Diverse new tropical land snail species from mid-Cretaceous Burmese amber (Mollusca: Gastropoda: Cyclophoroidea, Assimineidae)

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ABSTRACT

The amber fossil record of land snails is poorly studied, with few described species relative to other invertebrate groups (e.g., insects and chelicerates). Recently discovered land snail amber fossils from Myanmar present an important opportunity to understand the tropical land snail fauna of the Cretaceous, which was a time when many terrestrial invertebrates were rapidly diversifying. We describe 12 new land snail species in 3 families from mid-Cretaceous Burmese amber: *Eotrichophorus kachin* gen. et sp. nov., *Perissocyclos kyrtostoma* gen. et sp. nov., *Macropupina electricus* gen. et sp. nov., *Paleodiplommatina spelomphalos* gen. et sp. nov., *Xenostoma lophopleura* gen. et sp. nov. and *Assiminea striatura* sp. nov. and six species of uncertain taxonomic affinity. We also discuss the fossil history of the Cyclophoroidea. We report the first mid-Cretaceous land snail species with periostracal hairs and discuss their adaptive significance, as well as the general paleoecology of Burmese mid-Cretaceous tropical land snails.

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1. Introduction

Fossil terrestrial gastropods, particularly those from tropical forests, are relatively poorly known compared to fossil marine molluscs. This is a result of the poor preservational environment for terrestrial gastropods as tropical forest soils promote shell dissolution (Říhová et al., 2018). This relatively limited terrestrial fossil record has restricted our understanding of the timing and extent of early land snail diversification, particularly in geographic regions we expect to harbor relatives of explosively diverse modern land snail faunas, which are the tropics.

Gastropod transitions to land paved the way for subsequent diversification, but detailed knowledge about the timing of these events and the evolution of land snail families derived from them is incomplete. Broadly speaking, land snails compose a polyphyletic grade that includes at least 15 independent transitions to terrestriality within the clades Heterobranchia (Kameda and Kato, 2011; Romero et al., 2016), Neritimorpha (Rosenberg, 1996), and Caenogastropoda (Rosenberg, 1996; Vermeij and Dudley, 2000; Romero et al., 2016). The most species-rich clades of terrestrial or primarily terrestrial gastropods include the Stylommatophora (Heterobranchia) with roughly 20,000 known extant species, and the Cyclophoroidea (Caenogastropoda) with over 3000 species. The majority of these species are known from the tropics where their diversity is also likely underestimated due to their high rates of endemism and cryptic morphology (Lydeard et al., 2004). Orders closely related to the Stylommatophora, the Systellommatophora and the Ellobiida, also contain several independent transitions to terrestriality, as do the members of Neritimorpha and the caenogastropod clade Littorinimorpha.

The first apparent fossil land snails are from the Carboniferous (ca. 300 Ma). The taxa *Dawsonella* Bradley (1874) and *Anthracopupa* Whitfield (1881), both described from the Pennsylvanian (Solem and Yochelson, 1979; Bandel, 1997), have sometimes been ascribed to the extant clades Helicinidae (Neritimorpha) and Stylommatophora (Heterobranchia) respectively. However, recent authors have questioned these affinities. It is likely, as Kano et al. (2002) note, that *Dawsonella* is in the Neritiomorpha, but as an independent transition to land rather than part of the extant Helicinidae. There are unconvincing morphological synapomorphies placing *Anthracopupa* within the Stylommatophora (Naggs, 1997;

Naggs and Raheem, 2005), and molecular phylogenetic estimates of Stylommatophora place the age of the last common ancestor of all stylommatophorans comfortably in the Jurassic or Cretaceous (Dinapoli and Klussmann-Kolb, 2010; Zapata et al., 2014). Thus, the Carboniferous land snails likely belong to clades with no extant representatives.

However, it is likely that two to three clades of extant terrestrial gastropods had transitioned to land by the Cretaceous: the Stylommatophora (Dinapoli and Klussman-Kolb, 2010), the Cyclophoroidea (Xing et al., 2018; Yu et al., 2018), and perhaps the Carychiinae (Romero et al., 2016). Mesozoic fossils from these taxa can be more convincingly allied with their modern relatives, and the fossil record is concordant with the dated molecular phylogenies cited above. Further examination of Mesozoic land snail fossils can contribute direct evidence that tests these age estimates and provide minimum age ranges for the origin of these diverse taxa.

Amber fossil deposits provide a potential window into the early species diversity that marks snails' evolutionary success as they proliferated on land. Amber fossils have been instrumental in advancing our understanding of other terrestrial invertebrate clades such as insects, chelicerates and onychophorans (Grimaldi et al., 2002; Huang et al., 2016; Oliveira et al., 2016; Selden and Ren, 2017; Wang et al., 2018), but amber fossils of land snails are seldom recovered or studied. Only 30 amber fossil land snails have been previously described: 19 from Baltic (Eocene) amber (Klebs, 1886; Sandberger, 1887; Larsson, 1978; Stworzewicz and Pokryszko, 2006, 2015), seven from Dominican amber (Eocene to Oligocene; Poinar and Roth, 1991), one from Lebanese (Early Cretaceous) amber (Roth et al., 1996), and three from Burmese (Cretaceous) amber (Yu et al., 2018; Xing et al., 2018). Cretaceous amber is also known from Spain (mid-Cretaceous), Siberia, Canada, and New Jersey (North America; Late Cretaceous), although land snails have yet to be found in amber from these deposits.

Cretaceous amber from Myanmar (Burma) is of particular interest for understanding early land snail diversity because of its age and its potential to contain fossilized animals. Burmese amber (also known as burmite) has been mined for nearly 2000 years from the Hukawng valley of northeastern Myanmar (Zherikhin and Ross, 2000; Grimaldi and Ross, 2017). Amber deposits of northern Myanmar have been radiometrically dated at 98.72 ± 0.62 Ma, earliest Cenomanian, based on U−Pb zircon dating of the volcanoclastic matrix (Shi et al., 2012). Of the major sources of amber inclusions in the world, Burmese amber is by far the most species-rich amber from the Cretaceous and one of the most diverse from the Mesozoic (Grimaldi and Ross, 2017).

In this paper we describe 12 previously unidentified mid-Cretaceous Burmese amber land snails using light microscopy and micro-CT scans, and discuss these taxa in the context of the fossil history of the Cyclophoroidea and paleoecology of these specimens.

2. Materials and methods

Specimens BuKL-20-20, JZC Bu-1454, JZC Bu-1840, Bu1852, JZC Bu-307, JZC Bu-333, JZC Bu-538, and AMNH B-0099 were from the American Museum of Natural History Division of Invertebrate Zoology (New York, New York, USA) and specimens PRI80020, PRI 80021, PRI78119, and PRI78120 were from the Paleontological Research Institution (Ithaca, New York, USA). Burmite is largely mined in the Hukawng River valley in Kachin State in Northeast Myanmar (Zherikhin and Ross, 2000), though a smaller, younger (Campanian-aged) deposit is known from the Kabaw Formation at Tillin, Gangaw District, Magway Region, central Myanmar (Zheng et al., 2018). Called "Tilin amber", inclusions in it are typically compressed and distorted, and in fact molecular composition indicates

significant diagenetic alteration (Zheng et al., 2018). Molecular compositions of Kachin and Tilin amber are distinct (Zheng et al., 2018). While the exact provenance of most of our amber specimens is unknown, they are likely to have been collected somewhere in the Hukawng River valley in and around Noije Bum summit mine (26.246°N, 96.556°E) (Grimaldi and Ross, 2017).

Except where specified as "amber specimens," the term "specimen" herein refers to the land snail within the amber matrix. The term "amber specimen" then refers to the whole piece of amber and all inclusions preserved within. Specimens that were damaged or poorly preserved and of uncertain taxonomic affinity are described as Incertae sedis. Observations of the snail shell morphologies were assisted by light microscopy and X-ray micro-computed tomography (micro-CT). Micro-CT scanning was performed at the American Museum of Natural History Microscopy and Imaging Facility. Land snail specimens within opaque or debris-filled amber pieces were imaged using micro-CT in an effort to resolve internal shell features as well as shell surfaces. Scans were taken with a GE Phoenix v|tome|x s240 micro-CT system (Germany). Amber pieces were scanned at a range of voltages and currents, depending on land snail specimen characteristics and the quality of the intermediate or 'working' images during the image data collection process. For each specimen, a total of 1800 images were taken, most with an exposure time of 500 ms each. Voxel sizes ranged from 5 to 10 μm, depending on the resolution required for the snail specimen. Volume reconstruction of X-ray images was achieved with semi-automatic geometry correction. Volumes were post-processed using Fiji/ImageJ 2.0.0-rc-59/1.5lj (Schindelin et al., 2012). Datasets were volume rendered and segmented with 3D Slicer versions 4.7 (nightly builds), 4.8, and 4.9 (nightly builds) (Fedorov et al., 2012). Print-quality images were rendered with Blender 2.79 and the Cycles render engine (Blender Online Community, 2017).

