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Short communication

New terrestrial gastropods of Pupinidae and Diplommatinidae (Cyclophoroidea) from mid-Cretaceous Burmese amber

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ABSTRACT

Land snails in mid-Cretaceous Burmese amber have aroused interest from palaeontologists in recent years. Here we describe three newly discovered species and a new genus belonging to families Pupinidae and Diplommatinidae: *Cretatortulosa cretakachinensis* sp. nov., *Rhaphaulus zhuoi* sp. nov. and *Pulchraspira teneristoma* gen. et sp. nov., using classic light microscopy and modern micro-CT scans with computer 3D reconstructions. *Rhaphaulus zhuoi* sp. nov represents the earliest fossil record of the genus *Rhaphaulus*. Our discoveries increase known species diversity of families Pupinidae and Diplommatinidae (Cyclophoroidea) during the Cretaceous of Asia. We compare these new taxa with fossil and extant representatives, discuss their significance in the context of the Pupinidae and Diplommatinidae fossil record, and consider habitats and feeding habits with reference to extant cyclophoroideans.

1. Introduction

Cyclophoroidea are characteristic and dominant terrestrial gastropods of tropical forests in East and South Asia (Kongim et al., 2013; Neubert and Bouchet, 2015). There has been increasing research interest of this species-rich superfamily due to its diversity of shell shapes, including molecular systematics, taxonomy and evolutionary history (e.g. Tielecke, 1940; Barker, 2001; Ponder et al., 2008; Hirano et al., 2019). In the past three years, fifteen well-preserved fossil species (five assigned to Cyclophoridae, four to Diplommatinidae, and six to Pupinidae; mostly new genera and species) from Burmese amber have been described, pushing back the early records of Asian Cyclophoroidea, and of Pupinidae in particular, to the mid-Cretaceous (Yu et al., 2018; Xing et al., 2019; Neubauer et al., 2019; Hirano et al., 2019; Bullis et al., 2020; Balashov, 2020).

Pupinidae Pfeiffer, 1853 is a rather large family of terrestrial snails, generally characterized by the pupoid shell, with a circular aperture and thickened peristome, which in most cases is interrupted by canals (Thiele, 1992). The Diplommatinidae Pfeiffer, 1857 are characterized by small conical, spindle-shaped or almost cylindrical shells, with a usually irregularly coiled spire and a more or less distinctive constriction of the last whorl (Nurinsiyah and Hausdorf, 2017), though several genera have regularly-coiled shells, such as *Kontschania* Páll-Gergely and Grego, 2020 and *Habeastrum* Simone, 2019. Furthermore, diplommatinid species are often equipped with internal lamellae and plicae (Kobelt, 1902; Thiele, 1929), though in some taxa (e.g., *Arinia* H. Adams and A. Adams, 1856, *Helicomorpha* Möllendorff, 1890, *Opisthostoma* W. T. Blanford and H. F. Blanford, 1860, *Palaina* O. Semper, 1865, *Plectostoma* H. Adams, 1865) these are strongly reduced or entirely absent (Páll-Gergely and Grego, 2020), especially in genera spread over Southeast Asia, which is probably the most important biodiversity hotspot of this family (Egorov, 2013). Furthermore two diplommatinid genera from Burmese amber also display reduced internal barriers: *Euthema* Yu, Wang and Pan, 2018 and *Xenostoma* Bullis, Herhold, Czekanski-Moir, Grimaldi and Rundell, 2020.

