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First freshwater gastropod preserved in amber suggests long-distance dispersal during the Cretaceous Period

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Abstract

Burmese amber continues to provide unique insights into the terrestrial biota inhabiting tropical equatorial forests during mid-Cretaceous time. In contrast to the large amount and great diversity of terrestrial species retrieved so far, aquatic biota constitute rare inclusions. Here we describe the first freshwater snail ever preserved in amber. The new species *Galba prima* sp. nov. belongs in the family Lymnaeidae, today a diverse and near globally distributed family. Its inclusion in terrestrial amber is probably a result of the amphibious lifestyle typical of modern representatives of the genus. The finding of a freshwater snail on the Burma Terrane, back then an island situated at some 1500 km from mainland Asia, has implications for the dispersal mechanisms of Mesozoic lymnaeids. The Cenomanian species precedes the evolution of waterfowl, which are today considered a main vector for long-distance dispersal. In their absence, we discuss several hypotheses to explain the disjunct occurrence of the new species.

1. Introduction

Amber fossils provide a unique window into the geological past of the Earth's biosphere. The exceptional preservation of fossils in amber frequently provides access to the finest morphological details and occasionally even the shapes of organic material such as soft bodies or feathers (e.g. Poinar & Hess, 1985; Henwood, 1992; Grimaldi *et al.* 1994; Xing *et al.* 2019, 2020; Wang *et al.* 2020).

Burmese amber in northern Myanmar has provided among the most abundant fossils from amber deposits. Descriptions of amber inclusions dating back to the early 20th century (Cockerell, 1916) indicate that the region has been mined for over 100 years. Since the turn of the century, scientists have become increasingly aware of the outstanding potential of Burmese amber to advance palaeontological research. Burmese amber has provided a rare insight into mid-Cretaceous terrestrial forest environments that were creeping, crawling and slithering with insects, arachnids, myriapods, crustaceans, nematodes, annelids, snails, amphibians and reptiles (Ross, 2019). Particularly over the last decade, the excavation of exceptional fossils has attracted researchers worldwide and sparked a major wave of species discoveries (Ross, 2019). Approximately 1200 species of animal and plants have been described and many more are awaiting description (Ross, 2019; Sokol, 2019). In addition, a number of marine animals have been recorded trapped in the treacherous resin (Smith & Ross, 2018; Xing *et al.* 2018*a*; Yu *et al.* 2019).

Here, we present a novel finding of two freshwater snails of the family Lymnaeidae preserved in Burmese amber. We describe a new species and discuss the implications of this record for palaeoecology and biogeography of the Lymnaeidae. We propose five hypotheses to explain the disjunct occurrence on an island in the mid-Cretaceous Tethys Sea.

2. Materials and methods

The material derives from a former amber mine near Noije Bum in Tanaing Township in northernmost Myanmar. We are aware of the toxic situation associated with the mining of Burmese amber, involving armed conflict and civilian casualties since November 2017. While we clearly condemn the actions violating international human rights and humanitarian law, we argue in line with Haug *et al.* (2020) that our specimens were mined legally before November 2017 and do not qualify as "blood amber".

Dating of zircons embedded in the volcanoclastic matrix containing the amber yielded a maximum age of *c.* 99 Ma (Shi *et al.* 2012). This agrees with biostratigraphic data based on ammonites found in the amber-bearing beds and within the amber, indicating a late Albian – early Cenomanian age (Cruickshank & Ko, 2003; Yu *et al.* 2019).

The amber pieces containing the two shells are translucent yellow. The specimens were photographed using a Zeiss AXIO Zoom V16 microscope system with the stacking function at the State Key Laboratory of Palaeobiology and Stratigraphy, Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences (NIGPAS). The final images are composites of approximately 50 individual focal planes that were combined with the software Helicon Focus 6.

Additionally, the holotype and paratype individuals were scanned with a ZEISS Xradia 520 versa 3D X-ray microscope at the micro-CT lab of NIGPAS. A charge-coupled device detector and a 0.4× objective, providing isotropic voxel sizes from 0.5 mm with the help of geometric magnification, were used to obtain high resolution. The running voltage for the X-ray source was set at 50 kV (for NIGP1) and 60 kV (for NIGP2), and a thin filter (LE2) was applied to avoid beam-hardening artefacts. A total of 2001 projections over 360° were collected and the exposure time for each projection was set at 2 s (for NIGP1) and 2.5 s (for NIGP2) to obtain a high signal-to-noise ratio. Volume data were processed with the program VGSTUDIO MAX 3.0 (Volume Graphics, Heidelberg, Germany). Images were edited and arranged using the CorelDraw Graphics Suite X8.