3. Systematic palaeontology

Abbreviations: H = height, W = width, D = depth, L = length, Ah = aperture height, Aw = Aperture width.

Clade Caenogastropoda Cox (1960)
Superfamily Cyclophoroidea Gray (1847)
Family Cyclophoridae Gray (1847)

Genus ***Eotrichophorus*** gen. nov.
Type species. *Eotrichophorus kachin* sp. nov.

Diagnosis. Very small turbinate shell with transverse costae and periostracal hairs, 4-4 1/2 whorls, sub-circular aperture, angular body whorl periphery and narrow umbilicus.
Etymology. The name of the genus is a combination of the Greek words ἠώς meaning "dawn, or early," θρίξ meaning "hair," and φόρος or "bearing," and altogether meaning "early hair bearing."

Eotrichophorus kachin sp. nov.
(Fig. 1A−D)

Diagnosis. As for genus.
Etymology. The specific epithet is given as "kachin" after Kachin State, Myanmar where the specimen was recovered.
Material. Holotype: BuKL-20-20, an oval piece of amber, honey colored. Dimensions: D = 10 mm, L = 17 mm.
Type locality and horizon. Kachin State, Myanmar; mid-Cretaceous, at the Albian-Cenomanian boundary (approximately 100 Ma).
Description. Dextral, small shell, turbinate, approximately 4-4 1/2 whorls, rapidly increasing in diameter, shell apex blunt, apical
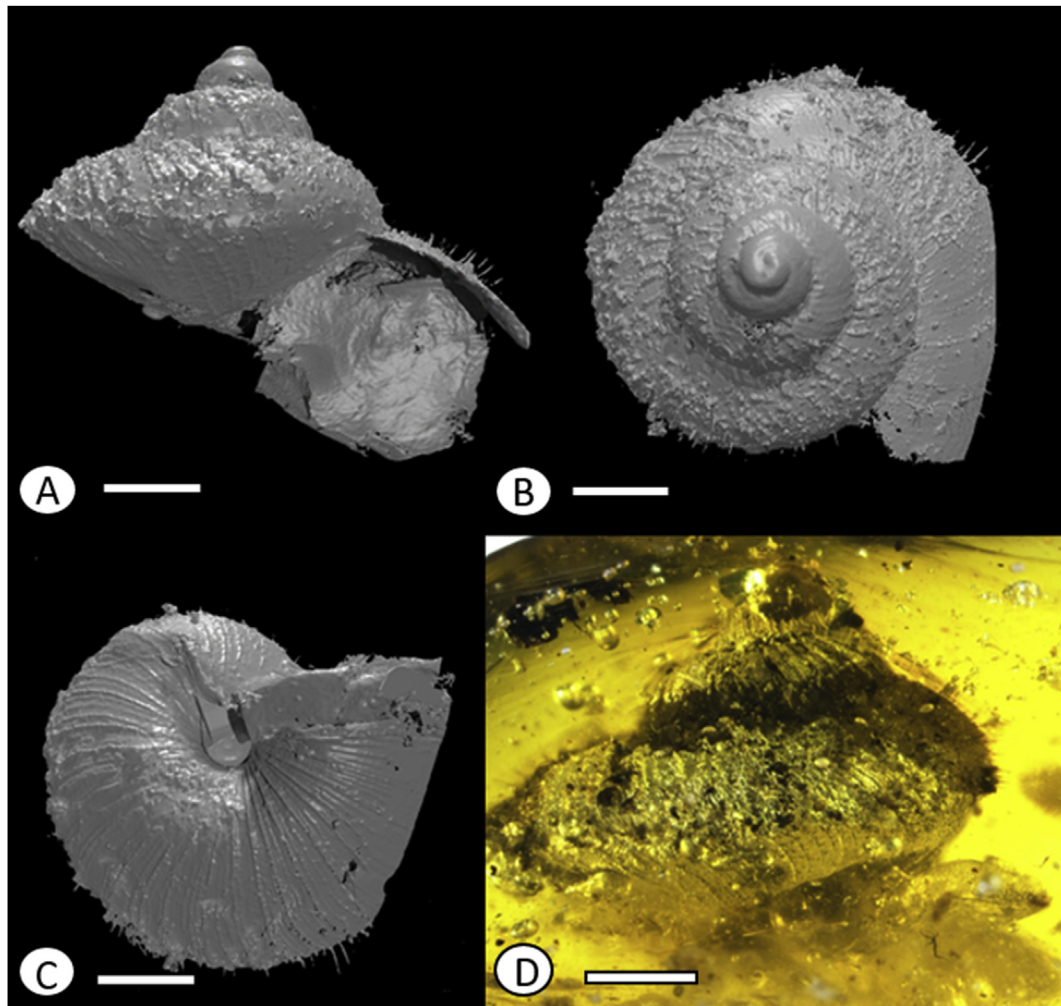
Fig. 1. Holotype of *Eotrichophorus kachin* gen. et sp. nov. from mid-Cretaceous Burmese amber (BuKL-20-20) MicroCT scans showing: **A**, apertural view; **B**, apical view; **C**, umbilical view; and **D**; *in situ* light micrograph. Scale bar = 1 mm.

angle 90°, protoconch apparently unsculptured. Teleoconch sculpturing prominent transverse costae and periostracal hairs on body whorl and penultimate whorl, body whorl with angular periphery, remaining whorls slightly rounded and moderately shouldered, sutures highly indented, aperture obliquely ovate attaching broadly to body whorl at the columellar edge, peristome absent, columellar edge slightly impinging on umbilicus, umbilicus narrow and <1/5th of shell width. Operculum multispiral. Dimensions: H = 3.75 mm, W = 4.75 mm.

Remarks. An operculum with the multispiral sculpturing and overall shape are characteristic of the Cyclophoroidea. Similar to *Lagocheilus* Blanford (1864) in turbinate shape, rate of whorl diameter increase and in some species the presence of periostracal hairs. In *Eotrichophorus* the body whorl is wider, umbilicus is perforate and the sculpturing is different (more pronounced costae than *Lagocheilus* and lacking spiral sculpturing). Like *Ihapasaw minuta* this species is significantly smaller than other species of its most similar genus *Lagocheilus* or potentially closely allied *Cyclophorus*. The genus *Mychopoma* Blanford (1869) is superficially similar in that many species possess periostracal hairs and have similar transverse sculpturing, but differs significantly in its pyramidal conical shell shape, irregular aperture shape, and possessing distinct radial sculpture. Only *Craspedotropis* Blanford (1864) and *Japonia* Gould (1859) are similar in size and shell shape; some

species also possesses periostracal hairs. These genera are different however in that they both possess strong radial sculpture and in the case of some *Craspedotropis* species also have irregularly increasing whorl diameter. The combination of overall shape, sculpturing, presence of hairs and unique aperture define this new genus and species.

Genus *Perissocyclos* gen. nov.
Type species. *Perissocyclos kyrtostoma* sp. nov.

Diagnosis. Medium sized discoidal shell with depressed spire, wide umbilicus and sub-circular aperture which narrowly attaches to the body whorl between parietal and columellar edge and has a slightly reflexed apertural lip.
Etymology. From the Greek περισσός meaning "beyond the usual number, or superfluous" and κύκλος meaning "circle, or whorl".

Perissocyclos kyrtostoma sp. nov.
(Fig. 2A−D).