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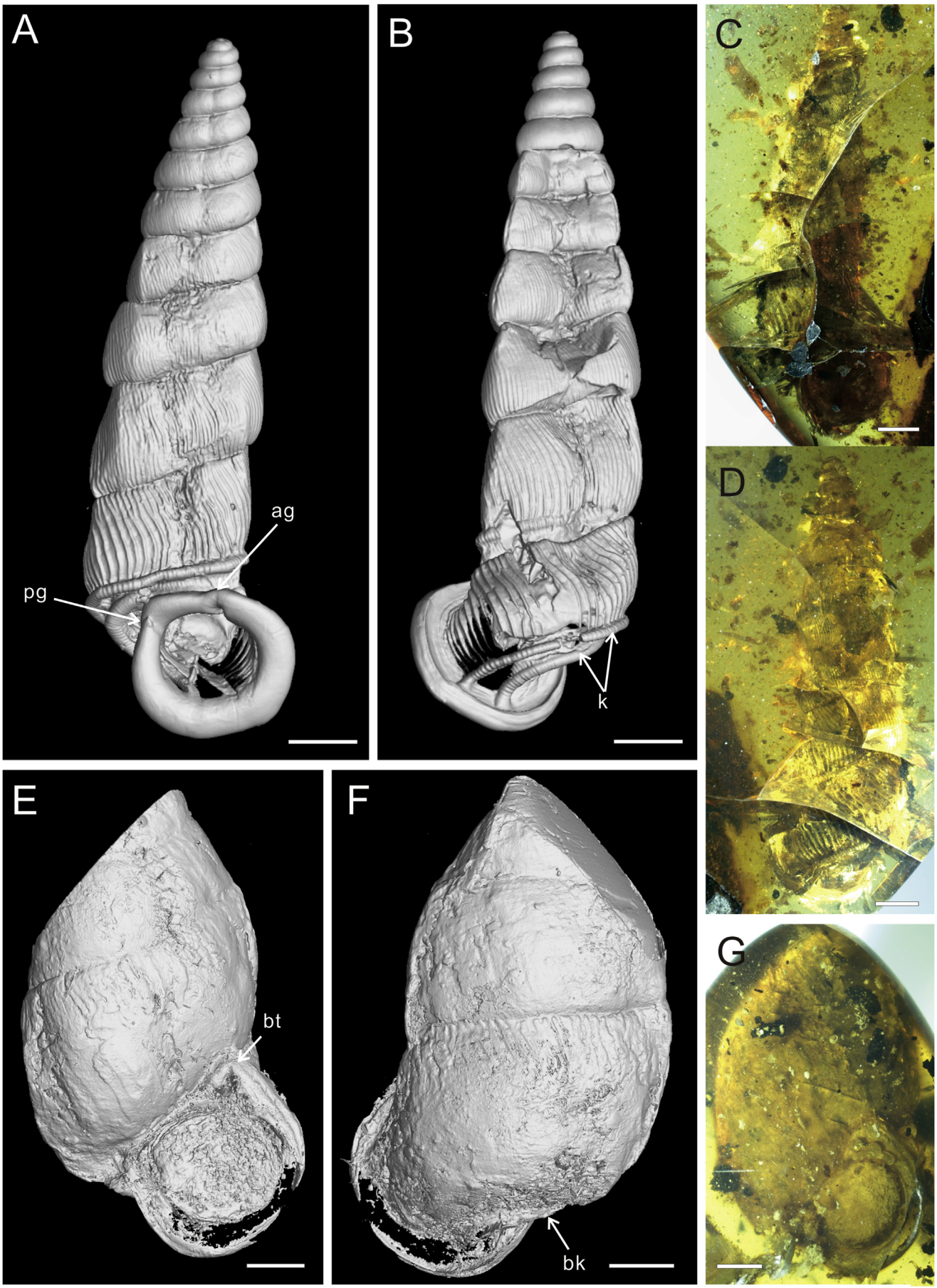
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Here we describe two new species of Pupinidae and one new genus and species of Diplommatinidae from mid-Cretaceous Burmese amber. Our finds increase known species diversity of families Pupinidae and Diplommatinidae in mid-Cretaceous tropical amber rainforest.

2. Material and methods

The specimens were obtained from a former amber mine located near Noije Bum Village, Tanaing Township, in northernmost Myanmar. The U–Pb dating of zircons from the volcanoclastic matrix of the amber indicated a maximum age of approximately 99 Ma for the deposits (Shi et al., 2012). Some ammonites found in the amber-bearing beds and within the amber corroborate a late Albian–early Cenomanian age (Cruickshank and Ko, 2003; Yu et al., 2019).

The amber pieces containing gastropods are translucent yellow. Photographs were taken using a Zeiss AXIO Zoom V16 microscope system at the State Key Laboratory of Palaeobiology and Stratigraphy, Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences (NIGPAS). All images are digitally stacked photomicrographic composites of approximately 50 individual focal planes that were obtained using the Helicon Focus 6 software for better illustration of the 3D structures. All images and figures were prepared with the aid of CorelDraw X4 and Adobe Photoshop CS3. The specimens are housed at NIGPAS.

