted right valve showing full extent of posterior lateral tooth; paratype, BSPG 2011 XXI 9a; **E**, anterior fragments of two nested right valves; paratype, GPIT/BI/5562; **G**, anterior fragment of left valve; paratype, BSPG 2011 XXI 11; **I**, interior view of slightly distorted left valve showing full extent of bifid posterior lateral tooth; paratype, BSPG 2011 XXI 9b; **K**, interior view of young adult right valve; paratype, GPIT/BI/5563; **L**, outside view of articulated specimen in butterfly position; paratype, GPIT/BI/5564. **F**, **H**, *Cuneopsis celtiformis* (Heude, 1874), right valve; Recent, Hunan Province, east-central China (SMF 14390); **F**, inside view; **H**, outside view showing pustules on the umbo. Scale bar = 10 mm.

?***Cuneopsis*** sp.
(Fig. 4A)

Material. Two specimens with contiguous valves, one specimen in butterfly position, one left valve. GPIT/BI/5565.

Dimensions. L = 48.5 mm, H = 28.5 mm, T = 22 mm.

Occurrence. Rinh Chua Formation, Palaeogene, Na Duong coalmine, Lang Son Province, northern Vietnam.

Description. Shell blunt-triangular, markedly inflated, relatively thick. Anterior margin well rounded, gradually passing into almost straight ventral margin. Posterodorsal margin almost straight, down-sloping. Posterior end slightly to strongly tapering, with rounded tip. Umbones prominent, prosogyrous, positioned at approximately one-third of total shell length. Shell surface covered with densely spaced commarginal growth lines. Hinge structures preserved as negatives on internal moulds only. Strong, elongate, triangular pseudocardinal tooth and extensive posterior lateral tooth present in both valves. Pseudocardinals internally structured by vertical furrows. Anterior adductor muscle scar large and deep.

Remarks. The few specimens from the Rinh Chua Formation are preserved as internal moulds, in part with remnants of shell. Consequently, assignment to *Cuneopsis* is provisional, and a specific designation is not possible. However, the presence of large, elongate pseudocardinal hinge teeth observed as negatives in the moulds, and the triangular shape and tapering posterior part of the shell relatively closely resemble features seen in the extant *Cuneopsis capitatus* (Heude, 1874) (Fig. 4B), strongly suggesting a potential relationship.

Genus ***Lanceolaria*** Conrad, 1853

Type species. *Unio grayanus* Lea, 1834.

Remarks. The genus *Lanceolaria* is distributed across eastern Asia, including the Amur-Beringia, Yangtze-Huang and Indochina bio-provinces *sensu* Graf & Cummings (2007), likely with fewer than 10 extant species. The taxonomic status of several (sub-)species remains unresolved, and the genus therefore is clearly in need of revision. The fossil record of *Lanceolaria* is sparse. In *L. pisciformis* (Yokoyama, 1932) from the Oligocene of Japan (e.g. Suzuki 1941a, b), *L. convexa* Huang & Wei in Gou *et al*., 1976 from the Miocene of China, and *L.* cf. *fruhstorferi* (Bavay & Dautzenberg, 1901) from the 'Tertiary' of Gansu Province, China (Gou *et al*. 1976), internal shell characters are unknown, and generic assignment remains tentative. Fossil shells assigned to several extant species of *Lanceolaria* are documented from the Pleistocene of China and Japan (Suzuki 1949; Huang 1981; Huang & Guo 1982).

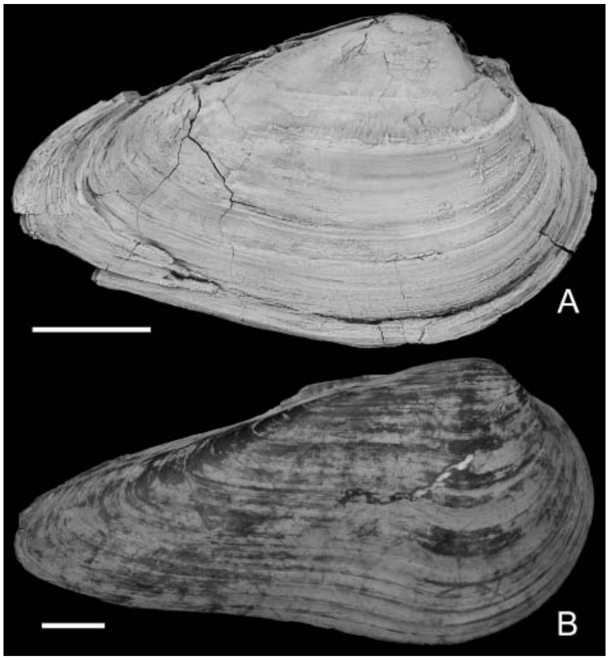

Figure 4. **A**, ?*Cuneopsis* sp., articulated specimen, internal mould with remnants of shell, right valve view; Rinh Chua Formation, Palaeogene, Na Duong coalmine; GPIT/BI/5565. **B**, *Cuneopsis capitatus* (Heude, 1874), right valve; Recent, Chi-an-hsien, Kiangsi, China; SMF 14386. Scale bars = 10 mm.

?***Lanceolaria*** sp.
(Fig. 5A)

Material. A single, almost undistorted left valve. GPIT/BI/5566.

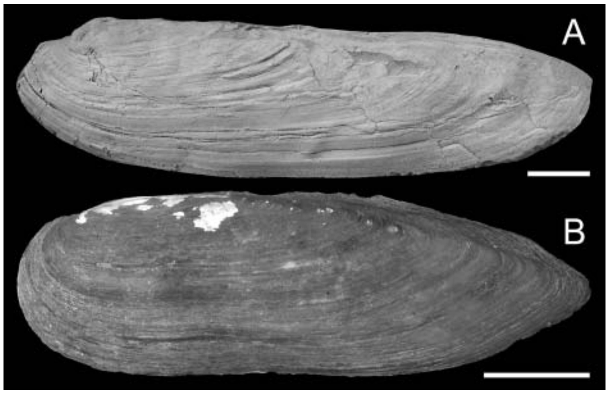

Figure 5. **A**, ?*Lanceolaria* sp., Na Duong Formation, Palaeogene, Cao Bang brickyard; GPIT/BI/5566. **B**, *Lanceolaria bilirata* (von Martens, 1902), outside of left valve; Recent, Tonkin = northern Vietnam; paratype of *Nodularia* (*Lanceolaria*) *bilirata* von Martens, 1902, SMF 3573. Scale bars = 10 mm.

Dimensions. L = 45.5 mm, H = 13 mm, T = 3.5 mm.

Occurrence. Na Duong Formation, Palaeogene, Cao Bang brickyard, Cao Bang Province, northern Vietnam.

Description. Shell strongly elongate, lancet-shaped (L:H = 3.5), relatively shallow; anterior end well-rounded; posterior end bluntly tapering towards dorsal half of shell height. Shell thin, very fragile. Umbo weakly pronounced, slightly prosogyrous; positioned distinctly behind the anterior end, at ~15% of total shell length. Shell surface smooth, with distinct growth lines. Shell proportions more or less stable throughout ontogeny; no marked allometric growth. Internal characters largely unknown; hinge almost un-preparable due to fragility of shell; no obvious strong pseudocardinal tooth.

Remarks. The specimen differs from similarly sized specimens of *Cuneopsis quangi* by the shell being distinctly less inflated, significantly more elongated and approximately one-third longer. Additionally, the umbo is somewhat less pronounced, and positioned nearly twice as far from the anterior end of the shell than in *C. quangi*. Overall, the shell most closely resembles that of the extant *Lanceolaria bilirata* (von Martens, 1902). This species is regarded as a subspecies of *L. oxyrhyncha* (von Martens, 1861) by Haas (1969). However, the former occurs in northern Vietnam, while the latter is endemic to Lake Biwa (Honshū, Japan; Takahashi 1989), thus suggesting that these forms represent two independent species. However, this supposition is still to be tested using molecular data. *Lanceolaria* sp. from Cao Bang is very similar in outline to *L. bilirata*, but lacks the posterodorsal ridge seen in the extant species (Fig. 5B). Moreover, the tapering posterior end of the shell is positioned more dorsally in the fossil. As only one specimen is present, and attribution to *Lanceolaria* remains tentative because data on hinge characters are lacking, I refrain from specific assignment.

Tribe **Anodontini** Rafinesque, 1820
Genus ***Cristaria*** Schumacher, 1817

Type species. *Cristaria tuberculata* Schumacher, 1817 (= *Cristaria plicata* [Leach, 1815]).

Remarks. The genus *Cristaria* is characterized by the absence of pseudocardinal teeth and presence of a single, simple posterior lateral tooth in each of the valves. In some extant species these lateral teeth are weak or absent (Haas 1969). The similarly shaped *Hyriopsis* can be easily distinguished from *Cristaria* by the presence of a bifid posterior lateral tooth in the left valve.

According to Graf & Cummings (2007), *Cristaria* comprises at least four extant species, all of which are indigenous to East Asia. Fossil representatives of *Cristaria* from East Asia include several species from the Eocene to Pleistocene of China, Korea, Taiwan and Japan (e.g. Suzuki 1949; Huang 1981, 1983; Huang & Guo 1982). Whether these species really belong to *Cristaria*, or have only been assigned to this genus because of their anodontiform shape, cannot be decided without examination of the type material. Curiously, Gou *et al*. (1976) did not list a single fossil species of *Cristaria* from China.

Cristaria mediterranea Schütt, 1973 from the Pleistocene of Chios, Greece (Schütt & Besenecker 1973) closely resembles the extant *C. plicata* from East Asia with regard to shell shape. However, *C. plicata* has only a simple posterior lateral tooth in its left valve, while *C. mediterranea* clearly shows a bifid posterior lateral tooth. Thus, *C. mediterranea* certainly is not a representative of *Cristaria*, but rather belongs to a different genus.

Cristaria mothanica sp. nov.
(Fig. 6)

pp. 1991 *Anodonta* sp. Khuc: 79, pl. 42, fig. 8 only.