Diagnosis. As for genus.
Etymology. From the Greek κυρτός meaning "curved" and στόμα meaning "mouth".
Material. Holotype: JZC Bu-1454, a rectangular piece of amber, yellowish-orange colored. Dimensions: D = 1−1.5 mm, W = 16 mm, L = 19 mm.
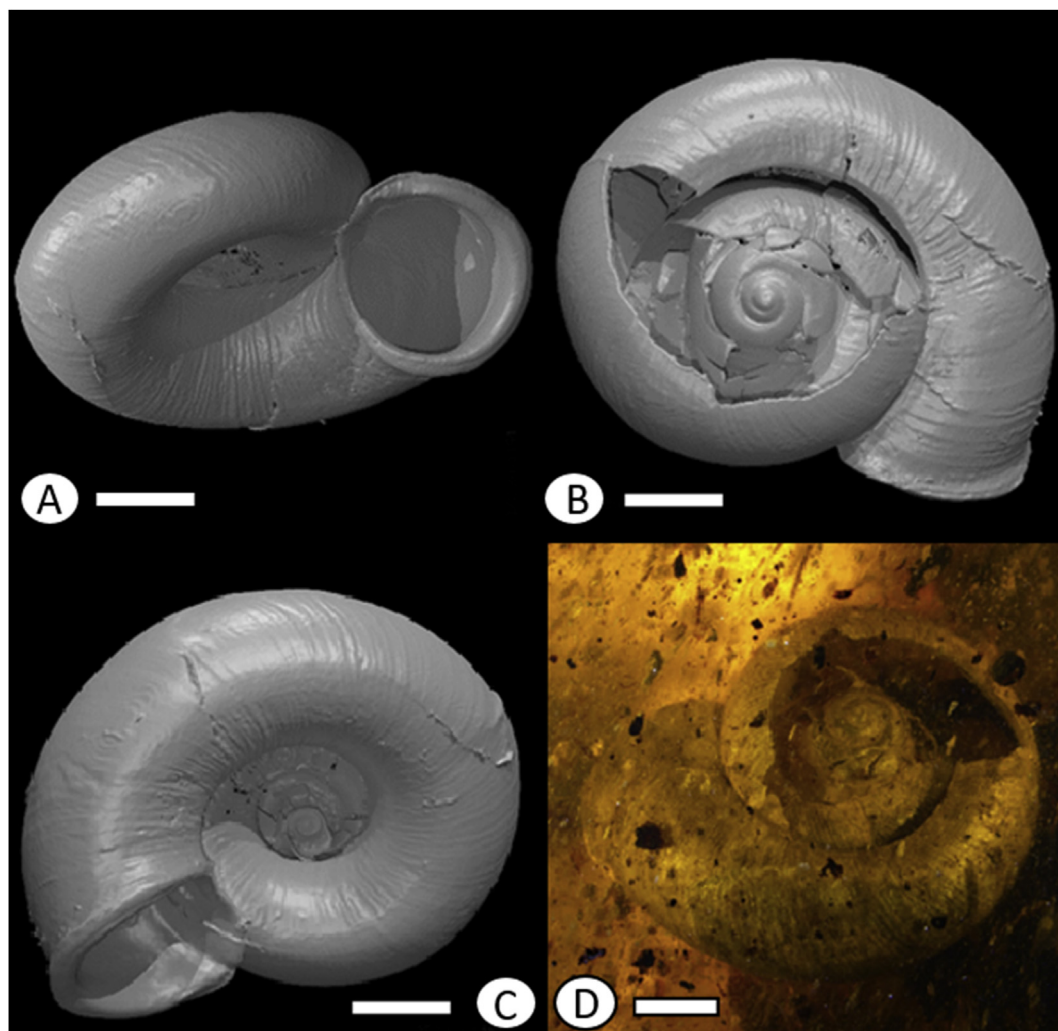
Fig. 2. Holotype of *Perissocyclos kyrtostoma* gen. et sp. nov. from mid-Cretaceous Burmese amber (JZC Bu-1454) MicroCT scans showing: **A**, apertural view; **B**, apical view; **C**, umbilical view; and **D**; *in situ* light micrograph. Scale bar = 2 mm.

Type locality and horizon. Kachin State, Myanmar; mid-Cretaceous, at the Albian-Cenomanian boundary (approximately 100 Ma).

Description. Dextral, medium shell, discoidal, depressed spire damaged, approximately 5 ½ whorls, tightly coiled, sutures slightly indented, rounded body whorl periphery, protoconch apparently unsculptured. Teleoconch sculpturing transverse striate on body whorl and penultimate whorl, aperture subcircular with thick slightly reflexed peristome, aperture narrowly appressed to body whorl between the columellar and parietal edges, parietal edge of the aperture extending approximately 4.8 mm further forward than the basal edge. Umbilicus wide, approximately 1/3 shell width. Dimensions: H = 5 mm, W = 11.5 mm, D = 9 mm, Aw = 5.5 mm.

Remarks. The very non-distinct shape of *Perissocyclos* presented challenges to classification. Pulmonate genera such as *Vallonia* Risso (1826) bear a strong resemblance in key aperture features and overall shape. The micro-CT scans and still images suggest resorption of inner shell whorls and thus is likely not a Pulmonate. In addition, characteristic radial sculpture present in *Vallonia* is absent in *Perissocyclos*. Despite the damage to the spire of the shell this specimen possesses characteristics of extant members of the Cyclophoridae. This species is very similar to the extant genera *Theobaldius* G. Nevill (1878), *Scabrina* W.T. Blanford (1863), *Cyclotus* Swainson (1840), *Spirostoma* Heude (1885) and *Ptychopoma*

Möllendorff (1885) which are all small discoidal cyclophorids with narrowly attached apertures, similar patterns of sculpturing and occur in South-East Asia. It is unique from these however in number of whorls (approx. 5 ½), the manner of attachment of the aperture to the body whorl and the morphology of the peristome. The peristome in *Perissocyclos* differs in being comparatively thin and becoming less prominent on the columellar edge above which it only narrowly contacts the body whorl. In this respect it is most similar to the genus *Cyclotus*.

Family **Pupinidae** Pfeiffer (1853)

Genus ***Macropupina*** gen. nov.
Type species. *Macropupina electricus* sp. nov.

Diagnosis. Large elongate conical shell with 8 ½ whorls, minimally indented sutures, and a well-developed parietal breathing tube.
Etymology. From the greek *makros* meaning "long, or large" and the type genus of the family *Pupina* Vignard (1829).

Macropupina electricus sp. nov.
(Fig. 3A–C).

Diagnosis. As for genus.
Etymology. From the Greek ἤλεκτρον meaning "amber" from its origin in Burmese amber.

Material. Holotype: JZC Bu-1840, a sub-triangular piece of amber, deep orange colored, Dimensions: D = 1–1.5 mm, W = 56 mm, L = 44 mm.

Type locality and horizon. Kachin State, Myanmar; mid-Cretaceous, at the Albian-Cenomanian boundary (approximately 100 Ma).

Description. Dextral, large shell, elongate conical, high spired, apical angle <30°, approximately 8 ½ whorls, tightly coiling, body whorl approximately 50% of shell height, sutures barely indented, whorl periphery very slightly rounded, protoconch apparently unsculptured. Teleoconch unsculptured, aperture circular with thick peristome, parietal lip with breathing tube, columellar wall with small denticle, columellar lip impinging on umbilicus, umbilicus perforate to absent. Dimensions: H = 21 mm, W = 6.75 mm, Aw = 4.5 mm.

Remarks. This specimen was slightly damaged with fractures on the body whorl. The breathing tube on the parietal lip of the aperture and overall shape of the shell are very characteristic of extant members of Pupinidae. While this species is pupiniform in overall shape it does not closely resemble any extant or fossil genus. *Macropupina* most closely resembles *Schistoloma* Kobelt (1902) in size and elongate conical shape and *Pollicaria* Gould (1856) in apertural morphology. The breathing tube elaboration on the parietal edge of the aperture resembles that of the genus *Pollicaria* and to a lesser degree some species of *Rhaphaulus* Pfeiffer (1856), but is novel in its length and degree of openness.

Family Diplommatinidae Pfeiffer (1857)

Genus ***Paleodiplommatina*** gen. nov.
Type species. *Paleodiplommatina spelomphalos* sp. nov.

Diagnosis. Very small elongate conical shell with penultimate whorl wider than the body whorl. Distinct transverse costae numbering approximately 12/mm (becoming less densely spaced toward the aperture) along the teleoconch. Small columellar tooth, with doubly expanded peristome and appressed parietal callus.