Shell measurements include shell height (H), greatest width of shell perpendicular to height (D), aperture height parallel to shell height (h) and aperture width perpendicular to aperture height (d). All specimens are stored at the collection of NIGPAS. The publication and the nomenclatural act contained here are registered under http://zoobank.org/urn:lsid:zoobank.org:pub:6A5BFAA2-D508-4D63-861A-6DDDB071B689.

3. Systematic palaeontology

Class GASTROPODA Cuvier, 1795
Subclass HETEROBRANCHIA Burmeister, 1837
Superorder HYGROPHILA Férussac, 1822
Superfamily LYMNAEOIDEA Rafinesque, 1815
Family LYMNAEIDAE Rafinesque, 1815
Genus *Galba* Schrank, 1803
Type species. *Galba truncatula* O. F. Müller, 1774; type by subsequent designation; Recent, Europe.

Galba prima sp. nov.

(Fig. 1)

ZooBank LSID: urn:lsid:zoobank.org:act:095524C3-D5A1-4DC5-A26B-5142A2D39B5A

Derivation of name. The species epithet refers to it being the first freshwater gastropod species found in amber.

Holotype. NIGP173920.

Paratype. NIGP173921.

Type locality and horizon. Former amber mine near Noije Bum Village, Tanaing Township, Myitkyina District, Kachin State, northern Myanmar (26° 15' N, 96° 33' E); unnamed horizon, mid-Cretaceous, lower Cenomanian, *c.* 99 Ma.

Diagnosis. Small shell with slightly coeloconoid spire, weakly stepped whorls separated by deep suture, large and inflated body whorl, slender ovate aperture, nearly straight columella without fold, and small, circular umbilicus.

Description. Shell small, consisting of about 6–6.5 whorls. Height:width ratio is 1.66 (paratype) and 1.84 (holotype). Protoconch blunt, low domical; no surface details visible. Spire slightly coeloconoid, spire angle 60–65°. Whorls stepped, with straight-sided or weakly convex lower part and strongly convex upper part; whorls separated by deep suture; spire whorls increase gradually in height, with the last whorl being broad, slightly inflated and 71–78% of total shell height. Columella not twisted, forming almost straight pillar from apex to umbilicus. Peristome thin and sharp all around aperture; columellar lip slightly reflected towards umbilicus. Umbilicus small, circular, *c.* 0.25 mm in diameter. Aperture slender ovoid, adapically angulated, not expanded; height of aperture attains 57–63% of total height. Surface smooth except for faint, weakly prosocline growth lines.

Measurements. Holotype: $H = 7.89$ mm, $D = 4.28$ mm, $h = 4.34$ mm, $d = 2.38$ mm; paratype: $H = 6.19$ mm, $D = 3.74$ mm, $h = 3.69$ mm, $d = 1.61$ mm.

Remarks. Modern genus classification of extant Lymnaeidae is largely based on anatomical characteristics and molecular data (e.g. Correa *et al.* 2010; Vinarski 2013), while fossil shells can only be distinguished based on general morphology, sculpture and protoconch characteristics. We attribute the species to the genus *Galba* due to the small shell with stepped whorls, the inflated and expanded body whorl, the comparatively small, non-expanded aperture, the thin peristome without columellar fold (Fig. 1c, g, h) and the presence of an umbilicus (Fig. 1f).

Species of *Aenigmomphiscola* Kruglov & Starobogatov, 1981, *Hinkleyia* Baker, 1928, *Ladislavella* Dybowski, 1913, *Omphiscola* Rafinesque, 1819, *Stagnicola* Jeffreys, 1830 and *Walterigalba* Kruglov & Starobogatov, 1985 have more elongated shells, often with cyrtoconoid spires, and columella folds, while *Ampullaceana* Servain, 1882, *Peregriana* Servain, 1882 and *Radix* Montfort, 1810 species are typically more globular with broader apertures (Vinarski & Grebennikov, 2012; Vinarski *et al.* 2017, 2020*a*; Glöer, 2019). Even the more slender representatives of *Radix*, such as *Radix labiata* (Rossmässler, 1835), can be well distinguished from *Galba prima* sp. nov. by their expanded apertures. *Lymnaea* s.s. species are much larger and have a twisted axis (Vinarski, 2015; Anistratenko *et al.* 2018; Glöer, 2019). Similarly, shells of *Bulimnea* Haldeman, 1841 have a twisted columella and lack an umbilicus (Baker, 1911). The Australian *Austropeplea* Cotton, 1942 also bears a more expanded aperture and no umbilicus (Dell, 1956; Ponder *et al.* 2020).