We scanned the holotypes in the micro-CT lab of NIGPAS using a 3D X-ray microscope (3D-XRM), Zeiss Xradia 520 versa for additional detail. Unlike conventional micro-CT, which relies on maximum geometric magnification and a flat panel detector to achieve high resolution, the 3D-XRM uses CCD-based objectives to get higher spatial resolution. A CCD-based 0.4× objective was used, providing isotropic voxel sizes from 0.5 mm with the help of geometric magnification. During the scan, the running voltage for the X-ray source was set at 60 kV (NIGP173321) and 50 kV (NIGP173322, NIGP173323), and a thin filter (LE2) was used to avoid beam-hardening artefacts. To get a high signal-to-noise ratio, 2001 projections over 360° were collected and the exposure time for each projection was set at 2s (for NIGP173321), 4.5s (for NIGP173322) and 3s (for NIGP173323). Volume data processing was performed using the software Vgstudio Max (version 3.0, Volume Graphics, Heidelberg, Germany).

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.

3. Systematic palaeontology

Superfamily: Cyclophoroidea Gray, 1847
Family: Pupinidae L. Preiffer, 1853

Cretatortulosa Yu, Wang and Pan, 2018
Type species: *Cretatortulosa multilinea* Yu, Wang and Pan, 2018, mid-Cretaceous; northern Myanmar.