Etymology. From the Greek παλαιός meaning "old" and the genus *Diplommatina* Benson (1849).
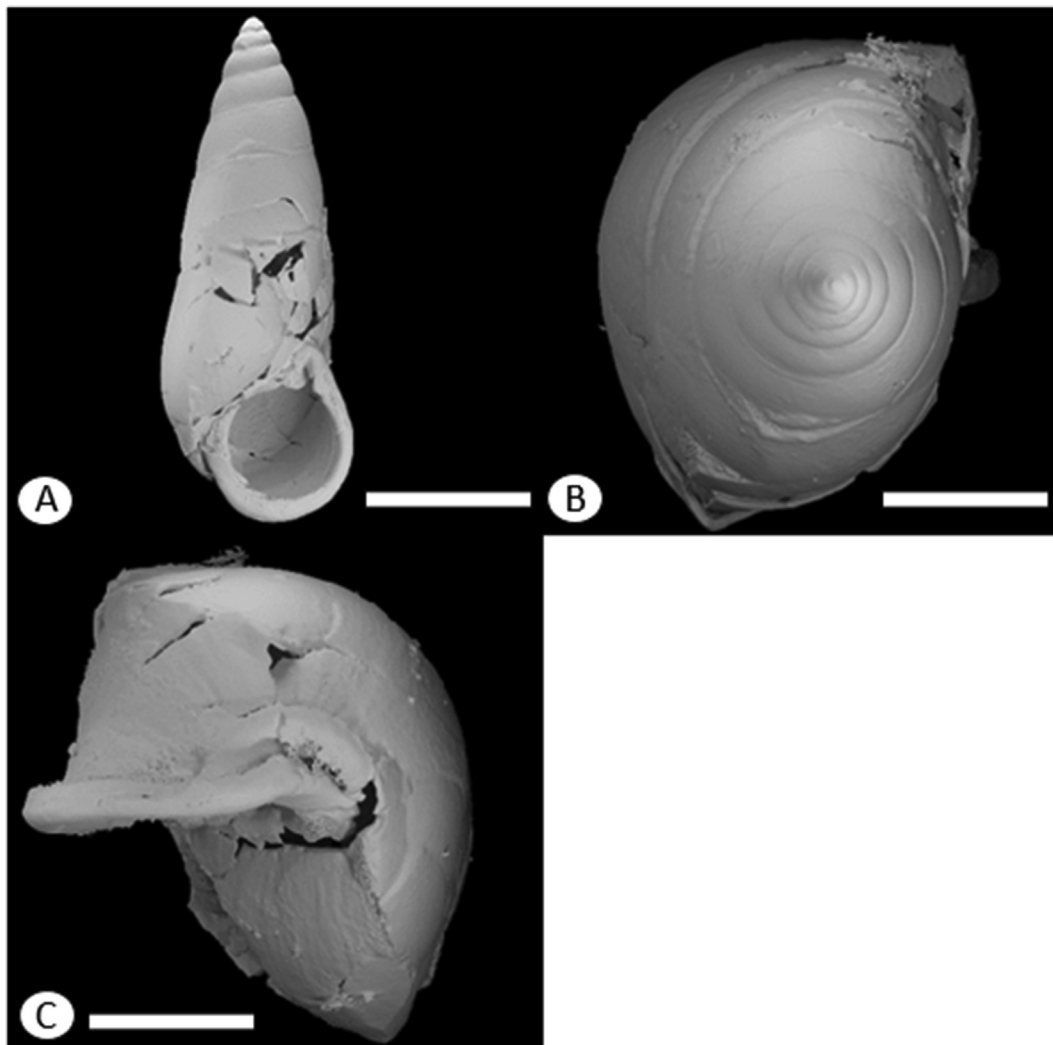
Paleodiplommatina spelomphalos sp. nov.
(Fig. 4A–D)

Diagnosis. As for genus.
Etymology. From the Greek σπήλαιο meaning "cave" and ομφαλός meaning "navel, or umbilicus".

Material. Holotype: PRI 80020, a rectangular piece of amber, yellowish-orange colored. Dimensions: D = 1–1.5 mm, W = 16 mm, L = 19 mm.

Fig. 3. Holotype of *Macropupina electricus* gen. et sp. nov. from mid-Cretaceous Burmese amber (JZC Bu-1840) MicroCT scans showing: **A**, apertural view, scale bar = 7 mm; **B**, apical view, scale bar = 2.25 mm; **C**, umbilical view, scale bar = 4 mm.

Type locality and horizon. Kachin State, Myanmar; mid-Cretaceous, at the Albian-Cenomanian boundary (approximately 100 Ma).

Description. Dextral, small shell, elongate conical, high spired, approximately 6 whorls, tightly coiling, penultimate whorl larger than ultimate whorl, sutures indented, whorl periphery rounded, protoconch apparently unsculptured. Teleoconch sculpturing distinct transverse costae (12/mm) becoming less densely spaced closer to the aperture, aperture subcircular, peristome double expanded with thick inner lip surrounded by a thinner outer lip with an irregular margin, parietal callus strongly appressed to the body whorl, small columellar tooth visible within the aperture. Umbilicus open, nearly 1/3rd the width of the shell. Dimensions: H = 3.25 mm, W = 1.25 mm, Aw = 0.5 mm.

Remarks. The earliest record of the Diplommatinidae was recovered from Burmese amber (Yu et al., 2018). This specimen does not resemble *Euthema naggsi* Yu et al. (2018) in being larger, having more regularly increasing whorl diameter and lacking the characteristic S-shaped transverse costae of that species. Compared to extant genera this species possesses similar morphology to *Diplommatina* species in Southeast Asia. The presence of a columellar tooth in *Paleodiplommatina* is also common in many species of *Diplommatina*, *Moussonia* Semper (1865a), and *Nicida* Blanford (1868) and thus not characteristic. However the degree of openness of the umbilicus and attachment of the aperture to the body whorl separates this genus from *Diplommatina* and other similar diplommatinid genera such as *Palaina* Semper (1865b), and *Diancta* E. von Martens (1864). The unique attachment of the aperture can also be seen in *Arinia* Adams and Adams (1853), however *Arinia* differs in its overall cylindrical shell shape. In particular *Paleodiplommatina* differs from *Nicida* in sculpturing (*Nicida* often lacking sculpture or having spiral lirae), possessing a columellar tooth and having an open umbilicus and from *Diancta* in sculpturing, having more prominent and sinuate costae and having an open umbilicus.
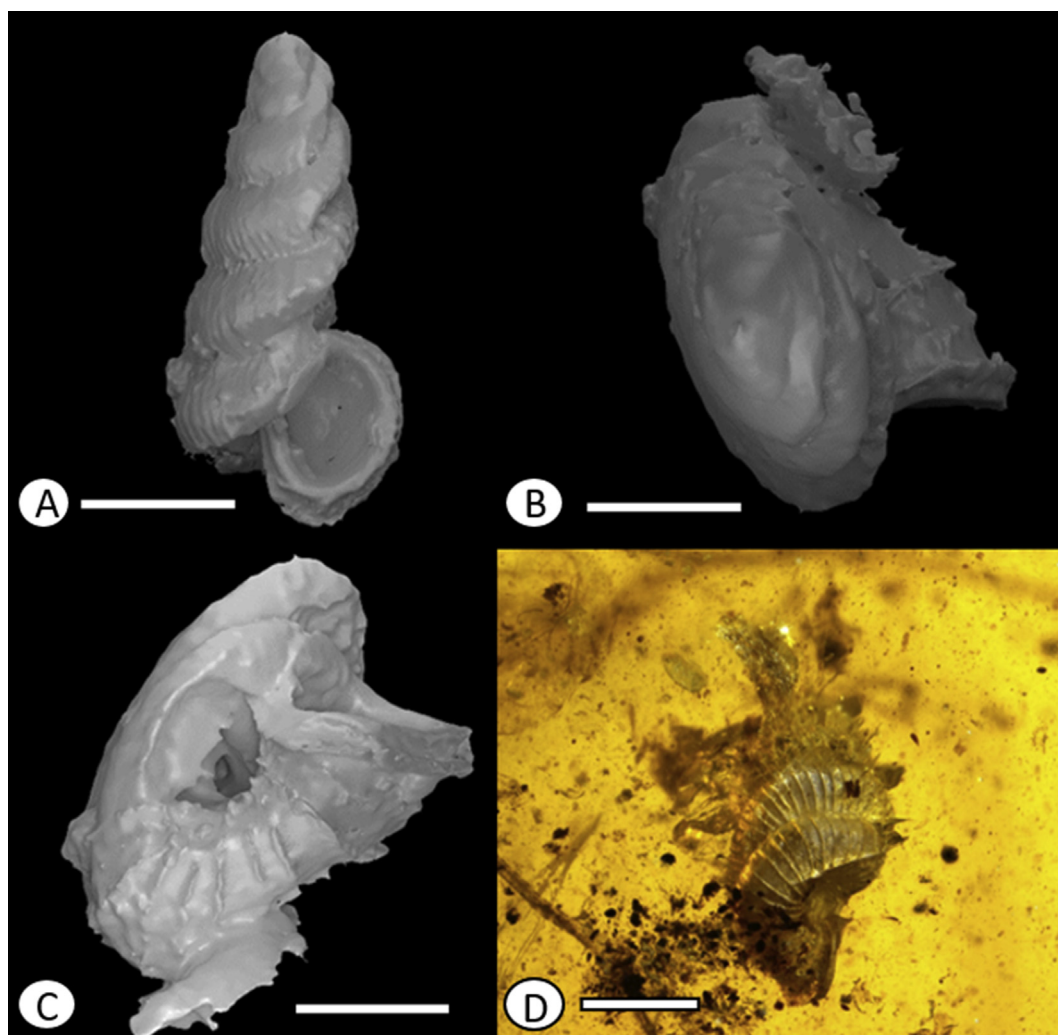
Genus ***Xenostoma*** gen. nov.
Type species. *Xenostoma lophopleura* sp. nov.