Diagnosis. Oblique-oval *Cristaria* with markedly anterior-positioned, slightly prosogyrous umbones, posterior half markedly higher than anterior part, and low posterior wing. Anterior wing minute but present. One set of relatively short posterior lateral teeth present.

Derivation of name. From the Vietnamese words 'Mỏ than', meaning coalmine, referring to the type locality, the Na Duong coalmine.

Material. Na Duong Formation: 28 specimens with contiguous or slightly gaping valves; 4 left valves. Rinh Chua Formation: 5 specimens with contiguous valves.

Type specimens. Holotype: GPIT/BI/5567. Paratypes: GPIT/BI/5568, GPIT/BI/5569, BSPG 2011 XXI 6, BSPG 2011 XXI 7, BSPG 2011 XXI 8.

Dimensions. L = 61–89 mm, H = 46–68 mm, T = 20–? mm.

Type locality and occurrence. Na Duong coalmine, Lang Son Province, northern Vietnam.

Type stratum. Na Duong and Rinh Chua formations, Palaeogene.

Description. Shell very thin, fragile. Undistorted shells (Fig. 6A, B, D, E) oblique-oval in outline, with posterior shell portion markedly higher than anterior part of shell. Umbones low; faintly prosogyrous; positioned in anterior portion of shell, at about one-third of total shell length. Young growth stages slightly less elongate than adult shells; modest allometric growth directed towards

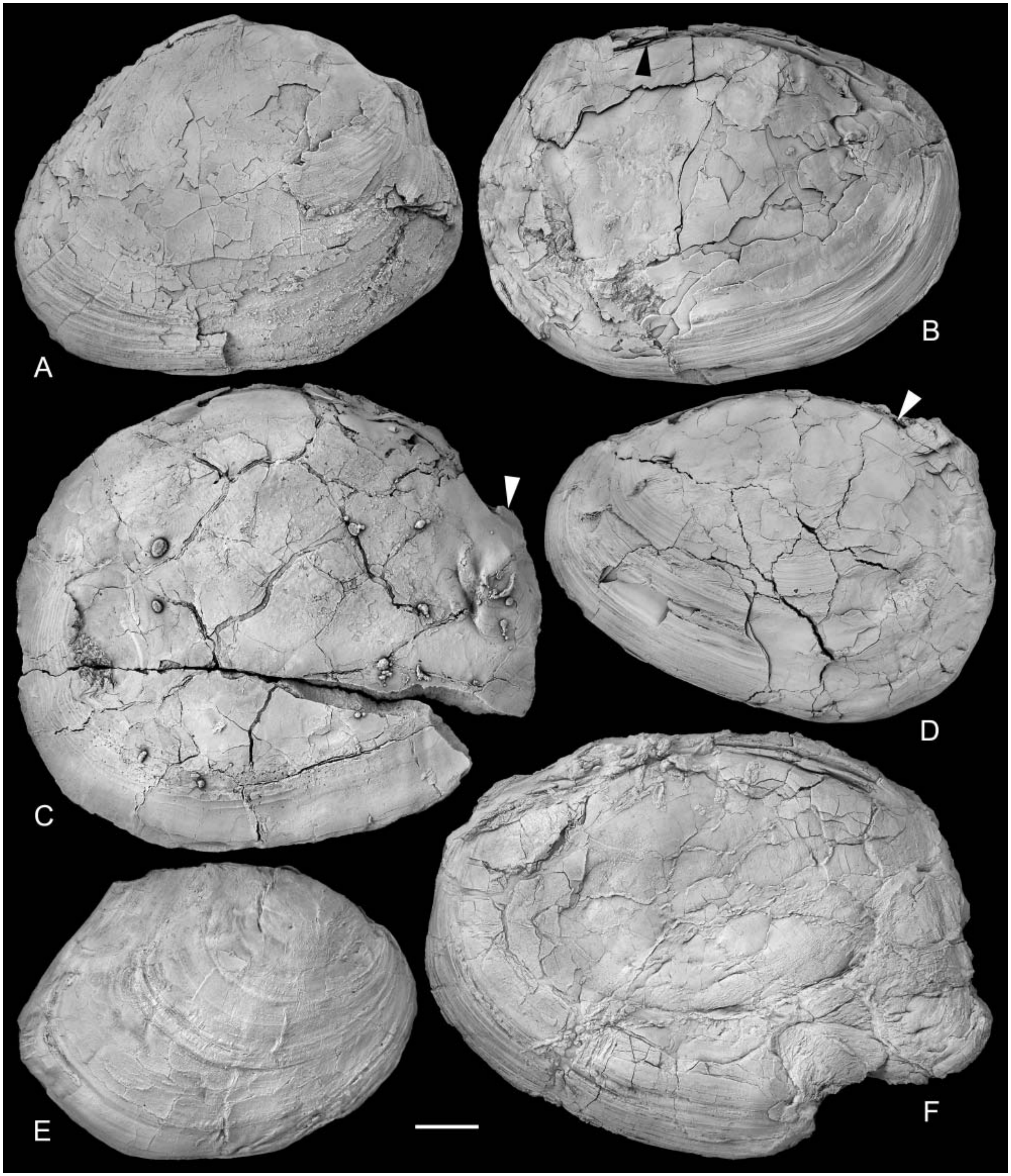

Figure 6. *Cristaria mothanica* sp. nov., Na Duong Formation, Palaeogene, Na Duong coalmine. **A**, articulated specimen with remnants of shell, right valve view; paratype, GPIT/BI/5568. **B**, articulated specimen, partial mould, showing imprint of claustrum (black arrow); right valve view; paratype, BSPG 2011 XXI 6. **C**, internal mould, showing distinct adductor muscle scars and several growth stages of mantle line; internal mould of anterior wing indicated by white arrow; right valve view; paratype, BSPG 2011 XXI 7. **D**, articulated specimen with large parts of shell preserved; imprint of claustrum indicated by white arrow; left valve view; paratype, GPIT/BI/5569. **E**, articulated specimen with fully preserved shell, right valve view; holotype, GPIT/BI/5567. **F**, large, slightly compressed articulated specimen with remnants of shell; left valve view; paratype, BSPG 2011 XXI 8. Scale bar = 10 mm.

posteroventral end. Anterior and ventral shell margins well-rounded. Posteroventral shell portion faintly tapering. Posterior shell margin slightly rounded to almost straight. Posterior portion of dorsal shell margin straight. Dorsal and posterior margin forming sharp corner, meeting at an angle of approximately 110°. Posterior wing (= shell portion superior to lateral teeth, not enclosing soft parts of the mussel) low; partly broken in most specimens, including the holotype. Minute anterior wing present, but visible only from perfectly preserved anterior mould (arrow in Fig. 6C); usually broken in individuals preserved with shell. Anterior portion of dorsal margin slightly rounded. Inflation low to moderate, with largest swelling in an oblique region extending from below the umbones in posteroventral direction.

Shell surface covered with numerous distinct, irregular, commarginal growth lines. Ornamentation of umbones absent or not preserved. Centre of hinge edentulous, with simple, relatively short, slightly incurved posterior lateral teeth (arrows in Fig. 6B, D). Anterior adductor muscle scar deep and large, more or less fused with pedal protractor muscle scar (Fig. 6C). Posterior adductor muscle scar indiscernible.

Remarks. Due to the presence of distinct, simple posterior lateral teeth, this species can be confidently assigned to *Cristaria*. Moreover, several additional features are similar to those seen in the extant *C. plicata* (Fig. 7D). Both species show a distinct posterior and small anterior wing. The area of largest inflation extends from below the umbones in a posteroventral direction. The anterior adductor muscle scar and pedal protractor muscle scar are distinct and almost fused, while the posterior adductor muscle scar is faint. In fact, the differences between *C. mothanica* and some of the morphs of the highly variable *C. plicata* are rather small. *C. mothanica* is generally less inflated and the anterior wing less developed. Most striking, the umbones of *C. mothanica* are positioned further towards the anterior end, and slightly prosogyrous, while they are almost rectigyrous and somewhat closer to the centre in *C. plicata*. Considering the difference in geological age, it could hardly be imagined that both forms are conspecific.

Cristaria falcatocostata sp. nov.

(Fig. 7A–C, E)

Diagnosis. Large, thin-shelled, rounded-rhomb-shaped *Cristaria* with sharp anterodorsal and posterodorsal corners and bow- to sickle-shaped ridge running from umbo towards tapering posteroventral end.

Derivation of name. From a combination of the Latin words ‘falcatus’, meaning sickle-shaped and ‘costatus’ meaning ribbed, referring to the presence and shape of the characteristic posterior ridge seen in the shells.

Material. 7 specimens with contiguous valves, 4 fragmentary specimens.

Type specimens. Holotype: GPIT/BI/5570). Paratypes BSPG 2011 XXI 5, GPIT/BI/5572, GPIT/BI/5571.

Dimensions. L = ~120–145 mm, H = ~60–80 mm.

Type locality and occurrence. Cao Bang brickyard, Cao Bang Province, northern Vietnam.

Type stratum. Na Duong Formation, Palaeogene.

Description. Shell large (up to ~145 mm in length), fragile, rounded-rhomb-shaped, modestly inflated; anterior and ventral shell margins well-rounded; anterodorsal corner sharp, elevated, forming small, distinct anterior wing; posterodorsal shell margin slightly and constantly incurved, extended, forming relatively high posterior wing; posterodorsal corner sharp, with dorsal and posterior shell margins meeting more or less at right angles; posterior margin markedly and regularly incurved, leading towards tapering, but well-rounded posteroventral end. Umbones low, only slightly inflated, rectigyrous. Shell surface covered with clearly visible, irregular commarginal growth lines. Distinct, broadly-rounded, bow- to sickle-shaped ridge running from the umbo towards posteroventral end of shell; shell at ridge faintly thickened; slightly bent outwards in cross-section. Ridge becoming less distinct with growth (Fig. 7B).