Some species of *Orientogalba* Kruglov & Starobogatov, 1985, a genus native to Asia, have a similar shell habitus with inflated body whorl and short spire, such as *O. viridis* (Quoy & Gaimard, 1833–1835) and *O. ollula* (Gould, 1859), but they lack the umbilicus (Vinarski *et al.* 2020*a*). Also, *O. viridis* has an expanded aperture (Vinarski *et al.* 2020*a*). *Orientogalba lenaensis* (Kruglov & Starobogatov, 1985), in turn, is much more slender and has a high spire (Sitnikova *et al.* 2014).

The fossil Mesozoic genus *Proauricula* Huckriede, 1967, which was tentatively considered a basal basommatophoran and predecessor of modern Lymnaeidae by Bandel (1991), has a more slender shell with columellar plicae and distinct spiral striation on the teleoconch (Huckriede, 1967; Bandel, 1991; Pan & Zhu, 2007). In fact, the overall shape and especially the distinct columellar plicae make a relationship to Lymnaeidae very unlikely. The shape and apertural characteristics are more similar to Ellobiidae, where the genus was originally placed by Huckriede (1967) and which

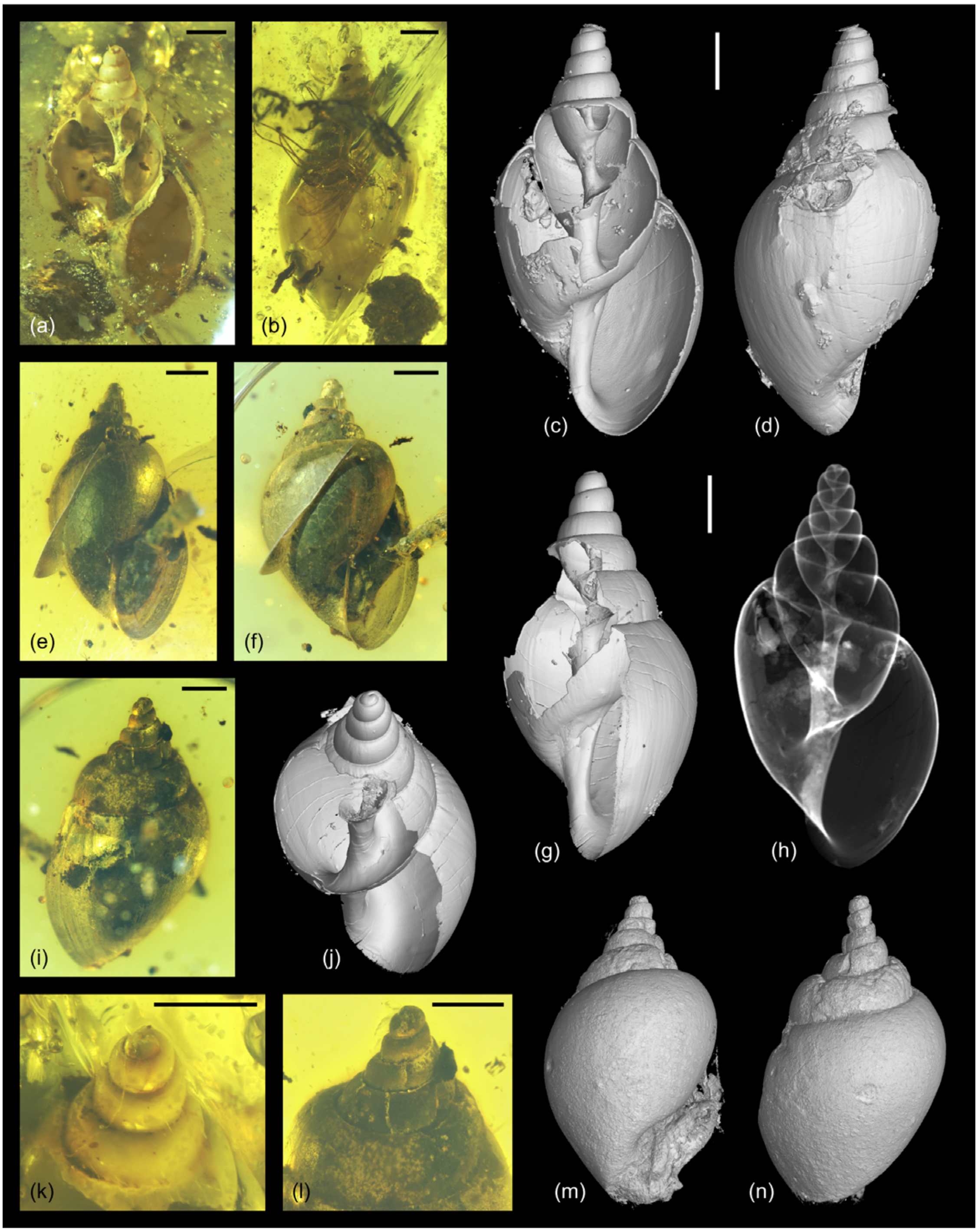

Fig. 1. (Colour online) *Galba prima* sp. nov. (a–d, g, h, j, k) holotype (NIGP173920). (e, f, i, l–n) paratype (NIGP173921); note the spire is slightly deformed. (c, d, g, j, m, n) are microtomographic reconstructions; (h) shows surface rendering with transparency. All scale bars represent 1 mm.

was also adopted by Pan & Zhu (2007). Here, we accept this original classification and place Proauricula tentatively in the Ellobiidae. That family was well represented during the Mesozoic Era by several genera and species (Yen, 1951, 1952*a*, *b*, 1954; Bandel, 1991; Bandel & Riedel, 1994; Pan & Zhu, 2007; Isaji, 2010).

Of the 13 mid-Cretaceous lymnaeids, only two species are currently classified in *Galba*, that is, *G. yongkangensis* Yü in Yü & Pan, 1980 and *G. meikiensis* Yü in Yü & Pan, 1980 from the Albian Guantou Formation in China. The former is more elongate and has a cyrtoconoid spire, while the latter can be distinguished from *Galba prima* sp. nov. by its higher last and penultimate whorl (Yü & Pan, 1980). Similarly, *Radix undensis* Martinson, 1956 from Aptian–Albian strata of Siberia has a higher, globular last whorl and a very short spire. The four Cenomanian species from France, introduced in the genus “*Limnaea*” by Repelin (1902), are more slender and have higher spires; only some specimens of *L. munieri* Repelin, 1902 have a similar