Diagnosis. Very small elongate conical shell with penultimate whorl wider than body whorl, narrowly umbilicate, and uniquely oblique-ovate aperture with doubly expanded peristome.

Etymology. From the Greek ξενος meaning "strange" and στόμα meaning "mouth".

Xenostoma lophopleura sp. nov.
(Fig. 5A–D)

Fig. 4. Holotype of *Paleodiplommatina spelomphalos* gen. et sp. nov. from mid-Cretaceous Burmese amber (PRI 80020) MicroCT scans showing: **A**, apertural view; **B**, apical view; **C**, umbilical view; and **D**; *in situ* light micrograph. Scale bar = 1 mm.

Diagnosis. As for genus.

Etymology. From the Greek λόφος meaning "hill" and πλευρα meaning "side".

Material. Holotype: PRI 80021, a drop-shaped piece of amber, deep orange colored. Dimensions: W = 11 mm, L = 30 mm.

Type locality and horizon. Kachin State, Myanmar; mid-Cretaceous, at the Albian-Cenomanian boundary (approximately 100 Ma).

Description. Dextral, small shell, elongate conical, high spired, approximately 6 whorls, penultimate whorl slightly larger than ultimate whorl, sutures highly indented, whorl periphery highly rounded, protoconch with very slight striae. Teleoconch sculpturing distinct transverse costae (12/mm), aperture obliquely ovate narrowly attached at parietal edge of the aperture, peristome double expanded with thin inner and outer lip, peristome margin entire, umbilicus narrowly open 1/6th width of maximum diameter. Dimensions: H = 2.25 mm, W = 1.5 mm.

Remarks. The oblique ovate aperture of this specimen and its attachment to the body whorl is very unique in the Diplommatinidae, most genera having a circular or sub-circular aperture being either detached or closely appressed to the body whorl. The broadly ovate conical shape of the shell is also fairly distinct, with the whorls increasing in width very regularly until the penultimate whorl after which the body whorl is the same width as the antepenultimate whorl. Protoconch sculpturing is also uncommon within the Diplommatinidae, making the striations on this specimen unique. Teleoconch sculpturing in this specimen is not sinuate like in other diplommatinid genera such as *Diplommatina* and *Euthema,* but instead is nearly straight. While different from *Xenostoma* in teleoconch sculpturing, *Euthema* is similar in size and in having highly rounded whorl peripheries. The genus most similar to *Xenostoma* is *Nicida* particularly in overall shape, the degree of whorl diameter increase, and possessing an umbilicus. However species of *Nicida* possess a circular or subcircular aperture and very often have spiral lirate sculpturing which *Xenostoma* lacks. The genus *Palaina* is also similar to *Xenostoma* but differs in lacking an umbilicus and the orientation and attachment of the aperture in relation to the coiling axis.

Superfamily Truncatelloidea Gray (1840)
Family Assimineidae Adams and Adams (1853)

Genus ***Assiminea*** J. Fleming (1828)
Type species. *Assiminea grayana* J. Fleming (1828)

Diagnosis. A description of the characteristics of the genus *Assiminea* can be found in Abbott (1958).

Remarks. The genus *Assiminea* occurs globally in tropical and subtropical environments particularly on the edge of marine
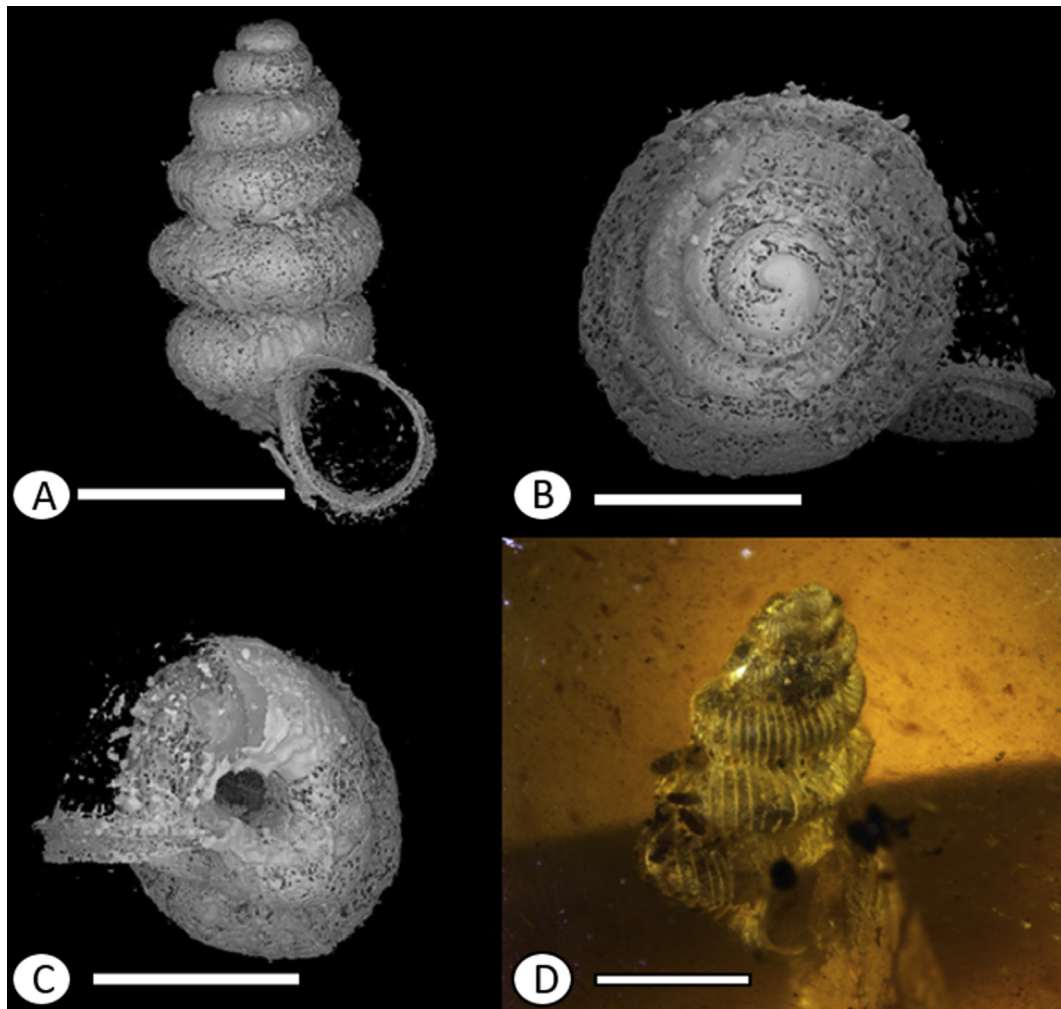
Fig. 5. Holotype of *Xenostoma lophopleura* gen. et sp. nov. from mid-Cretaceous Burmese amber (PRI 80021) MicroCT scans showing: **A**, apertural view; **B**, apical view; **C**, umbilical view; and **D**; *in situ* light micrograph. Scale bar = 1 mm.

habitats, being either amphibious or fully terrestrial. While the genus is thought to comprise 50–60 species a revision of the genus is desperately needed and has been problematic for over 60 years (Abbott, 1958). The earliest reported species of *Assiminea* in the fossil record is *Assiminea (Ovassiminea) obesa* Pan (1977). This species was described from the Zhanghe formation of Yunnan, China (Middle Jurassic) putting the age of the genus at 171.7–167.7 Ma.