Internal characters inferred from a single internal mould: Anterior adductor muscle scar large, sub-quadrate, relatively deep. Foot protractor muscle scar pronounced and relatively large, clearly separated from anterior adductor muscle scar. Posterior adductor muscle scar indiscernible. Posterior lateral teeth absent or extremely weak.

Remarks. As far as can be evaluated based on the single internal mould from Cao Bang, this species seems to lack posterior lateral teeth, or has only a weakly developed set of these structures. According to the concepts of the genus as discussed above, it can still be assigned to *Cristaria* based on general shell shape, including distinct wings and lack of pseudocardinal teeth. Certain morphs of the extant *C. plicata* also show a markedly incurved posterior margin and strongly tapering posteroventral end as seen in *C. falcatocostata*. However, *C. falcatocostata* clearly differs from all extant and fossil species of *Cristaria* by the presence of a marked, incurved posterior ridge. In cross-section, the slight thickening of the shell in this area becomes visible. Additionally, the shell forming this ridge is slightly inflated, and thus bent outward, presumably achieving additional stabilization by this kind of construction. All more or less complete specimens from Cao Bang are moderately to

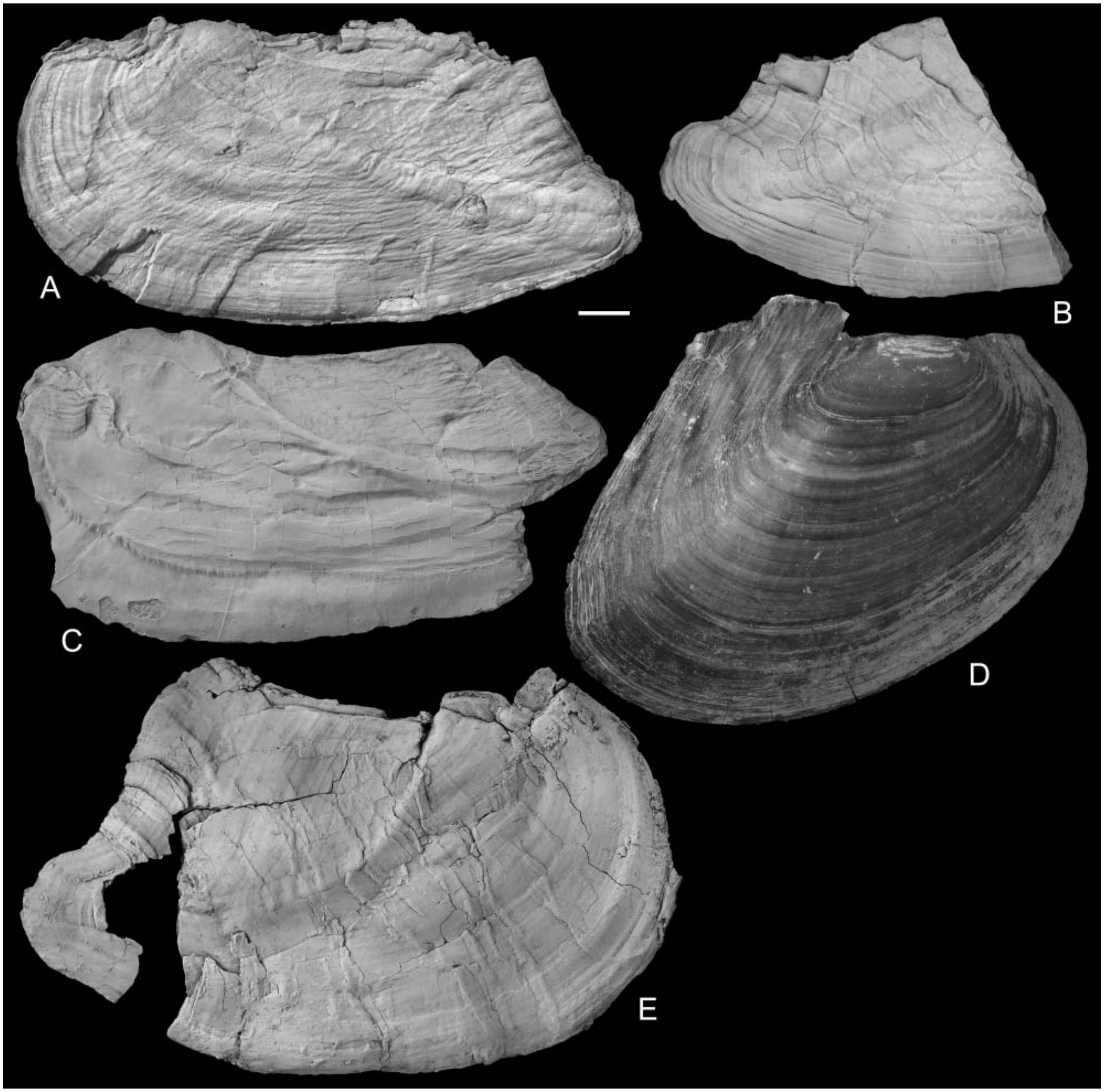

Figure 7. **A–C**, *Cristaria falcatocostata* sp. nov., Na Duong Formation, Palaeogene, Cao Bang brickyard; **A**, laterally compressed specimen with contiguous valves; left valve view; paratype, BSPG 2011 XXI 5; **B**, posterior portion of undistorted specimen with contiguous valves; right valve view; paratype, GPIT/BI/5572; **C**, internal mould of specimen with contiguous valves, showing anterior adductor muscle scar, pallial line, and posterior ridge; left valve view; paratype, GPIT/BI/5571. **D**, *Cristaria plicata* (Leach, 1815), right valve from outside view, 'Nordfluss oberh. Kanton', southern China; SMF 13171. **E**, *Cristaria falcatocostata* sp. nov., Na Duong Formation, Palaeogene, Cao Bang brickyard; laterally compressed specimen with contiguous valves; right valve view; holotype, GPIT/BI/5570. Scale bar = 10 mm.

strongly compressed, and thus measurements have to be interpreted with care. As can be inferred from fragments that were not distorted during diagenesis, the valves of this species generally were only moderately inflated. Thus, at least lateral compression (which occurs most frequently) did not significantly affect the general shell characters.

Anodontini sp.
(Fig. 8)

Material. Na Duong Formation: 3 specimens with contiguous valves, one specimen in butterfly position, 2 left valves. BSPG 2011 XXI 4, GPIT/BI/5573, GPIT/BI/5573.

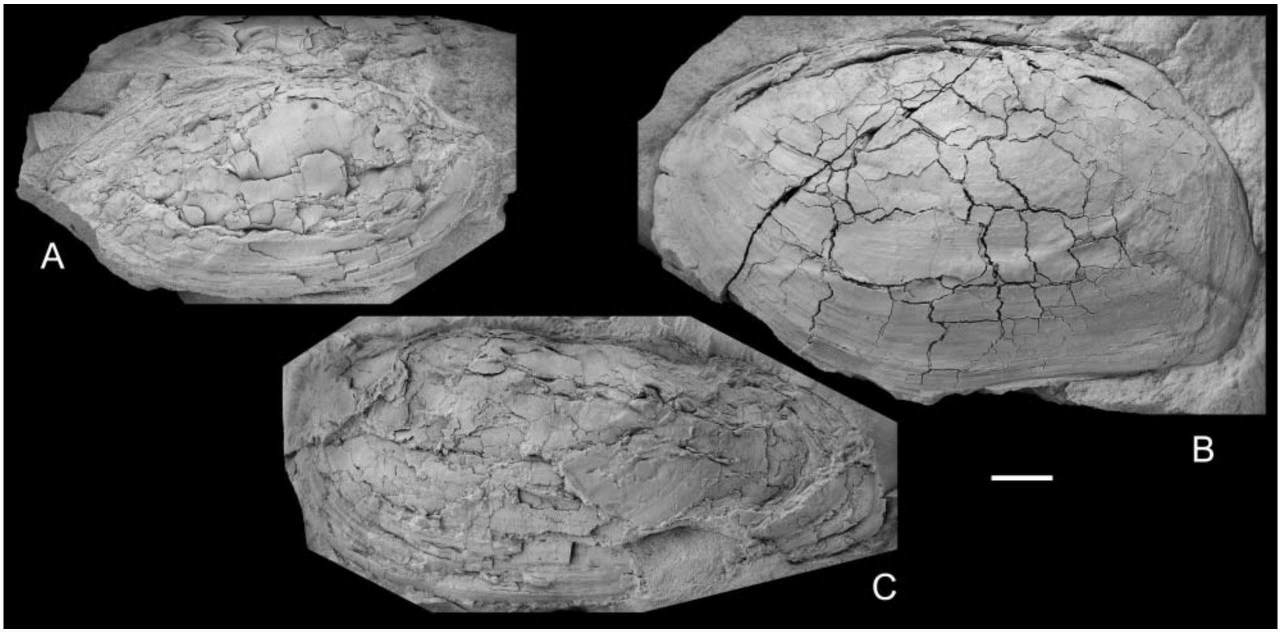

Figure 8. **A–C**, Anodontini indet., Na Duong Formation, Palaeogene, Na Duong coalmine. **A**, elongate, oval specimen; right valve, BSPG 2011 XXI 4; **B**, large, slightly angular specimen with contiguous valves; left valve view; GPIT/BI/5573; **C,** elongate specimen with slightly tapering posterior end; left valve, GPIT/BI/5574. Scale bar = 10 mm.

Dimensions. L = 73–95 mm, H = 36–55 mm.

Description. Relatively large, sub-oval, elongate-anodontiform shells. Two morphotypes present, one of them markedly elongate, with slightly tapering posterior end, the second one with high, slightly truncated posterior shell margin; dorsal and posterior margins meet at a blunt angle. Umbones faintly prosogyrous, low, only slightly inflated; positioned in anterior shell portion, at about 30% of total shell length. Shell surface smooth, with clearly distinguished growth lines. Internal shell characters unknown.