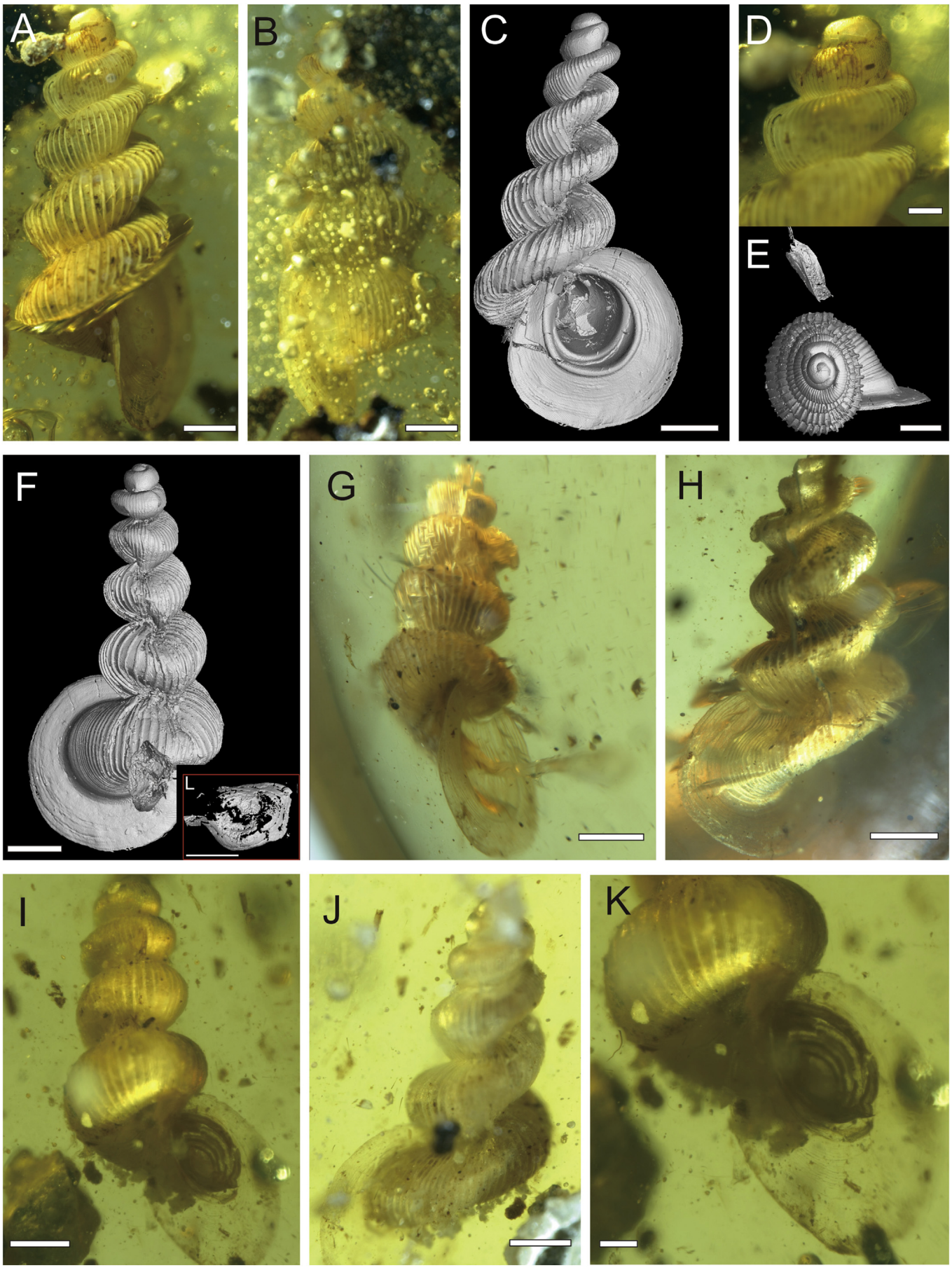
Remarks. The slender turriform shell shape of *Cretatortulosa* is easily distinguishable from typical pupinid genera with pupoid shell shape (e.g., *Pupina* Vignard, 1829, *Pupinella* Gray, 1850, *Pollicaria* A. Gould, 1856, *Streptaulus* Benson, 1857, *Rhaphaulus* L. Pfeiffer 1856, and *Schistoloma* Kobelt, 1902). It can also be instantly distinguished from species with turriform shells such as *Csomapupa* Páll-Gergely, 2015 and *Pseudopomatias* Möllendorff 1885, which have no keels around the whorls (Páll-Gergely et al., 2015). It also differs from *Tortulosa* Gray, 1847, *Nodopomatias* Gude, 1921 and *Vargapupa* Páll-Gergely, 2015 in having two keels. The basal keel of *Tortulosa* and *Nodopomatias* terminates just behind the peristome lip and that of *Vargapupa* flattens gradually on the ventral side of the body whorl, whereas that of *Cretatortulosa* terminates on the dorsolateral side of the penultimate whorl. *Cretatortulosa* further differs from *Tortulosa* in not having a fully detached body whorl and lacking a hemispherical opening well to the left and above the lowest point of the lip, plus a basal canal on the inner margin. *Cretatortulosa* also differs from *Streptaulus* and *Rhaphaulus* in having no complete tube at the posterior edge of the aperture (Páll-Gergely et al., 2014).

Cretatortulosa cretakachinensis sp. nov.
Fig. 1(A–D)

ZooBank LSID rn:lsid:zoobank.org:act:1B49A124-B6DB-4297-AD50-EA8740812E4B

Etymology. This species name is a combination of the prefix *creta-* referring to the age of the fossil (Cretaceous) and the location where the specimen was found (Kachin State, northern Myanmar).
Holotype. NIGP173321.
Type locality and horizon. Noije Bum Village, Tanaing Township, Myitkyina District, Kachin State, northern Myanmar (26°15′ N, 96°33′ E); unnamed horizon, mid Cretaceous, upper Albian or lower Cenomanian.
Diagnosis. Shell medium sized, slender, turriform, high-spired, regularly ribbed; aperture rounded, peristome thickened, broadened, somewhat relaxed and interrupted by two grooves; anterior groove situated on parietal–palatal transition and forming a deep one; posterior groove situated on columellar–parietal region and forming a shallow one; two keels exist on low part of shell, main keel starting from back side of bottom apertural rim and terminating on dorsolateral side of penultimate whorl; second keel present between main keel and umbilicus, starting from back side of most basal point of apertural rim, and terminating on ventrolateral side.
Description. Shell minute, apparently slightly compressed, with slender turriform shape, and about 11 regularly increasing, rather flat whorls; teleoconch highly spired, penultimate whorl and body whorl occupying nearly half of shell height; suture distinct, impressed and slightly oblique at low part of shell; surface ornamented with prominent ribs without spiral striation; ribs visible at lower part of shell; aperture rounded, peristome thickened, broadened, somewhat reflexed and interrupted by two grooves; anterior groove situated on parietal–palatal transition and forming a deep one; posterior groove situated on columellar–parietal region and forming a shallow one; bottom incisions (on basal part of aperture) are starting points of upper keel and lower keel separately, lower keel starting from lowermost point of apertural rim and terminating on ventrolateral side, whereas upper keel starts from slightly left of lowermost point; upper keel and lower keel visible inside aperture as two shallow canals situated on bottom of apertural rim; umbilicus narrow.
Measurements. H 20.03 mm, D 5.93 mm; h 4.25 mm, d 4.69 mm.
Remarks. *Cretatortulosa cretakachinensis* sp. nov. shares some similarities with *C. multilinea* Yu, Wang and Pan, 2018 in having a