Assiminea striatura sp. nov.
(Fig. 6A and B)

Diagnosis. As for genus.
Etymology. From the Latin *striatura* for "furrow".
Material. Holotype: Bu1852, an irregular rectangular piece of amber, yellowish orange colored. Dimensions: W = 7 mm, L = 11.5 mm, D = 4 mm.
Type locality and horizon. Kachin State, Myanmar; mid-Cretaceous, at the Albian-Cenomanian boundary (approximately 100 Ma).
Description. Dextral, small shell, ovate conical, high spired, 4 whorls, 70° apical angle, apex blunt, protoconch unsculptured, sutures indented marginally, whorls unshouldered, whorl periphery slightly rounded. Teleoconch sculpturing transverse striate, body whorl more than half shell height, aperture rounded lunate with slight flare at columellar and basal edges, umbilicus absent. Dimensions: H = 3.75 mm, W = 2.25 mm, Aw = 2.25 mm.
Remarks. Most similar to extant *Assiminea* in overall shape, size, and aperture morphology. However, *Assiminea* species tend to have 5–7 whorls. Also superficially similar to *Omphalotropis* Pfeiffer (1851) in sculpturing, overall shape and apertural morphology but different in having an angular body whorl periphery (as opposed to rounded), presence of an umbilicus, having a narrow apical angle and smaller in size. Unique in its degree of sculpturing from other assimineid species, and the connection of the aperture at the parietal edge to the body whorl. While this is not the oldest *Assiminea* described from the fossil record it is the first to be recovered in amber and is only the second reported for the Mesozoic, the next specimens not appearing again until the Oligocene nearly 65 million years later (Pan, 1977).
All taxonomic placements and environmental interpretations of fossils are hypotheses, and our hypothesis that this specimen is a

terrestrial species in the genus *Assiminea* is the most parsimonious given the morphology and fossilization environment. However, it is possible that the placement of this and older specimens in the extant genus *Assiminea* renders extant members of this genus paraphyletic with respect to other extant genera in this genus. Zapata et al. (2014) infer that the Littorinomorpha may have diverged from other Caenogastropoda between 180 and 100 Ma. The fossils that they use to date their phylogeny are all considerably older than this, so it is likely that there is some unaccounted-for rate heterogeneity driving this early divergence. As a result, it is also possible that both *Assiminea striatura* and *Assiminea obesa* are members of stem-group genera within the Assimineidae that unfortunately lack any convincing synapomorphies that would make the creation of a new genus justifiable on morphological grounds alone.

Incertae Sedis
Species 1
(Fig. 7A).

Material. PRI78119, an ovoid piece of amber, yellowish orange colored, Dimensions: W = 23 mm, L = 42 mm, D = 5 mm.
Locality and horizon. Kachin State, Myanmar; mid-Cretaceous, at the Albian-Cenomanian boundary (approximately 100 Ma).
Description. Dextral, large shell, ovate conical, high spired, 6 whorls, 30° apical angle, apex slightly blunted, protoconch sculpturing intermittently costate, indented sutures, whorl periphery slightly rounded. Teleoconch sculpturing very slight transverse striae, body whorl more than half shell height, rounded ovate aperture, umbilicus absent. Dimensions: H = 10.75 mm, W = 4.5 mm.
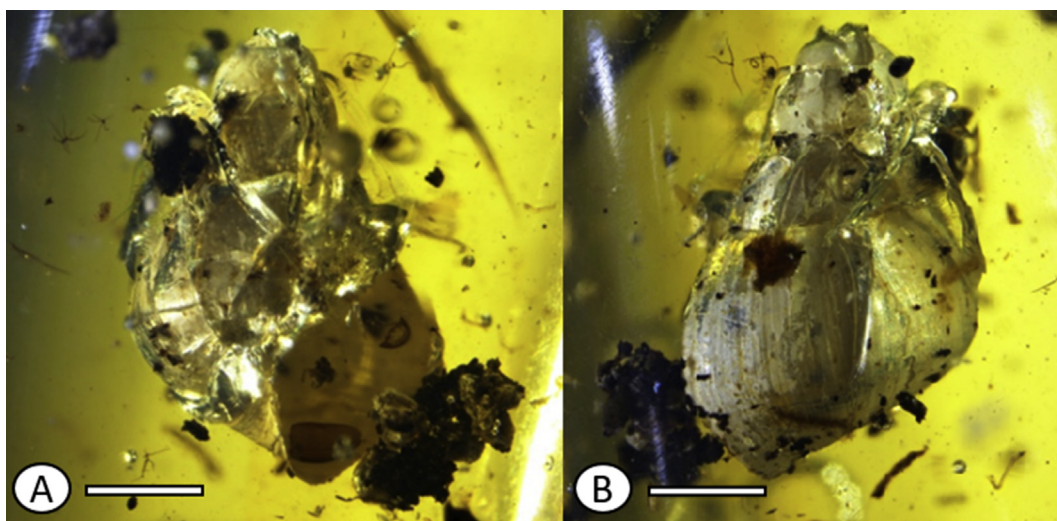
Species 2
(Fig. 8A and B)

Material. PRI78120, an oval piece of amber, pale yellow colored, Dimensions: W = 12 mm, L = 18 mm, D = 4 mm.
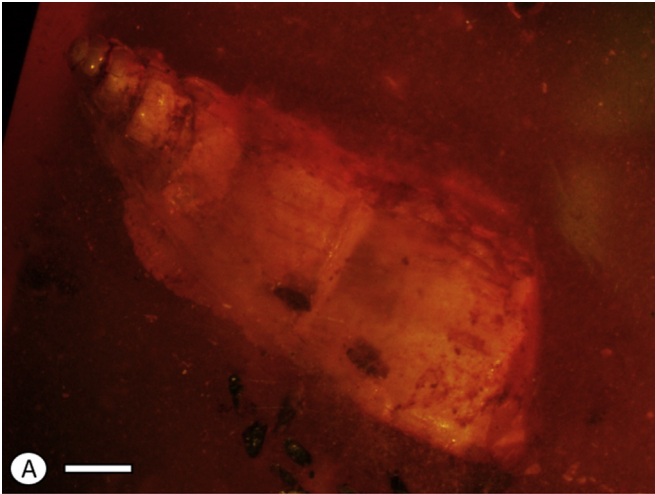**Locality and horizon.** Kachin State, Myanmar; mid-Cretaceous, at the Albian-Cenomanian boundary (approximately 100 Ma).
Description. Dextral, small shell, pyramidal conical shell, 5 whorls, apical angle 40°, apex slightly blunted, protoconch apparently unsculptured. Teleoconch lacking sculpture with sutures slightly indented, body whorl with slight angular periphery, and remaining

Fig. 6. Holotype of *Assiminea striatura* sp. nov. from mid-Cretaceous Burmese amber (Bu1852) *in situ* light micrographs showing: **A**, apertural view; **B**, abapertural view. Scale bar = 1 mm.

Fig. 7. Incertae sedis Species 1 from mid-Cretaceous Burmese amber (PRI78119) *in situ* light micrograph showing: **A**, lateral view. Scale bar = 2 mm.

whorls very slightly rounded. Aperture ovoid being broadly attached to body whorl by the parietal edge, basal and parietal edges of aperture slightly flared, umbilicus absent. Dimensions: H = 9.5 mm, W = 5.25 mm, Aw = 3 mm.

Species 3
(Fig. 9A–D)

Material. JZC Bu-307, an irregular ovoid piece of amber, brown colored, Dimensions: D = 18–21 mm, L = 35 mm, W = 30 mm. Syninclusions: large adult Blattodean, Dipteran.
Locality and horizon. Kachin State, Myanmar; mid-Cretaceous, at the Albian-Cenomanian boundary (approximately 100 Ma).
Description. Dextral, small shell, heliciform shell with highly depressed spire, at least 3 whorls, body whorl rounded periphery, sutures slightly indented, protoconch not preserved. Teleoconch sculpturing indeterminate, aperture circular with apertural lip slightly reflexed, umbilicus wide approximately 2/3 shell width. Overall shape: H = 2.75 mm, W = 7 mm.