Remarks. The unspecific shape and lack of internal shell features prevent assignment of these specimens to any genus or species. From *Cristaria mothanica*, which occurs in the same horizons at Na Duong, the specimens are clearly distinguished in their more elongate shape. Although somewhat variable in outline, the six individuals are provisionally placed in the same taxon. Considering the state of preservation of most of the specimens, it is virtually impossible to evaluate whether these deviations represent a primary feature or are caused by partial compression or distortion.

Unionidae ***incertae sedis*** *sensu* Graf & Cummings, 2007

Genus ***Lamprotula*** Simpson, 1900

Type species. *Chama plumbea* Dillwyn, 1817.

Remarks. *Lamprotula* was established as a subgenus name by Simpson (1900, p. 796), with *Chama plumbea* Chemnitz, 1795 as the type species. However, today the *Neues Systematisches Conchylien-Cabinet* of Martini & Chemnitz (1769–1795) is listed in the official index of rejected and invalid works in zoological nomenclature (ICZN 1954). Apparently, Dillwyn (1817, p. 215) was the first scholar to redescribe *Chama plumbea* using valid binominal nomenclature. He clearly referred to the type specimen figured by Martini & Chemnitz (1769–1795), and thus made the name available.

Recently, *Lamprotula* has been shown to be diphyletic based on the presence of two different types of glochidia and molecular evidence. Consequently, a new genus, *Aculamprotula* Wu *et al*., 1999, was introduced for one of the groups (Wu *et al*. 1999; Zhou *et al*. 2007). Up to now, only a few out of some 20 species have been tested for their affinity to either of the genera. In particular, the studies did not include the type species, and thus the generic status of all taxa formerly included in *Lamprotula* is obscure. Consequently, *Lamprotula* is interpreted *sensu lato* herein, and retained in Unionidae *incertae sedis* following Graf & Cummings (2007).

The genus *Lamprotula* in its broad sense has a good fossil record. The stratigraphically earliest record to date comes from the ?Upper Oligocene of Japan (Ueji 1934). Several species are known from the Miocene of Mongolia (Leroy 1940) and Japan (Mizuno 1966), and from Pleistocene strata in China (e.g. Leroy 1940; Gou *et al*. 1976;

Huang 1981; Huang & Guo 1982). The specimen described as "*Lamprotula* (?) sp." by Suzuki (1944) from the Upper Oligocene of Hokkaido (Japan) is too poorly preserved to be generically assigned.

Numerous Mesozoic Unionoidea have also been assigned to *Lamprotula*. Most were placed in the subgenus *Eolamprotula* Ku (e.g. Gou *et al*. 1976). In the author's opinion, *Eolamprotula* should be elevated to genus rank and placed in the Qiyangiidae J. Chen, 1983 to include all these mainly Jurassic forms. For differences between Mesozoic and Cenozoic unionoids, see Remarks on *Cuneopsis* above.

Lamprotula hungi sp. nov.

(Figs 9, 10)

Diagnosis. Medium large, sub-circular *Lamprotula* with relatively thin shell. Ornamentation of irregular wrinkles on umbo; posterior area and posterior part of flank optionally ornamented with outward-bent flabellae and densely spaced, drop-shaped knobs. Lateral teeth strongly arcuate, keel-like, without serration.

Derivation of name. Named in honour of Nguyễn Việt Hung, retired director of the Geology Museum, Hanoi.

Material. Three compressed specimens with contiguous valves, two incomplete separate valves of a single individual, 7 (incomplete) left valves, 7 (incomplete) right valves, several smaller fragments.

Type specimens. Holotype: GPIT/BI/5575. Paratypes: BSPG 2011 XXI 2, BSPG 2011 XXI 3, BSPG 2011 XXI 1, GPIT/BI/5576, GPIT/BI/5577.

Dimensions. Min: L = 18 mm, H = 15 mm, T = 5.5 mm; Max: L = ~75 mm, H = 66.5 mm, T = 23 mm.

Type locality and occurrence. Cao Bang brickyard, Cao Bang Province, northern Vietnam.

Type stratum. Na Duong Formation, Palaeogene.

Description. Shell medium large, relatively light and thin for *Lamprotula*; well-rounded quadrate to sub-circular; anteroventral and posteroventral corners slightly angled. Umbones inflated, distinctly prosogyrous, positioned in anterior portion of shell. Faint, blunt ridge running from umbo towards posteroventral shell margin. Shell slightly but not markedly thickened in anteroventral region. Shell surface covered with distinct irregular growth lines, becoming more pronounced in anterior shell portion, some of them almost forming ridges. Umbo ornamented with several horizontal rows of strong, irregular wrinkles (Fig. 10). Some shells additionally ornamented with several slightly outward-bent flabellae extending from posterior ridge towards posterodorsal margin and closely spaced, drop-shaped knobs covering flank below posterior ridge. Knobs arranged in commarginal rows in zipper-like manner.

Hinge plate broad and massive, with a pillar-like strengthening at anterior end below umbo. Nymph moderately prominent, not protruding above shell margin, extending on posterior quarter of shell length. Hinge of left valve with massive, triangular, central pseudocardinal tooth positioned right at umbo; two faint, radially arranged anterior pseudocardinals; one narrow anterior pseudocardinal positioned almost parallel to shell margin. Pseudocardinals swelling markedly with age; central pseudocardinal becoming radially striate; anterior pseudocardinals becoming sharp, lamella-like, with deep incisions in between. Bifid, strongly arcuate posterior lateral tooth emerging from hinge plate shortly behind central cardinal tooth; branches running parallel to shell margin towards posterodorsal end of shell. Branches smooth, keel-like, almost triangular in cross-section. Hinge plate of right valve showing an almost rectangular central indentation corresponding to left valve central pseudocardinal tooth. Two narrow-lamellate rudimentary anterior pseudocardinals corresponding to indentations in left valve. Small knob-like anterior pseudocardinal next to shell margin. Single arcuate, keel-like posterior lateral tooth without serration emerging directly behind umbo.

Inner shell surface smooth. Pallial line distinct and continuous, with faint radial mantle attachment striae at inner side. Anterior adductor muscle scar deep, circular to high-oval, positioned on elevate, thickened shell region directly below hinge; internally subdivided into two or three main portions. Posterior adductor muscle scar faint to invisible. Foot protractor scar deep but small.

Remarks. Although the shell of *Lamprotula hungi* is more or less circular in outline, this species seems to be more closely related to Recent forms with elongate shells. First of all, its ornamentation of drop-shaped knobs is similar to that seen in *L. cornuumlunae*. However, in *L. hungi* these knobs are more densely spaced than in *L. cornuumlunae*. Furthermore, anterior shell weighting in *L. hungi* is much less pronounced than in extant roundish-inflated forms of similar size. Most striking, however, the specimens of *L. hungi* from Cao Bang show non-serrated, smooth posterior lateral teeth. From all extant species of *Lamprotula sensu lato*, *L. hungi* differs by the presence of a large gap in the hinge plate of the right valve, occurring directly behind the major pseudocardinal tooth. The same feature is found in *Cuneopsis quangi* from Cao Bang (see description above). Whether this feature is a synapomorphy, or rather represents an analogy, remains to be tested.