morphology, but the species clearly differs from *G. prima* sp. nov. in having convex, non-stepped whorls. The American “*Lymnaea*” *nitidula* (Meek, 1860), “*Lymnaea*” *ativuncula* White, 1886 and “*Lymnaea*” *tengchieni* Kadolsky, 1995 (= *L. cretacea* Yen, 1951, non Thomä, 1845) are distinctly more slender, while "*Lymnaea*" *sagensis* Yen, 1946 has a globular shell and more reminiscent of a viviparid than a lymnaeid. An unidentified ?*Austropeplea* sp. from Albian–Cenomanian strata of New Zealand is only incompletely preserved, but the species appears to be broader and bears spiral microsculpture.

4. Discussion

Unsurprisingly, amber mostly preserves terrestrial biota, but a number of freshwater organisms are also known from amber deposits, including arthropods, nematodes and amoebae (Gray, 1988; Schmidt *et al.* 2004; Yu *et al.* 2019). The species described herein is the first freshwater snail ever recorded in amber. This mode of preservation is likely due to the species' lifestyle and aquatic niche: several extant members of the Lymnaeidae, including species of *Galba*, are amphibious (Dillon, 2000). For example, *Galba truncatula* (Müller, 1774) is commonly found outside the water and can withstand droughts for an extensive period of time; some individuals have been found surviving for over a year in aestivation (Kendall, 1949). However, extensive droughts were rather unlikely in the Cenomanian tropical forests of the Burma Terrane (Poinar *et al.* 2007; Xing *et al.* 2018*b*; Yu *et al.* 2019). Rather, the snail might have been captured in resin flowing down or dropping from trees close to a water body. Since extant *Galba* is typically found in stagnant and often temporary water bodies, such as lakes, ponds, ditches, mires and puddles (Kendall, 1949; Økland, 1990), we assume a similar aquatic biome close to the place of deposition.

The present finding also has implications for the biogeography of the family Lymnaeidae. *Galba prima* sp. nov. is among the few fossil Lymnaeidae known from early Late Cretaceous time. The only other relatives of similar age have been reported from Cenomanian strata of France (Repelin, 1902) and the Albian–Cenomanian deposits of New Zealand (Beu *et al.* 2014; see also Section 3 above on Systematic Palaeontology). Slightly older records have been documented from Aptian–Albian strata of North America (White, 1886; Yen, 1946, 1951, 1954), Russia (Martinson, 1956) and China (Yü & Pan, 1980; Pan & Zhu, 2007).