Fig. 1. *Cretatortulosa cretakachinensis* gen. et sp. nov. (A–D), holotype NIGP173321. (A) and (C) apertural view. (B) and (D) lateral view. (A) and (B) micro-CT reconstruction. *Rhaphaulus zhuoi* sp. nov. (E–G), holotype NIGP173322. (E) and (G) apertural view. (F). lateral view. (E) and (F) micro-CT reconstruction. Scale bars = 2 mm. Abbreviations: pg–(posterior grooves); ag–(anterior grooves); k–(keel); bt–(breathing tube); bk–(basal keel).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turriform shell with many narrow whorls ornamented with regular ribs, but it differs from the latter in having the main and lower keels running around the umbilicus and body whorl regions, and two grooves present on the peristome (Yu et al., 2018). It also resembles *Vargapupa oharai* Páll-Gergely, 2015 in shell shape, sculpture and in having two keels (albeit one of them is very faint in *V. oharai*), but the main keel of *V. oharai* ends on the ventrolateral side of the penultimate whorl, whereas that of *C. cretakachinensis* sp. nov. ends on the dorsolateral side (Páll-Gergely et al., 2015).

It also differs from other five pupinids species derived from Burmese amber: *Macropupina electricus* has a large elongate conical shell with minimally indented sutures, and a well-developed parietal breathing tube; *Pseudopomatias*? *lyui* (Yu, Wang and Jarzembowski, 2019) and *Pseudopomatias*? *zhuoi* (Yu, Wang and Jarzembowski, 2019) are much smaller and have a simple apertural margin; *Schistoloma electrothauma* Asato and Hirano, 2019 has a turriform/pupiniform shell without any ribs (Yu et al., 2019; Hirano et al., 2019; Bullis et al., 2020).

Genus *Rhaphaulus* L. Pfeiffer, 1856
Type species: *Rhaphaulus bombycinus* L. Pfeiffer, 1855. Recent, Sarawak.

Remarks. The present specimen is assigned to *Rhaphaulus* based on its pupoid to ovate shell with a thickened and expanded apertural margin, which also has a breathing tube at the posterior edge. As illustrated by Kongim et al. (2013), the most crucial difference between *Rhaphaulus* and other closely related genera such as *Pupina*, *Pupinella*, *Schistoloma* and *Tortulosa* lies in the presence of a complete posterior tube. Moreover, *Rhaphaulus zhuoi* sp. nov. resembles *Rhaphaulus* rather than closely related *Streptaulus* as it does not have a very long tube attached to the suture, with minor perforations; instead, the tube is short and unperforated.

Rhaphaulus zhuoi sp. nov.
Fig. 1(E–G)