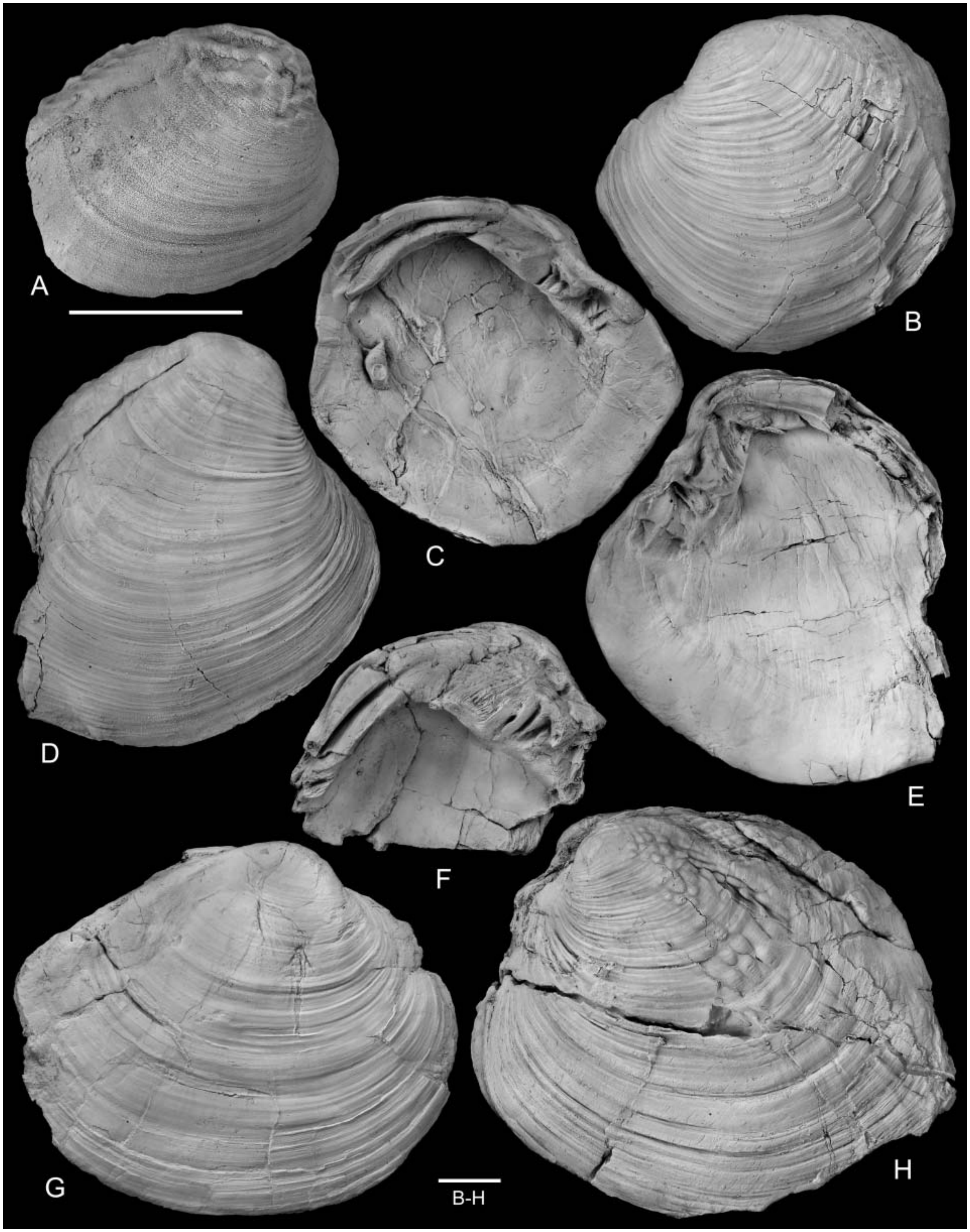

Figure 9. *Lamprotula hungi* sp. nov., Na Duong Formation, Palaeogene, Cao Bang brickyard. **A**, juvenile right valve; paratype, BSPG 2011 XXI 1. **B**, **C**, adult left valve; **B**, outside view, showing distinct growth lines; **C**, inside view; hinge teeth and deep anterior adductor muscle scar clearly visible; holotype, GPIT/BI/5575. **D**, **E**, adult right valve; **D**, outside view; **E**, inside view, showing hinge teeth and anterior adductor muscle scar; paratype, BSPG 2011 XXI 2. **F**, fragment of gerontic left valve, showing massive central pseudocardinal tooth and strongly incurved, branching posterior lateral tooth; paratype, GPIT/BI/5576. **G**, compressed, articulated adult specimen with smooth surface, right valve view; paratype, GPIT/BI/5577. **H**, slightly compressed, articulated adult specimen with strong ornamentation of densely spaced, drop-shaped knobs on posterior shell portion; paratype, BSPG 2011 XXI 3. Scale bars = 10 mm.

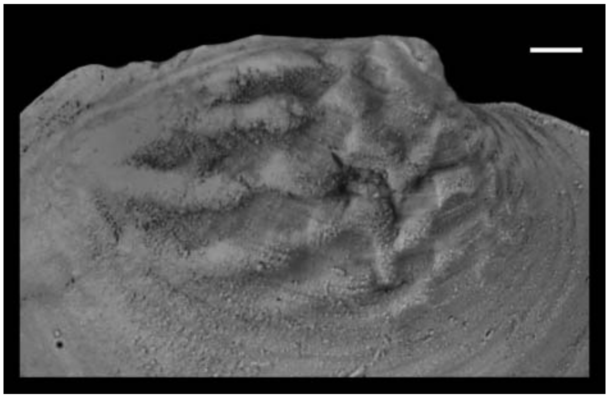

Figure 10. *Lamprotula hungi* sp. nov.; detail of Figure 9A; oblique-dorsal view, showing ornamentation of strong, irregular wrinkles; paratype, BSPG 2011 XXI 1. Scale bar = 1 mm.

?*Lamprotula* sp.

(Fig. 11A)

Material. A single, mostly undistorted external mould of an individual in butterfly position. GPIT/BI/5578.

Dimensions. L = 44 mm (fragmentary; estimated total length ~50 mm), H = 31 mm, T = ~13 mm.

Occurrence. Na Duong Formation, Palaeogene; Cao Bang brickyard, Cao Bang Province, northern Vietnam.

Description. Shell rounded-rectangular in outline, with more or less angular anterodorsal and posterodorsal corners; moderately inflated; ventral margin well-rounded. Umbones moderately pronounced, opisthogyrous, rising slightly above shell margins. Blunt, oblique ridge running from umbo towards posteroventral edge of shell. Shell surface covered with distinct, dense growth lines. Ornamentation divided into three domains. Small anterior field directly below umbones ornamented by several tiny, but strongly pronounced, rounded pustules. Central and posterior shell flank below posterior ridge covered by oblique rows of nodes, running from umbo in posteroventral direction down to ~75% of shell height. Nodes well raised from shell surface, gaining quickly in size with shell growth; almost circular during early shell growth, becoming laterally elongate with age; more or less regularly spaced, with interstices almost as wide as nodes. Area above posterior ridge ornamented with closely spaced, short, oblique, slightly incurved ridges, gaining in strength towards dorsal margin. Interior shell characters unknown.

Remarks. Since no internal shell characters are available from the specimen, assignment to *Lamprotula* cannot be verified. Nevertheless, the rounded-rectangular outline and complex ornamentation of the shell closely resemble the characters seen in several extant species of *Lamprotula*, e.g. *Lamprotula leai* (Gray in Griffith & Pidgeon, 1834) (Fig. 11B), *L. leleci* (Heude, 1875) and *L. cornuumlunae* (Heude, 1883). The latter three species have been synonymized by Haas (1969). Preliminary results from morphometry applied to the type series of several similar taxa, however, indicate certain differences (work in progress).

From *Lamprotula hungi* (L:H = ~1.1) the specimen clearly differs by its less rounded outline (L:H = ~1.6), more prominent, widely spaced and regular ornamentation, and the ornamented field below the umbones.

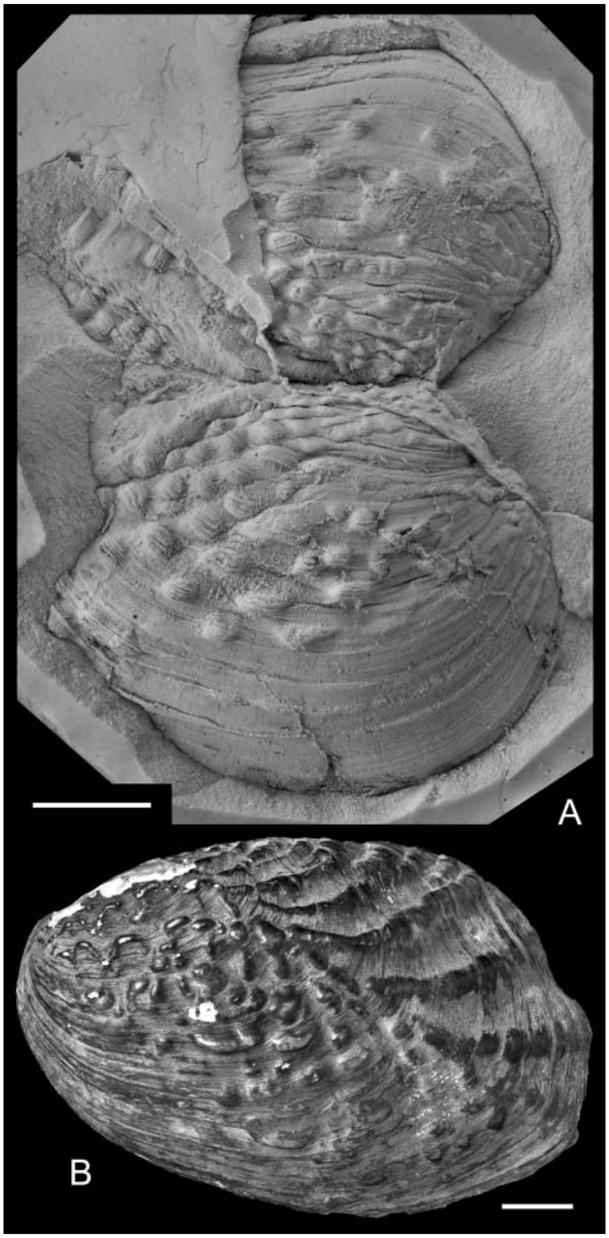

Figure 11. **A**, ?*Lamprotula* sp., composite mould of specimen in butterfly position; Na Duong Formation, Palaeogene, Cao Bang brickyard; GPIT/BI/5578. **B**, *Lamprotula leai* (Gray in Griffith & Pidgeon, 1834), outside of left valve with strong ornamentation; Recent, Tonkin (= northern Vietnam); "*Unio* (*Quadrula*) *richthofeni* v. Mrts. F. *minor*", Messager Collection, SMF 168015. Scale bars = 10 mm.

Table 1. Occurrence data for fossil unionid taxa from the Palaeogene of northern Vietnam.

Taxon	Na Duong Basin	Cao Bang Basin
?*Nodularia cunhatia* sp. nov.	×	—
Cuneopsis quangi sp. nov..	—	×
?*Cuneopsis* sp.	×	—
?*Lanceolaria* sp.	—	×
Cristaria mothanica sp. nov.	×	—
Cristaria falcatocostata sp. nov.	—	×
Anodontini sp.	×	—
Lamprotula hungi sp. nov.	—	×
?*Lamprotula* sp.	—	×

Discussion

Comparison of the Na Duong and Cao Bang basins

Although assumed to be of similar age and dominated by lacustrine environments, the Na Duong and Cao Bang basins do not share a single bivalve (or gastropod) species, and perhaps only two unionid genera (Table 1). A similar pattern can be observed with regard to the fish faunas (Böhme *et al*. 2011, unpublished data). Several explanations for this contrast can be offered: (1) a similar age is currently assumed for both basins, but still awaits confirmation by robust data from Cao Bang; this assumption could well turn out to be false; (2) the two basins were perhaps colonized by different species from independent stocks, and thus could not develop similar faunas; and (3) although both areas were flooded by lakes, the habitats at Na Duong and Cao Bang may have been significantly different. The presence of coal seams and the high content of dispersed pyrite in the sediments at Na Duong (Böhme *et al*. 2011) indicate highly eutrophic conditions, where organic material was accumulated rather than being readily degraded. Similar to modern unionids from soft water environments, the mussels from Na Duong show corroded umbones, presumably resulting from humic acid. In contrast, plant remains are scarce in the sediments from Cao Bang, and pyrite seems to be absent, pointing to a well-oxygenated lake bottom. Moreover, the umbones of all unionid species found at Cao Bang are well preserved.

At present, explanation (3) seems to be most plausible, as differences in ecology are obvious and verifiable. However, knowledge of the palaeoecology is still scarce and the stratigraphy of the outcrops unsettled, so that future research may well identify other causes of faunal differentiation.