Species 4
(Fig. 10A–D)

Material. JZC Bu-333, an irregular triangular piece of amber, deep orange colored, Dimensions: D = 12 mm, L = 28 × 27 × 24 mm.
Locality and horizon. Kachin State, Myanmar; mid-Cretaceous, at the Albian-Cenomanian boundary (approximately 100 Ma).
Description. Dextral, small shell, heliciform with highly depressed spire, at least 3 whorls, sutures indeterminate, protoconch not preserved. Teleoconch sculpturing prominent transverse costae, large subcircular aperture with evidence of a basal lip flare, wide umbilicus approximately ½ shell width. Dimensions: H = 1 mm, W = 2.5 mm.

Species 5
(Fig. 11A–D)

Material. JZC Bu-538, an irregularly ovate piece of amber, dark brown colored. Dimensions: D = 7 mm, H = 22 mm, L = 12 mm.
Locality and horizon. Kachin State, Myanmar; mid-Cretaceous, at the Albian-Cenomanian boundary (approximately 100 Ma).
**Description.** Dextral small shell, conical, high spired, approximately 5–6 whorls. Shell apex very blunt, apical angle 50°, protoconch unsculptured. Teleoconch unsculptured, body whorl representing approximately ½ of shell height, whorl periphery slightly rounded and moderately shouldered, sutures indented, aperture damaged extending ½ whorl inward, columellar lip impinging on umbilicus which is perforate. Dimensions: H = 3.5 mm, W = 2.75 mm.
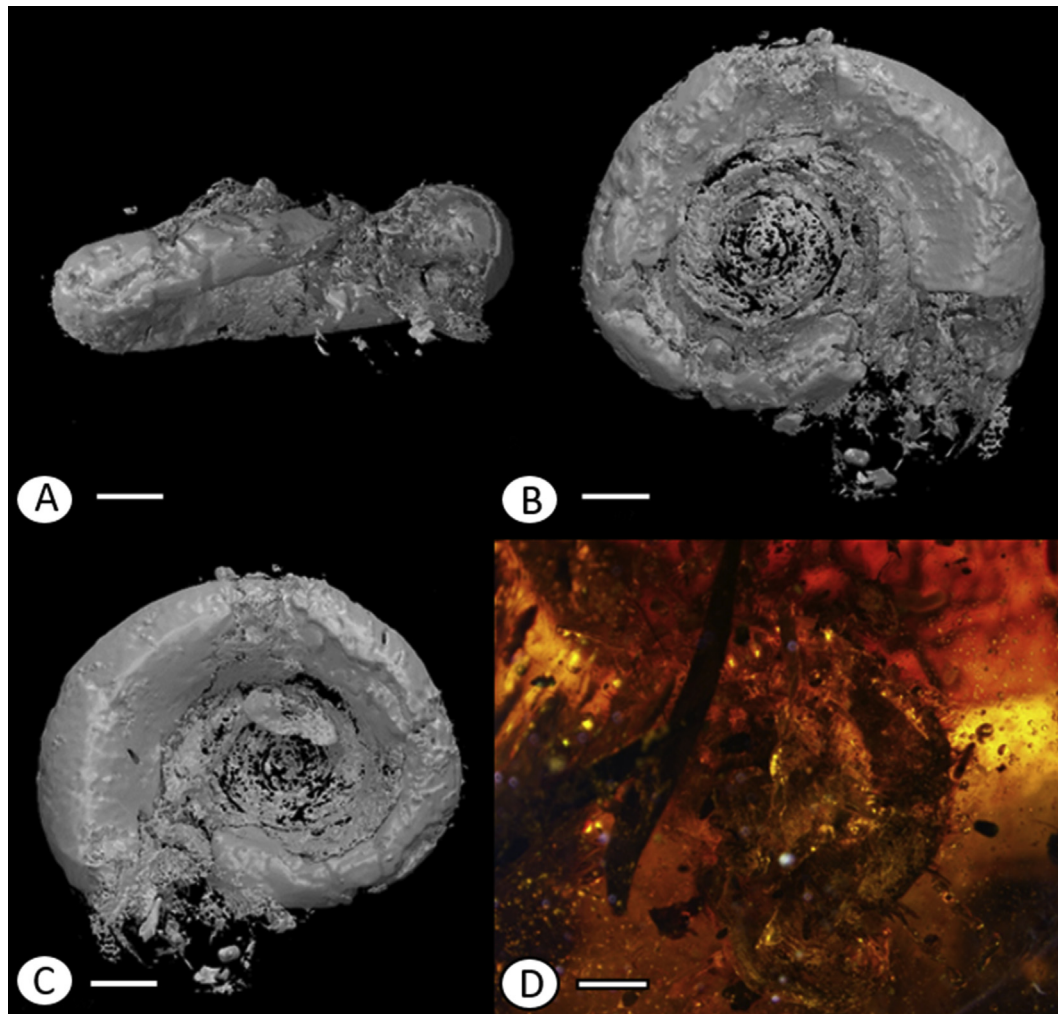
Species 6
(Fig. 12A–D)

Material. AMNH B-0099, a cracked piece of amber embedded in composite, honey colored. Dimensions: D = 4–5 mm, W = 17 mm, L = 11–17 mm. Syninclusions: Male Cecidomyiidae, cercal forceps of a dermapteran, three Acari, and Auchenorrhyncha wing.
Locality and horizon. Kachin State, Myanmar; mid-Cretaceous, at the Albian-Cenomanian boundary (approximately 100 Ma).
Description. Dextral, small shell, turbinate, approximately 4 whorls, tight elliptical coiling. Shell apex blunt from damage, apical angle 90°, protoconch with indeterminate sculpturing, spire subtriangular. Teleoconch sculpturing transverse striate, body whorl
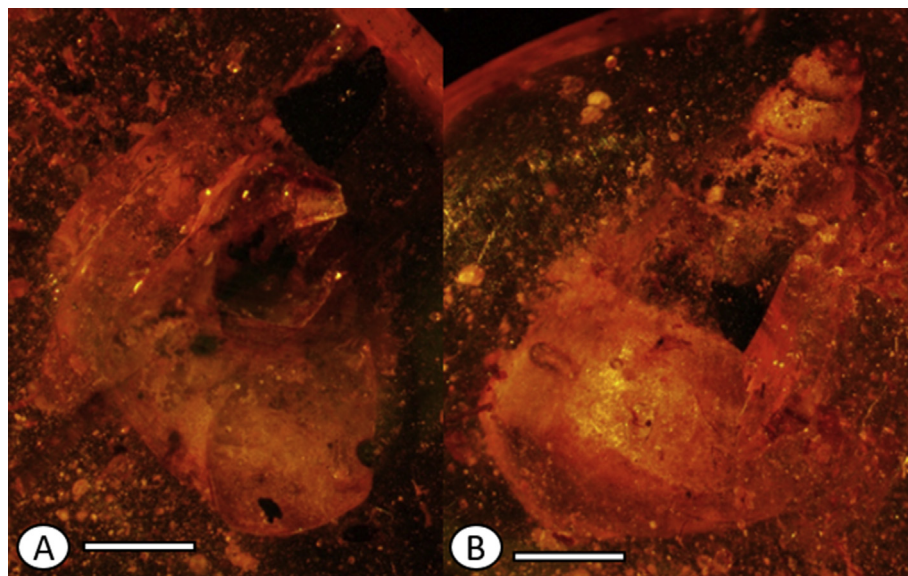
Fig. 8. Incertae sedis Species 2 from mid-Cretaceous Burmese amber (PRI78120) *in situ* light micrograph showing: **A**, apertural view; **B**, abapertural view. Scale bar = 1 mm.

Fig. 9. Incertae sedis Species 3 from mid-Cretaceous Burmese amber (JZC Bu-307) MicroCT scans showing: **A**, apertural view; **B**, apical view; **C**, umbilical view; and **D**; *in situ* light micrograph. Scale bar = 1 mm.

with angular periphery, body whorl ¾ shell height, suture between body whorl and penultimate whorl impressed, suture between penultimate whorl and antepenultimate whorl slightly impressed, aperture rounded lunate with damage along out lip, palatal lip absent, evidence of perforate umbilicus. Dimensions: H = 5 mm, W = 5 mm, D = 5.5 mm.