ZooBank LSID. urn:lsid:zoobank.org:act:B242A65A-DE6B-4663-B0EE-11B63B464B9F

Etymology. This species is named after Mr. De Zhuo, the collector of this specimen.
Holotype. NIGP173322.
Type locality and horizon. Noije Bum Village, Tanaing Township, Myitkyina District, Kachin State, northern Myanmar (26°15′ N, 96°33′ E); unnamed horizon, mid Cretaceous, upper Albian or lower Cenomanian.
Diagnosis. Shell medium size, tumid, pupoid to ovate shape, with several flat whorls, body whorl extremely inflated, basal keel present on umbilical region, starting from back side of most basal point of apertural rim, and terminating on ventrolateral side, aperture circular, peristome thickened, apertural margin with triangular (in transverse section) breathing tube at posterior edge.
Description. Medium size, tumid, pupoid to ovate shell consisting of four flat whorls; early whorls damaged, body whorl extremely inflated, more than half of shell height; suture very shallow; shell surface ornamented by rather regular, inconspicuous growth lines; aperture circular, peristome thickened, broadened and somewhat reflexed; peristome not continuous, lacking parietal region; umbilicus slit-like; basal keel present on umbilical region, starting from back side of most basal point of apertural rim, and terminating on ventrolateral side; apertural margin with triangular (in transverse section) breathing tube at posterior edge; operculum very thin, circular, lamellate, multispiral and slightly concave.
Measurements. H 15.20 mm, D 9.26 mm; h 6.52 mm, d 5.62 mm.
Remarks. This new species can be distinguished from other *Rhaphaulus* spp. by the basal keel on the umbilical region. Besides that, *Rhaphaulus zhuoi* sp. nov. differs from *R. tonkinensis* Páll-Gergely, 2014 from north-western Malaysia in having a much more oblique body whorl and discontinuous peristome; from *R. aborensis* Godwin-Austen, 1917, *R. assamicus* Godwin-Austen, 1886 and *R. oakesi* Godwin-Austen, 1917 from north-eastern India in having a much smaller size, pointed apex, and (from the latter two species only) in having a wider peristome on the umbilical region; from *R. chrysalis* L. Pfeiffer, 1852 from north-eastern India and Myanmar in having a larger aperture and a thicker apertural "plate" (Páll-Gergely, 2014); from *R. pachysiphon* Theobald and Stoliczka, 1872 from Myanmar in having a slender shape and higher spire; from *R. shimangensis* Godwin-Austen, 1917 from north-eastern India and *R. lorraini* L. Pfeiffer, 1856 from north-western Malaysia in having a much more streamlined whorl profile and much shallower sutures; and from *R. tonkinensis* Páll-Gergely, 2014 from northwestern Malaysia and *R. yamneyensis* Godwin-Austen, 1917 from north-eastern India in having a much flatter whorl profile.

Family Diplommatinidae L. Pfeiffer, 1856

Pulchraspira gen. nov.
ZooBank LSID. rn:lsid:zoobank.org:act:CB603979-C868-4CC1-AF18-C604C7B3D883

Type species. *Pulchraspira teneristoma* gen. and sp. nov., designated herein. Mid-Cretaceous; northern Myanmar.
Etymology. The genus name is a combination from the Latin *pulcher* (meaning beautiful), and *spira* (meaning coil).
Diagnosis. Shell minute, slim, turreted, with regularly increasing strongly stepped and compressed whorls; protoconch round and smooth; teleoconch sculptured with spaced axial ribs; aperture circular, peristome thin, double; the inner part of the peristome more or less exerted, the outer part broadly flared and expanded.
Remarks. We place *Pulchraspira* gen. nov. in the Diplommatinidae due to the small shell size and the regularly ribbed but irregularly convex and constricted whorls. The aperture and peristome structure (bearing a duplicated margin) of the present fossils are reminiscent of extant diplommatinid genus *Luzonocoptis* Páll-Gergely and Hunyadi, 2017 from the Philippines, but the former differs in having turreted shell with regularly increasing convex and constricted whorls and lack of a columellar tooth (Páll-Gergely et al., 2017). The slim turreted shell with a deeply impressed suture and a broadly flared and expanded peristome excludes placement in genera such as *Diancta* E. von Martens, 1864 and *Palaina* Semper, 1865 (Neubert and Bouchet, 2015). The lacking tooth-like lamella in the aperture of the present material differs it from *Moussonia* Semper, 1865 (Neubert and Bouchet, 2015). The constriction of whorls of genus *Arinia* H. Adams and A. Adams, 1856 is usually in the middle or the last quarter of the last whorl. Species of *Diplommatina* Benson, 1849 usually bear a parietal lamella and a columellar lamella (Nurinsiyah and Hausdorf, 2017). *Pulchraspira* gen. nov. differs from *Habeastrum* Simone, 2019 in having much constricted whorls and flaring peristome (Simone et al., 2020). *Xenostoma* Bullis, Herhold, Czekanski-Moir, Grimaldi and Rundell, 2020 from the same amber mine has a small elongate conical shell with oblique-ovate aperture with doubly expanded peristome (Bullis et al., 2020). *Pulchraspira* gen. nov. also shares some similarities with *Euthema* Yu, Wang and Pan, 2018 from Burmese amber in having a smooth and rounded protoconch, convex whorls, and densely spaced ribs on the shell surface, but differs in its elongated-