Evolution of drainage patterns and unionid faunas

Four out of the nine unionid taxa described from the Eocene/Oligocene sedimentary infill of the Na Duong and Cao Bang basins can be identified to species level based on a sufficient quantity of well-preserved specimens showing an adequate number of characters. These four species clearly and four additional taxa quite likely belong to extant genera. As a first important result, it can thus be assumed that the generic evolution of *Nodularia*, *Cuneopsis*, *Lanceolaria*, *Cristaria* and *Lamprotula* started in the Eocene/Oligocene or even earlier. Moreover, *Cuneopsis*, *Cristaria* and *Lamprotula* are represented by two species, and thus obviously had undergone a first radiation by that time.

Generally, the distribution of unionids is related to the evolution of drainage systems (Graf & Cummings 2007). Today, a major segment of northern Vietnam is drained by the Red River, which rises from Yunnan Province (southern China) and empties into the South China Sea in the Ha Noi–Hai Phong region (Fig. 12). A small territory in the north-western part of Vietnam – including the Na Duong and Cao Bang basins – is joined to the Pearl River flow system, which covers a large area of southern China and empties in Hong Kong. To the north, both drainage regions border the catchment area of the Yangtze, which rises from the Tibetan Plateau and drains large portions of southern and central China before it flows into the East China Sea at Shanghai. Together with the Yangtze, the Mekong, which borders the Red River flow system to the south, originates from the Tibetan Plateau. Its catchment area hardly touches Vietnam, but finally, after crossing Cambodia, the Mekong empties into the South China Sea directly to the south of Ho Chi Minh City (Saigon). Major parts of Vietnam, however, are not joined to one of the larger flow systems, but drained by numerous small and comparably short rivers (small coastal rivers of Fig. 12) that rise from the Annamite Range along the border to Laos.

During the Cenozoic, the fluvial systems of South-East Asia were subject to significant modifications, which resulted from the tectonic history of the area (see geological setting section above). Based on multi-proxy provenance analyses (radiometric dating, isotope geochemistry), Clift *et al*. (2008) and Hoang *et al*. (2009) attempted to reconstruct the evolution of the Red River and adjacent flow systems since Eocene times. For Eocene to Early Miocene times, they proposed a Palaeo-Red River that drained a much larger area than today, including the middle part of the present-day Yangtze catchment area and the headwaters of the modern Pearl River (Hoang *et al*. 2009). Further to the west, the headwaters of the present-day Yangtze and Mekong were likely directed southward and emptied into a Palaeo-Salween/Irawaddy, while the severely shortened Palaeo-Mekong originated as far south as Laos. The giant Palaeo-Red River catchment area resulted in a significantly higher sediment load that was deposited in an expansive delta complex at the Vietnamese coast, major parts of which are drowned in the South China Sea today. During the Miocene, the Palaeo-Salween/Irawaddy and the Palaeo-Red River lost the Yangtze portions of their

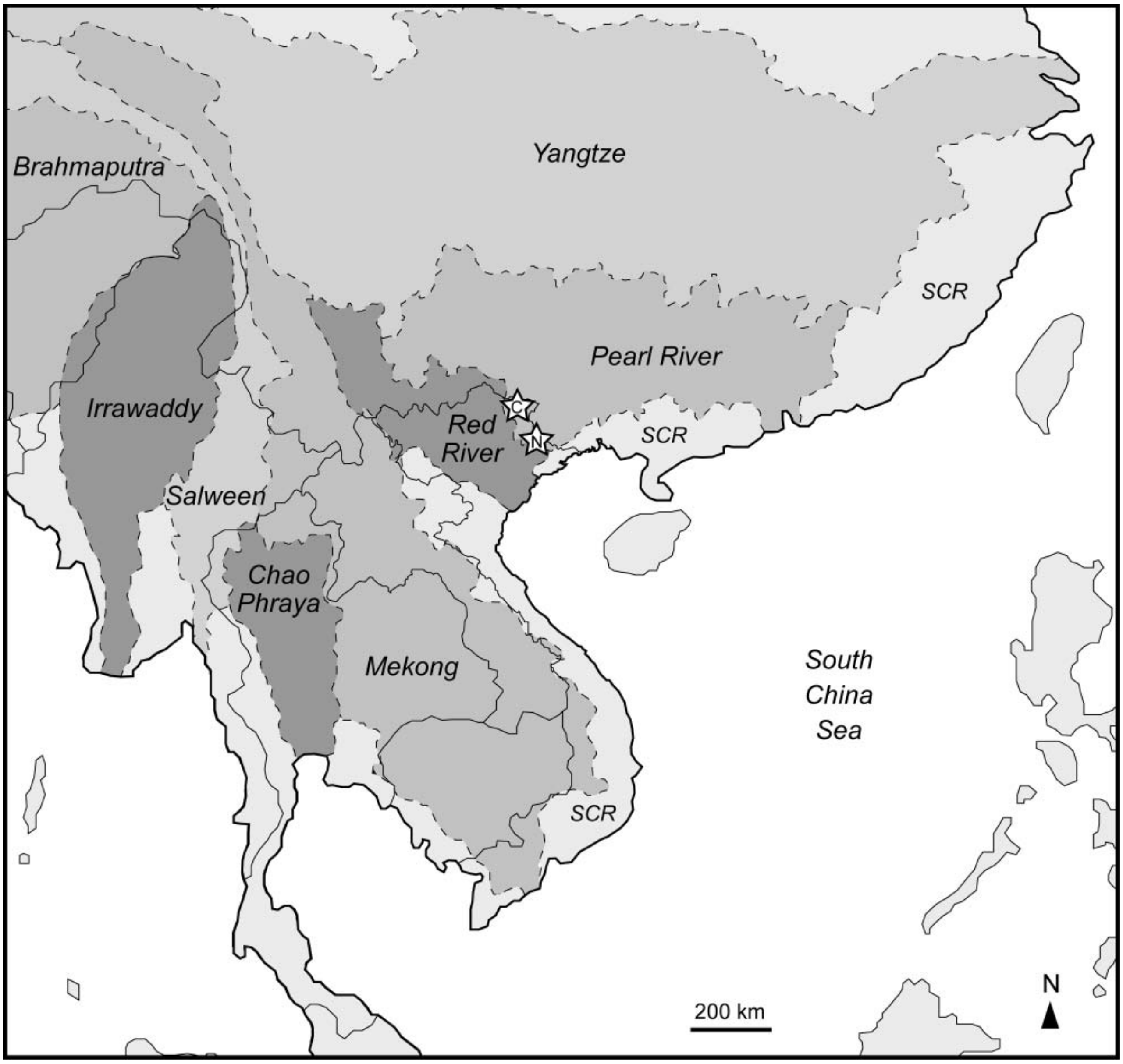

Figure 12. Overview of the drainage pattern in South-east Asia and adjacent areas of China. Catchment areas of major rivers are shaded in different tones of grey. The localities of Na Duong (N) and Cao Bang (C) are indicated by asterisks. SCA = small coastal rivers.

catchment areas, and the Yangtze was established largely in its present extent. Nevertheless, the Pearl River headwaters still supplied the Palaeo-Red River, until the rivers were disconnected in the Pliocene (Clift *et al*. 2008; Hoang *et al*. 2009).

The proposed scenario concurs with the present-day distribution of freshwater mussels and the palaeontological data presented in this study. The five genera documented as fossils from Na Duong and Cao Bang show fairly different modern distributional patterns. The distribution of *Cristaria*, namely of *C. plicata* (Leach), extends over major parts of East and South-East Asia, and the genus also enters the Mekong catchment area. However, many unionids that inhabit both rivers and lakes or ponds commonly occur over extraordinarily large areas and cross boundaries between drainage systems (Brandt 1974). Moreover, *C. plicata* may have become anthropogenically dispersed, as it has been cultured for centuries to produce nacre and pearls (e.g. Landmann *et al*. 2001). The genus *Cristaria* may thus not represent a reliable indicator for palaeogeographical reconstructions. *Nodularia* and *Lanceolaria* are spread over south-eastern Siberia, Korea, Japan, large parts of China, and northern to central Vietnam. Representatives of *Lamprotula sensu lato* inhabit rivers, lakes and ponds of

Korea, major parts of China, and northern Vietnam. Finally, the occurrence of *Cuneopsis* is restricted to east-central and south-eastern China and northern Vietnam. Summing up, all five genera share an area comprising the Yangtze, Pearl and Red River drainage systems, and probably some of the small coastal rivers of northern and central Vietnam. Considering that most of the above-mentioned genera originate from the Palaeogene, when the Palaeo-Red River was the major drainage system of the region and incorporated large areas that are drained by the Yangtze and Pearl rivers today (Clift *et al*. 2008; Hoang *et al*. 2009), this coincidence may be easily explained.

The modern faunas of the two currently largest rivers of the area, the Yangtze and Mekong, contain numerous unionid taxa indigenous and largely exclusive to one of these fluvial systems (see Haas 1969; Brandt & Temcharoen 1971; Brandt 1974; Dang *et al*. 1980; Prozorova *et al*. 2005; and Graf & Cummings 2007 for distributional data). Although both rivers originate in the mountains of southern Tibet, the major parts of their catchment areas have been well separated since the Eocene according to the models of Clift *et al*. (2008) and Hoang *et al*. (2009). Assuming that most of the modern mussel genera, including those taxa documented from Na Duong and Cao Bang, evolved earlier (i.e. during the early Palaeogene), the Yangtze and Mekong unionid faunas basically must have developed in independent radiations during this period of time. The large degree of faunal distinctness supports an effective detachment of the Yangtze and Mekong during the entire Cenozoic, preventing significant faunal exchange.

It may well be possible further to disentangle the structural geological evolution of East and South-East Asia by reconsidering particular phyletic traits in unionids from simple occurrence data. The lack of data on the actual distribution of extant Unionidae in these areas, however, prevents a more detailed analysis of the respective faunas. Moreover, the patchiness of the fossil record hampers a reconstruction of palaeogeographical patterns.