However, *Galba prima* sp. nov. is not the earliest member of the genus; alleged records of *Galba* date back to the Middle Jurassic Epoch of China (Pan, 1977; Yü & Pan, 1980). Their attribution to the genus (and in some cases even to the family Lymnaeidae) has not yet been confirmed with certainty and requires a detailed reassessment of the respective species.

The disjunct distribution of the family and particularly the isolated occurrence of *Galba prima* sp. nov. on the Burma Terrane are striking – how did a freshwater snail reach an island at least 1500 km from the nearest mainland (Fig. 2)? In the following, we propose five hypotheses that could explain the disjunct occurrence. Some of these hypotheses may also serve as an explanatory model for the existence of terrestrial and other freshwater biota on the Burma Terrane. All hypotheses rely on the recently published tectonic model for the Burma Terrane as an island in the Cenomanian Tethys Ocean (Westerweel *et al.* 2019; Fig. 2).

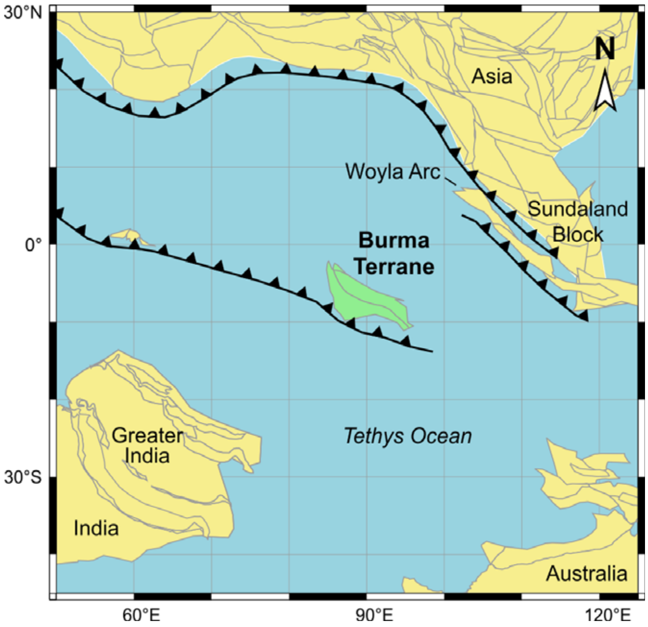

Fig. 2. (Colour online) Reconstruction of the Burma Terrane during the Cenomanian Age (95 Ma). Modified from Westerweel *et al.* (2019).

(1) Modern Lymnaeidae, as well as many other freshwater snails, are commonly distributed via waterbirds (Green & Figuerola, 2005; Kappes & Haase, 2012; van Leeuwen & van der Velde, 2012; van Leeuwen *et al.* 2012, 2013; Vinarski *et al.* 2020*b*). Although some species may occasionally be transported by song birds (e.g. Zenzal *et al.* 2017), this seems to be the exception rather than the rule. Passive transport of snails via travelling and migrating birds provides a unique opportunity for long-distance dispersal across watersheds. Snails travel attached to feathers or feet and can survive ingestion and defecation. Dispersal via waterfowl has been hypothesized to explain many a disjunct fossil occurrence in Cenozoic strata (Harzhauser *et al.* 2016; Aksenova *et al.* 2018; Esu & Girotti, 2018) and likely contributed markedly to the already large distribution of the family in Mesozoic strata. However, waterfowl (Anseriformes) did not evolve before latest Cretaceous time, and even the oldest neognathe bird is younger than the new Cenomanian Lymnaeidae (*c.* 85 Ma according to Claramunt & Cracraft, 2015). Little is known about the flight capabilities of Mesozoic birds. Early Cretaceous ornithurines already possessed anatomical features similar to those of modern migratory birds, such as a keeled sternum (Falk, 2011). Based on the appearance of the same types of bird routes across great distances, Falk (2011) suggested that ornithurine birds might have evolved long-distance migration in or before the Early Cretaceous Epoch, but clear evidence is lacking. Enantiornithines, a group widely represented in the global Cretaceous fossil record, have been recorded several times in Burmese amber (Xing *et al.* 2016, 2017, 2019, 2020). Their plumage would likely have been suitable for transporting the tiny snail, but current knowledge indicates that this group was only capable of flap-gliding and bounding flight (e.g. Liu *et al.* 2017; Serrano *et al.* 2018). Probably, enantiornithines were already present on the Burma Terrane before it detached from Gondwana during the Jurassic Period (Matthews *et al.* 2016).