Fig. 2. *Pulchraspira teneristoma* gen. et sp. nov. (A–F, holotype NIGP173323; G–H, paratype NIGP173324, I–K, paratype NIGP173325). (C), (E), (F) and (L) micro-CT reconstruction. (A), (C), (G), (I) and (K), apertural view. (B), (F), (H) and (J), lateral view. Scale bar = 0.5 mm. (D) and (E), apical view. Scale bar = 0.2 mm. (L), operculum, Scale bar = 0.85 mm.

turreted shell with regularly increasing convex whorls and double peristome (Yu et al., 2018).

The flaring peristome of the present material is also reminiscent of extant neotropical *Tomocyclus* Crosse and Fischer, 1872, *Megalomastoma* and *Farcimen* Troschel, 1847, belonging in the family Megalomastomatidae Blanford, 1864. However, all these representatives differ markedly in their more regular type of coiling. In addition to the morphological evidence, there are several diplommatinids known from Burmese amber, but not a single fossil representative of Megalomastomatidae has been reported previously from Asia.

Pulchraspira teneristoma sp. nov.
Fig. 2

ZooBank reg nr. rn:lsid:zoobank.org:act:8D1D70CA-ED61-4F83-9DDD-29464C414024

Etymology. This species is a combination from the Latin *tener* (meaning delicate) and *stoma* (meaning mouth). The specific epithet is a noun in apposition.

Holotype. NIGP173323. *Paratypes.* NIGP173324, NIGP173325.

Type locality and horizon. Noije Bum Village, Tanaing Township, Myitkyina District, Kachin State, northern Myanmar (26°15′ N, 96°33′ E); unnamed horizon, mid-Cretaceous, upper Albian or lower Cenomanian.

Diagnosis. As genus above.

Description. Shell dextral, very small, slim, elongated and turreted, consisting of about 5–6 regularly increasing strongly stepped and compressed whorls; apex obtuse, apical angle almost 70°; embryonic shell low conical, consisting of more than two smooth and rounded whorls; teleoconch sculpture of closely spaced orthocline ribs on initial whorls, turning to a more widely spaced pattern on central whorls, and becoming slightly coarser on penultimate whorl and body whorl; suture distinct, deeply impressed; umbilicus narrow, partly obscured by columellar wall; aperture circular, peristome thin, transparent and double; inner part of peristome more or less exerted; the outer part broadly flared and expanded, maximum diameter from inner edge to outer edge 0.48 mm; outer edge with concentric, closely spaced growth lines. Operculum poorly preserved, apparently circular, thin, with concentric growth lines.

Measurements. Holotype (NIGP173323), H 3.90 mm, D 1.94 mm; h 1.70 mm, d 1.64 mm; paratype (NIGP173324), H 3.36 mm, D 1.51 mm; h 1.49 mm, d 1.08 mm; paratype (NIGP173325), H 3.02 mm, D 1.14 mm; h 1.16 mm, d 0.82 mm.

Remarks. *Pulchraspira teneristoma* sp. nov. is very similar to Recent *Luzonocoptis antenna* Páll-Gergely and Hunyadi, 2017 and *L. angulata* Páll-Gergely and Hunyadi, 2017 in having a strongly expanded and reflected peristome, but it differs from them in having a much smaller shell, slender, turreted shape and lacking an interrupted columellar lamella. *Pulchraspira teneristoma* sp. nov. is also similar to *Diplommatina auriculata* Möllendorff, 1897 from Java in having a distinct extension of the peristome and closely-set ribs, but differs from it in lacking a prominent columellar lamella and having a narrower umbilicus, a much more slender shell, and more convex and constricted whorls (Nurinsiyah and Hausdorf, 2017).