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References

Bavay, A. & **Dautzenberg, P.** 1901. Description de deux *Unio* et d'un *Corbicula* nouveaux, provenant de l'Indo-Chine. *Journal de Conchyliologie*, **49**, 5–9.

Bieler, R., **Carter, J. G.** & **Coan, E. V.** 2010. Classification of bivalve families. *Malacologia*, **52** (2), 113–133.

Böhme, M., **Prieto, J.**, **Schneider, S.**, **Hung, N. V.**, **Quang, D. D.** & **Tran, D. N.** 2011. The Cenozoic on-shore basins of Northern Vietnam: biostratigraphy, vertebrate and invertebrate faunas. *Journal of Asian Earth Sciences*, **40**, 672–687.

Brandt, R. A. M. 1974. The non-marine aquatic Mollusca of Thailand. *Archiv für Molluskenkunde*, **105**, 1–423.

Brandt, R. A. M. & **Temcharoen, P.** 1971. The molluscan fauna of the Mekong at the foci of schistosomiasis in South Laos and Cambodia. *Archiv für Molluskenkunde*, **101**, 111–140.

Chen, J. 1983. Microstructure of Early and Middle Jurassic unionids. *Transactions of the Chinese Society of Malacology*, **1**, 221–222.

Chen, J. 1987. Microstructures of Lower-Middle Jurassic unionid (Bivalvia) shells. *Acta Palaeontologica Sinica*, **26**, 8–17.

Clift, P. D. & **Sun, Z.** 2006. The sedimentary and tectonic evolution of the Yinggehai–Song Hong basin and the southern Hainan margin, South China Sea: Implications for Tibetan uplift and monsoon intensification. *Journal of Geophysical Research*, **111**, B06405, doi:10.1029/2005JB004048.

Clift, P. D., **Van Long, H.**, **Hinton, R.**, **Ellam, R. M.**, **Hannigan, R.**, **Tan, M. T.**, **Blusztajn, J.** & **Duc, N. A.** 2008. Evolving east Asian river systems reconstructed by trace element and Pb and Nd isotope variations in modern and ancient Red River-Song Hong sediments. *Geochemistry, Geophysics, Geosystems*, **9**(4), doi:10.1029/2007GC001867.

Conrad, T. A. 1853. A synopsis of the family of Naïades of North America, with notes, and a table of some of the genera and sub-genera of the family, according to their geographical distribution, and descriptions of genera and sub-genera. *Proceedings of the Academy of Natural Sciences of Philadelphia*, **6**(7), 243–269.

Dang, N. T., **Thái, T. B.** & **Phum, V. M.** 1980. *Identification manual to the freshwater invertebrate fauna of northern Vietnam*. Faculty of Science and Technology Press, Hanoi, 569. pp. [in Vietnamese].

Deshayes, G. P. 1874. Description de quelques espèces de mollusques nouveaux ou peu connus envoyés de la Chine par M. l'Abbé A. David. *Bulletin des nouvelles archives du Muséum d'Histoire Naturelle, Paris*, **9**, 3–14.

Dillwyn, L. W. 1817. *A descriptive catalogue of Recent shells, arranged according to the Linnaean method; with particular attention to the synonymy. Volume 1*. John and Arthur Arch, London, xii + 580 pp.

Dy, N. D., **Trung, P. Q.** & **An, N. Q.** 1996. New paleontological data from Cenozoic sediments of the Na Duong depression. *Geological Resources*, **1**, 287–296.

Dzanh, T. 1996. Chrono-ecological vegetative assemblage and historical development of Neogene and Neogene-Quarternary floras of Vietnam. *Palaeobotanist*, **45**, 430–439.

Frech, F. 1911. Abschliessende palaeontologische Bearbeitung der Sammlungen F. von Richthofens, die Untersuchung weiterer fossiler Reste aus den von ihm bereisten Provinzen sowie den Entwurf einer erdgeschichtlichen Uebersicht China's. Pp. 1–195 in F. F. Richthofen (ed.) *China: Ergebnisse eigener Reisen und darauf gegründeter Studien,* **5**. Reimer, Berlin.

Gilley, L. D., **Harrison, T. M.**, **Leloup, P. H.**, **Ryerson, F. J.**, **Lovera, O. M.** & **Wang, J.** 2003. Direct dating of left-lateral deformation along the Red River shear zone, China and Vietnam. *Journal of Geophysical Research*, **108**, 2127, doi:10.1029/2001JB001726.

Gong, S.-Y., **Liu, J.**, **Zhang, X.-P.**, **He, X.-G.** & **Liu, C.-F.** 2003. Studies on the growth of *Lamprotula fibrosa*. *Acta Hydrobiologica Sinica*, **27**, 521–526.

Gou, Z., **Huang, B.**, **Chen, C.**, **Wen, S.**, **Ma, Q.**, **Lan, X.**, **Xu, J.**, **Liu, L.**, **Wang, S.**, **Wang, D.**, **Qiu, R.**, **Huang, Z.**, **Zhang, Z.**, **Chen, J.** & **Wu, P.** 1976. *Chinese fossils of all groups. Fossil Lamellibranchia of China*. Nanjing Institute of Geology and Palaeontology, Academia Sinica, Science Press, Nanjing, Beijing, 150 pp. [in Chinese].

Graf, D. L. & **Cummings, K. S.** 2007. Review of the systematics and global diversity of freshwater mussel species (Bivalvia: Unionoida). *Journal of Molluscan Studies*, **73**, 291–314.

Gray, J. E. 1854. A revision of the arrangement of the families of bivalve shells (Conchifera). *Annals and Magazine of Natural History, Series 2*, **13**(77), 408–418.

Griffith, E. & **Pidgeon, E.** 1834. *The Mollusca and Radiata arranged by the Baron Cuvier, with supplementary additions to each order*. Whittaker, London, 601 pp.

Haas, F. 1929. Beitrag zur Kenntnis ostasiatischer Binnenmollusken. *Senckenbergiana Biologica*, **11**(4), 211–218.

Haas, F. 1969. Superfamilia Unionacea. In R. Mertens, W. Hennig & H. Wermuth (eds) *Das Tierreich. Eine Zusammenstellung und Kennzeichnung der rezenten Tierformen,* **88 [for 1968]**. de Gruyter, Berlin, x + 663 pp.

Heude, R. P. 1874. Diagnoses molluscorum in fluminibus provincias Nankingensis collectorum. *Journal de Conchyliologie*, **22**, 112–118.

Heude, R. P. 1875–1885. *Conchyliologie fluviatile de la Province de Nanking*. Librairie F. Savy, Paris. Premier fascicule, pls 1–8 (1875); Deuxième fascicule: pls 9–16 (1877); Troisième fascicule, pls 17–24 (1877); Quatrième fascicule, pls 25–32 (1878); Cinquième fascicule, pls 33–40 (1879); Sixième fascicule, pls 41–48 (1880); Septième fascicule, pls 49–56 (1881); Huitième fascicule, pls 57–64 (1883); Neuvième fascicule, pls 65–72 (1885); Dixième fascicule, pls 1–8 (1880). [dates according to Johnson 1973].

Hoang, L. V., **Wu, F.-Y.**, **Clift, P. D.**, **Wysocka, A.** & **Swierczewska, A.** 2009. Evaluating the evolution of the Red River system based on in situ U-Pb dating and Hf isotope analysis of zircons. *Geochemistry, Geophysics, Geosystems*, **10**(11), doi:10.1029/2009GC002819.

Hu, A.-G., **Gong, S.-Y.**, **Zhang, X.-P.**, **He, X.-G.** & **Yang, X.-F.** 2007. Comparison of survival rate and activities for *Lamprotula fibrosa*'s glochidia at three different conditions. *Acta Hydrobiologica Sinica*, **31**, 286–289.

Huang, B. 1981. The freshwater lamellibranchs from the site of the Zhenpiyan Cave in Guilin, Guangxi. *Acta Palaeontologica Sinica*, **20**, 199–206.

Huang, B. 1983. Miocene non-marine lamellibranchs from Xiacaowan, Sihong, northern Jiangsu. *Acta Palaeontologica Sinica*, **22**, 123–128.

Huang, B. & **Guo, S.** 1982. Early Pleistocene fresh-water lamellibranch fauna from Nihewan, Hebei. *Bulletin of Nanjing Institute of Geology and Palaeontology*, **5**, 231–249.

Huang, Y., **Liu, H.**, **Wu, X.** & **Ouyang, S.** 2002. Testing the relationships of Chinese freshwater Unionidae (Bivalvia) based on analysis of partial mitochondrial 16S rRNA sequences. *Journal of Molluscan Studies*, **68**, 359–363.

Huber, M. 2010. *Compendium of bivalves*. Conchbooks, Hackenheim, 904 pp.

ICZN 1954. Direction 1. *Opinions and declarations rendered by the International Commission on Zoological Nomenclature*, **3**, 401–415.

Johnson, R. I. 1973. Heude's molluscan types, or Asian land and fresh water mollusks, mostly from the People's Republic of China, described by P. Heude. *Special occasional publication, Department of Mollusks, Museum of Comparative Zoology, Harvard University*, **1**, 1–111.

Khuc, V. (ed.) 1991. *Paleontological atlas of Vietnam. Volume 3. Mollusca*. Science and Technics Publishing House, Hanoi, 207 pp.

Khuc, V., **Thanh, T. D.** & **Tri, T. V.** 2005. New schema of subdivision and correlation of on-shore Tertiary sediments in Vietnam. *Journal of Geology (Hanoi)*, **B26**, 6–12.

Landmann, N. H., **Mikkelsen, P. M.**, **Bieler, R.**, & **Bronson, B.** 2001. *Pearls – a natural history*. Harry N. Abrams, New York, 232 pp.

Lea, I. 1834. Observations on the naiades; and descriptions of new species of that and other families. *Transactions of the American Philosophical Society*, **5**(N.S.), 23–119.