(2) An alternative winged animal group existing during the Cenomanian Age were pterosaurs (Order Pterosauria). So far, they have not been considered potential dispersal agents for invertebrates, but previous studies suggest that Cretaceous pterosaurs may have dispersed angiosperm seeds (Fleming & Lips, 1991). In addition to the aforementioned ornithurine birds, pterosaurs were likely capable of long-distance travels

(Witton & Habib, 2010). Some species probably fed on molluscs (Bestwick *et al.* 2018). Pterosaurs may therefore have dispersed freshwater snails via ingestion or by attachment to the feet or scales on the legs or tail, comparable to similar occurrences in modern birds. However, no pterosaur fossil has so far been retrieved from Burmese amber deposits that could potentially support this hypothesis. Other animal groups, such as amphibians or larger insects, which have occasionally been found carrying freshwater molluscs (e.g. Walther *et al.* 2008; Kolenda *et al.* 2017), are unlikely to play a significant role in long-distance dispersal.

(3) Driftwood is known to be a potential transoceanic vector for terrestrial and amphibious animals (e.g. Trewick, 2001; Measey *et al.* 2007) as well as brackish-water gastropods, such as Littorinidae (Reid, 1986) or estuarine Neritidae (Kano *et al.* 2013). While these brackish-water snails have a marine larval phase facilitating wider dispersal, Lymnaeidae are restricted to freshwater environments. We cannot exclude that *Galba prima* sp. nov. boarded driftwood in a river or estuary and survived the long journey (perhaps during aestivation), but we believe it is fairly unlikely given the great distance and ecological constraints. However, driftwood (or any kind of drifting islands) may have facilitated dispersal of Cenomanian land snails (compare Dörge *et al.* 1999), which may have had a higher chance of long-term survival due to their ability to close the shell with an operculum or epiphragm (Ożgo *et al.* 2016).

(4) Several studies have indicated the possibility of dispersal via wind, particularly strong storms. Numerous examples of "raining fishes" exist from the recent past as well as historical documents worldwide, where storms carried both marine and freshwater fishes over large distances (Rees, 1965). A case of freshwater *Anodonta*, a genus of unionid bivalves, raining down over Germany after a storm was reported in the 19th century (Rees, 1965). Ożgo *et al.* (2016) demonstrated land snail dispersal by strong storms in northern Europe. They concluded that wind currents associated with storm cells may also facilitate long-distance dispersal. A similar hypothesis was proposed by Vagvolgyi (1975) explaining how land snails could colonize remote Pacific islands. The terrestrial ecosystems in the area that comprises Southeast Asia today were also likely perturbed by tropical storms as long ago as during the Cenomanian Age. Considering the overall high temperature in the Cretaceous greenhouse (Mills *et al.* 2019), storm frequency and intensity were probably higher than today (Ghosh *et al.* 2018). The prevailing wind stress reconstructed for the mid-Cretaceous period by Poulsen *et al.* (1998) points from mainland Asia towards the Tethys Ocean, matching the required dispersal direction. Since the Burma Terrane was south of the equator during the Cenomanian Age according to the latest palaeogeographic model (Westerweel *et al.* 2019), the only storms that could potentially transport the snails towards the Burma Terrane would have originated in the southern Woyla Arc or the southern Sundaland Block and moved westwards along the Southern Hemisphere trade winds (Fig. 2). However, no fossil record is available to support this hypothesis.

(5) Finally, Lymnaeidae may have reached the Burma Terrane when it was still attached to Gondwana prior to the opening of the Neotethys Ocean during latest Jurassic time (Matthews *et al.* 2016) and they survived there until the Cenomanian Age (without fossil record). However, this still leaves open how the family got there in the Jurassic Period, when their fossil record was limited to the Northern Hemisphere. Despite the patchiness of the fossil record, especially for freshwater habitats during the Mesozoic Era, the lack of any evidence makes this, in our opinion, the least plausible hypothesis.

Given the uncertainties involved in many of these hypotheses, we do not support a particular explanation model. However, considering the great distance and ecological constraints, we believe airborne dispersal – whether via ornithurine birds, pterosaurs or storms – is the most plausible means.

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Conflict of interest. None.

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