4. Discussion

New taxa. Presently, approximately twenty pupinid genera are known from South Asia, East Asia to Southeast Asia, Melanesia, Micronesia and parts of Australia (Stanisic, 1998; Stanisic et al., 2010). They are more diverse in the tropical forests of East and South Asia (Wenz, 1938; Kongim et al., 2013; Sang, 2017). In contrast to their diversity and wider geographical distribution in the region, the Asian fossil record of this family is relatively sparse (Solem, 1959; Vaught, 1989; Stanisic, 1998; Stanisic et al., 2010), with one species from the Eocene of China (Yü and Pan, 1982), one from the earliest Miocene of Vietnam (Raheem et al., 2018) and six from mid-Cretaceous Burmese amber, all except one assigned to new genera (Yu et al., 2018; Hirano et al., 2019; Bullis et al., 2020). Members of *Rhaphaulus* are distributed today from north-eastern India through the Malay Peninsula to Borneo (Thiele, 1929; Páll-Gergely et al., 2014). *Rhaphaulus zhuoi* sp. nov. represents the earliest fossil record of the genus and widens the taxon's geographical distribution in the region.

Extant diplommatinids are represented by dozens of genera and more than 500 species in eastern and southern continental Asia, Sri Lanka, Japan, Taiwan, Indonesia, the Philippines, Northern Australia, Melanesia, Micronesia and Samoa, as well as a few genera in Central and South America and one genus in Madagascar (Kobelt, 1902; Thiele, 1929; Wenz, 1938–1939; Birckolz et al., 2016; Simone et al., 2020). In contrast, the fossil record of Diplommatinidae is very sparse, but the oldest representatives of the family have been reported from mid-Cretaceous Burmese amber.

Our finds increase known species diversity and what is presently known about conchological variation of Pupinidae and Diplommatinidae, both during the Cretaceous and overall. *Cretatortulosa cretakachinensis* sp. nov., for instance, has a turriform shell shape, unusual of the family, also bearing two keels on the body whorl. Likewise, the shell morphology of *Pulchraspira teneristoma* sp. nov. is very unusual among diplommatinids, with its strongly stepped and compressed whorls and extremely inflated disc-like peristome. In fact, the morphology of *Pulchraspira* is also a potential case of convergence with neotropical members of Megalomastomatidae.

Paleoecology. Most snails preserved in amber seem to belong to ground-dwelling taxa living under fallen leaves, logs, and rocks (Speiser, 2001), a habitat that is consistent with ecological preferences of extant tropical Cyclophoroidea. Cyclophoroids are detritivores and herbivores, and they graze on plant material, lichens, fungi, and humus (Speiser, 2001). Extant diplommatinids generally occur in leaf litter, damp rocks, deadwood, shrubs, vegetation, limestone rocks and calcareous environments in humid forests (Nurinsiyah and Hausdorf, 2017). Species of Pupinidae generally occur in tropical forest and most commonly and abundantly in limestone areas (Páll-Gergely et al., 2015). *Cretatortulosa cretakachinensis* sp. nov., *Rhaphaulus zhuoi* sp. nov. and *Pulchraspira teneristoma* gen. et sp. nov. occur in amber formed on a tropical island in the Neotethys Ocean (Westerweel et al., 2019). Therefore, the snails likely lived in a tropical humid forest, which is consistent with previous studies of Burmese amber fossils (Yu et al., 2018; Xing et al., 2019; Neubauer et al., 2019; Hirano et al., 2019; Bullis et al., 2020; Balashov, 2020).

5. Concluding remarks

Here we described new fossil land snails from mid-Cretaceous Burmese amber: two new species of Pupinidae and one new genus and species of Diplommatinidae. Our discoveries increase the known biodiversity of those families during the Cretaceous of Asia, adding to the previously reported six species of Pupinidae and four of Diplommatinidae. Furthermore, they also improve upon the known morphological variation in those families, as the

fossils reported here present distinct and unusual shell shapes and structures. Finally, we report the earliest record of the genus *Rhaphaulus*.

Acknowledgements

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