Leach, W. E. 1815. *The zoological miscellany; being descriptions of new, or interesting animals. Volume 1*. McMillan, London, 144 pp.

Leloup, P. H., **Lacassin, R.**, **Tapponier, P.**, **Schärer, U.**, **Dailai, Z.**, **Xiahoan, L.**, **Liangshang, Z.** & **Trinh, P. T.** 1995. The Ailao Shan-RRSZ (Yunnan, China), Tertiary transform boundary of Indochina. *Tectonophysics*, **251**, 3–84.

Leroy, P. 1940. The Late-Cenozoic unionids of China. *Bulletin of the Geological Society of China*, **19**, 393–453.

Linnaeus, C. 1758. *Systema naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis. Editio decima, reformata*. Holmiae, 823 pp.

Liu, X.-Q. & **Wang, H.-Z.** 2008. Food web of benthic macro invertebrates in a large Yangtze River-connected lake: the role of flood disturbance. *Fundamental & Applied Limnology*, **171**, 297–309.

Long, P. D. (ed.) 2001. *Geology and Mineral Resources Map of Vietnam, Chinh Si – Long Tan sheet, 1:200.000 (F-48-XI & XVII)*. Department of Geology and Minerals of Vietnam, Hanoi.

Martens, E. von 1861. Die Japanesischen Binnenschnecken im Leidner Museum. *Malakozoologische Blätter*, **7**, 32–61.

Martens, E. von 1902. Neue Unioniden aus Tonkin und Anam. *Nachrichtsblatt der Deutschen Malakozoologischen Gesellschaft*, **34**, 130–135.

Martini, F. H. W. & **Chemnitz, J. H.** 1769–1795. *Neues systematisches Conchylien-Cabinet*. Raspe, Nürnberg. **1**, 408 pp.

(1769); **2**, 362 pp. (1773); **3**, 434 pp. (1777); **4**, 344 pp. (1780); **5**, 324 pp. (1781); **6**, 375 pp. (1782); **7**, 356 pp. (1784); **8**, 372 pp. (1785); **9** (1), 151 pp. (1786); **9** (2), 194 pp. (1786); **10**, 376 pp. (1787–8); **11**, 310 pp. (1795).

Matsuoka, K. 1988. Pliocene freshwater bivalves (*Lamprotula* and *Cuneopsis*: Unionidae) from the Iga Formation, Mie Prefecture, central Japan. *Transactions and Proceedings of the Palaeontological Society of Japan, New Series*, **149**, 417–429.

Mizuno, A. 1966. On the new Miocene unionids from the Sasebo Coal Field, western Japan. *Report, Geological Survey of Japan*, **215**, 1–12.

Mongin, D. 1963a. Les lamellibranches du "Continental intercalaire" du Sahara (Crétacé inférieur). *Mémoires de la Société Géologique de France, Nouvelle Série*, **96**, 5–51.

Mongin, D. 1963b. Une naïade géante (lamellibranche limnique) dans le "Continental intercalaire" du Niger (Sahara méridional). *Bulletin de la Société Géologique de France, 7ème Série*, **5**, 62–63.

Morley, C. K. 2002. A tectonic model for the Tertiary evolution of strike-slip faults and rift basins in SE Asia. *Tectonophysics*, **347**, 189–215.

Newell, N. D. 1965. Classification of the Bivalvia. *American Museum Novitates*, **2206**, 1–25.

Oyama, K. 1978. Late Caenozoic freshwater Mollusca from Thailand. *Geology and Palaeontology of Southeast Asia*, **19**, 161–165.

Pan, Y.-H. & **Sha, J.-G.** 2009. Middle Jurassic unionids (nonmarine Bivalvia) from the Shiwandashan Basin, southern China, with special emphasis on *Cuneopsis* Simpson. *GFF*, **131**, 183–194.

Prozorova, L. A., **Sayenko, E. M.**, **Bogatov, V. V.**, **Wu, M.** & **Liu, Y.-Y.** 2005. Bivalves of the Yangtze River drainage. *The Bulletin of the Russian Far East Malacological Society*, **9**, 46–58.

Pubellier, M., **Rangin, C.**, **Phach, P. V.**, **Que, B.C.**, **Hung, D.-T.** & **Sang, C. L.** 2003. The Cao Bang-Tien Yen Fault: Implications on the relationships between the Red River Fault and the South China Coastal Belt. *Advances in Natural Sciences*, **4**, 347–361.

Rafinesque, C. S. 1820. Monographie des coquilles bivalves fluviatiles de la rivière Ohio, contenant douze genres et soixante-huit espèces. *Annales Générales des Sciences Physiques*, **5**(13), 287–322.

Schumacher, C. F. 1817. *Essai d'un nouveau système des habitations des vers testacés*. Schultz, Copenhagen, 287 pp.

Schütt, H. & **Besenecker, H.** 1973. Eine Molluskenfauna aus dem Neogen von Chios (Ägäis). *Archiv für Molluskenkunde*, **103**, 1–29.

Searle, M. P. 2006. Role of the Red River Shear zone, Yunnan and Vietnam, in the continental extrusion of SE Asia. *Journal of the Geological Society, London*, **163**, 1025–1036.

Simpson, C. T. 1900. Synopsis of the naiades, or pearly freshwater mussels. *Proceedings of the United States National Museum*, **22**, 501–1044.

Suzuki, K. 1941a. Some non-marine shells from the Oligocene Ishikari Series in the Ishikari Coal-field, Hokkaido. *Journal of the Faculty of Science, University of Tokyo, Section 2*, **6**, 1–11.

Suzuki, K. 1941b. Notes on the Tertiary non-marine Mollusca from the coal-field of Uryu, Hokkaido. *Journal of the Faculty of Science, University of Tokyo, Section 2*, **6**, 13–37.

Suzuki, K. 1944. Notes on some Tertiary non-marine Mollusca from North Nippon. *Journal of the Geological Society of Japan*, **51**(606), 100–109 [in Japanese].

Suzuki, K. 1949. Development of the fossil non-marine molluscan faunas in Eastern Asia. *Japanese Journal of Geology and Geography*, **21**, 91–133.

Takahashi, S. 1989. A review of the origins of endemic species in Lake Biwa with special reference to the goby fish, *Chaenogobius isaza*. *Journal of Paleolimnology*, **1**, 279–292.

Thanh, T. D. & **Khuc, V.** (eds) 2006. *Stratigraphic units of Vietnam*. Vietnam National University Publishing House, Hanoi, 526 pp.

Thuy, D. K. (ed.) 2001. *Geology and Mineral Resources Map of Vietnam, Lang Son sheet, 1:200.000 (F-48-XXIII)*. Department of Geology and Minerals of Vietnam, Hanoi.

Trung, P. Q., **Quynh, P. H.**, **Bat, D.**, **An, N. Q.**, **Khoi, D. V.**, **Hieu, D. V.** & **Ngoc, N.** 2000. New palynological investigation in the Na Duong mine. *Oil and Gas Journal (Hanoi)*, **7**, 18–27 [in Vietnamese].

Tsceltzov, Y. G. 1968. Tertiary and Quaternary fauna of Vietnam. *Bjulleten' Moskovskogo Obscestva Ispytatelej Prirody, Otdel geologiceskij*, **73**(1), 153 [in Russian].

Udomkan, B., **Ratanasthien, B.**, **Takayasu, K.**, **Fyfe, W. S.**, **Sato, S.**, **Kandharosa, W.**, **Wongpornchai, P.** & **Kusakabe, M.** 2003. Fluctuation of depositional environment in the Bang Mark coal deposit, Krabi Mine, southern Thailand: stable isotope implication. *ScienceAsia*, **29**, 307–317.

Ueji, T. 1934. *Lamprotula nojimensis* n. sp., a fossil unionid from the Kitamatsuura Coal-Field, northern Kyushu, Japan. *Venus*, **4**, 284–288.

Wood, W. 1815. *General conchology; or, a description of shells, arranged according to the Linnean System, and illustrated with plates, drawn and coloured from nature. Volume 1*. John Booth, London, 246 pp.

WoRMS 2010. World register of marine species [updated at http://www.marinespecies.org/; accessed November 2010].

Wu, X., **Liang, Y.**, **Wang, H.** & **Ouyang, S.** 1999. Morphological characters of glochidia of Unionidae and the taxonomic significance. *Acta Hydrobiologica Sinica*, **23** (supplement), 139–147.

Wysocka, A. 2009. Sedimentary environments of the Neogene basins associated with the Cao Bang – Tien Yen Fault, NE Vietnam. *Acta Geologica Polonica*, **59**, 45–69.

Xie, G.-P. 1999. Tertiary bivalves from the Xianshuihe Formation of Lanzhou Basin, Gansu. *Acta Palaeontologica Sinica*, **38**, 94–101.

Yen, T.-C. 1943. Review and summary of Tertiary and Quaternary non-marine mollusks of China. *Proceedings of the Academy of Natural Sciences of Philadelphia*, **95**, 267–346.

Yokoyama, M. 1932. Tertiary Mollusca from the coalfield of Uryu, Ishikari. *Journal of the Faculty of Science, Imperial University of Tokyo, Section 2*, **3**(6), 221–247.

Zhen, S., **Di, Z.**, **Zhihong, Z.**, **Bin, X.**, **Xuelin, Q.**, **Zuoxun, Z.** & **Jianqun, J.** 2006. Research on the dynamics of the South China Sea opening: Evidence from analogue modeling. *Science in China D*, doi:10.1007/s11430–006-1053–6.

Zhou, C.-H., **Ouyang, S.**, **Wu, X.-P.** & **Li, M.** 2007. Phylogeny of the genus *Lamprotala* (Unionidae) in China based on mitochondrial DNA sequences of 16S rRNA and ND1 genes. *Acta Zoologica Sinica*, **53**, 1024–1030.

Zhu, M., **Graham, S.** & **McHargue, T.** 2009. The Red River Fault zone in the Yinggehai Basin, South China Sea. *Tectonophysics*, **476**, 397–417.