Remarks. Turbinate shell shape is very characteristic of cyclophoroidean land snails but is also superficially similar to *Chondropometes* Henderson and Bartsch (1920) (Littorinoidea: Annulariidae) and *Tropidophora* Troschel (1847) (Littorinoidea: Pomatiidae). Overall shell shape and perforate umbilicus similar to that of extant *Leptopoma* Pfeiffer (1847) and *Cyclophorus* de Montfort (1810) (Cyclophoridae). In contrast, *Leptopoma* has a conical spire, possesses spiral sculpture and a circular or sub-circular aperture. Very blunt apex appears to be the result of damage from the apical view (Fig. 1B). The degree of angularity of the body whorl is fairly uncommon in *Cyclophorus* and only resembles *Cyclophorus acutimarginatus* Sowerby (1842).

4. Discussion

The new land snails we report herein represent a significant contribution to knowledge of the land snail fauna known from Burmese amber, increasing the total number from three to 15. The wealth of discoveries of new cyclophoroideans in Burmese amber compared to other land snail groups suggests that they may have been a major component of the snail fauna of Southeast Asia in the mid-Cretaceous (which is still true today), and that some families evolved earlier than was previously understood. Recent cyclophoroideans occur in temperate Europe but are largely pantropical (Old and New World tropics), reaching their highest diversity in India and Southeast Asia. Our results align with recent studies of mid-Cretaceous age Burmese amber that have also uncovered new diplommatinid, cyclophorid, and pupinid land snail species (Cyclophoroidea) (Neubauer et al., 2019; Xing et al., 2018; Yu et al., 2018). The earliest representatives of these families were previously known only from the Miocene (23 Ma) in the case of Cyclophoridae and Pupinidae (Raheem et al., 2017), and the Paleocene (Thanetian Age; 57 Ma) in the case of the Diplommatinidae (Glibert, 1962). Our study, combined with evidence from the Yu et al. (2018) and Xing et al. (2018) specimens, suggests a minimum divergence estimate of the Cyclophoroidea from the Viviparoidea in the mid-Cretaceous. The maximum age of the divergence of the Heterobranchia and Caenogastropoda is estimated to be in the early Devonian (418 Ma) (Zapata et al., 2014). Based on previous attempts at fossil-calibrated dating of molecular phylogenies of gastropods, several extant terrestrial clades were
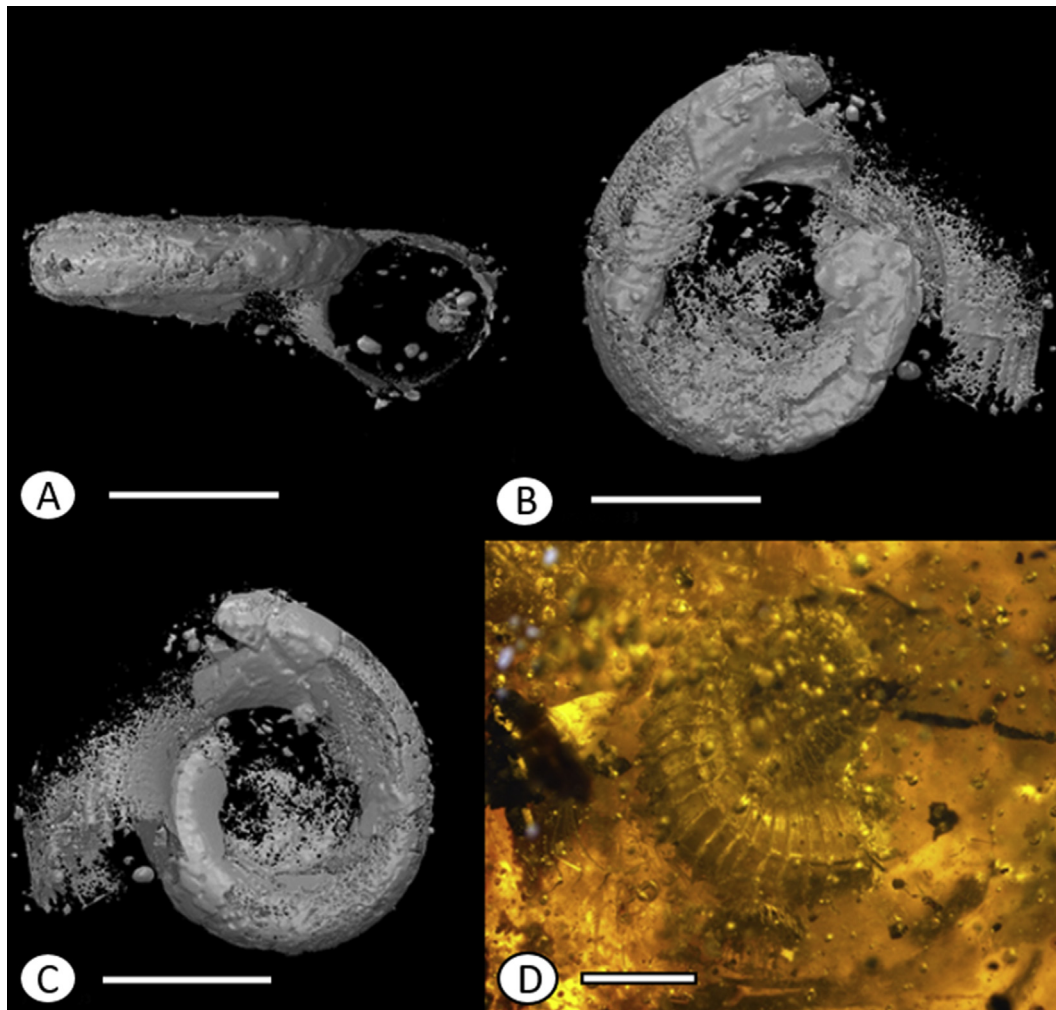
Fig. 10. Incertae sedis Species 4 from mid-Cretaceous Burmese amber (JZC Bu-333) MicroCT scans showing: **A**, apertural view; **B**, apical view; **C**, umbilical view; and **D**; *in situ* light micrograph. Scale bar = 1 mm.

present during the Mesozoic and would be possible to recover in future Burmite samples.

The paleoforests in which Burmese amber specimens were preserved were likely mixed conifer and angiosperm in composition. While angiosperms were still relatively rare in Early Cretaceous forests between the Aptian and Albian, they became a far more common component of Cretaceous forests between the Cenomanian and Santonian ages (Peralta-Medina and Falcon-Lang, 2012). This increasing angiosperm dominance in the paleoforests of Myanmar likely created more favorable conditions for the proliferation of land snails Solem (1984) noted that land snails generally are more rare and species-poor in today's conifer-dominated forests, so perhaps whatever the underlying cause of this pattern in space also drove a diversification of land snails along with the rise of the angiosperms in paleontological time.

Preservation of most of our land snail specimens as dead, empty shells suggests that their fossilization occurred after death, as amber tree-resin fell onto dead shells on the forest floor. The majority of the specimens examined for this study were preserved with damage consistent with what is observed in empty shells on the forest floor. This hypothesis is supported by land snails' typical avoidance of crawling on coniferous tree species (Solem, 1984; Kralka, 1986), as well as the likelihood that dead snail shells might accumulate in certain areas on the forest floor, as they do in

modern rainforests. Both emergent-vegetation (including tree-)-dwelling land snails and leaf litter-dwelling land snails accumulate on the forest floor, so it is difficult to know for certain whether our species were vegetation- or leaf litter-dwelling. All families represented in the present study contain many leaf litter-dwelling species. This, combined with the fact that the majority of extant tropical land snail species richness is in the leaf litter, supports the notion that many of these were leaf litter species.

The taphonomy and shell characteristics of Burmese land snails in amber are of interest because they can help us better understand the ecology of these species before and after death, and their environments of fossilization (Yanes, 2012). For example, are forest floor conditions conducive to long periods of shell "survival," while the animal is dead but before it is trapped in resin? In terrestrial habitats, persistence of shells after death is limited by the effects of chemical dissolution and physical breakage, as well as bioerosion by grazing organisms (Pearce, 2008). Chemical dissolution can be accelerated by acidic leaves in leaf litter, to which land shells' protective outer periostracum has adapted (Solem, 1974). While the rate at which shell breakdown processes occur in the environment can vary significantly, it has been shown that warm, humid tropical climates might speed shell breakdown overall, and that larger shells break down far more slowly than smaller shells (Říhová et al., 2018): in warm moist habitats this process occurs within three
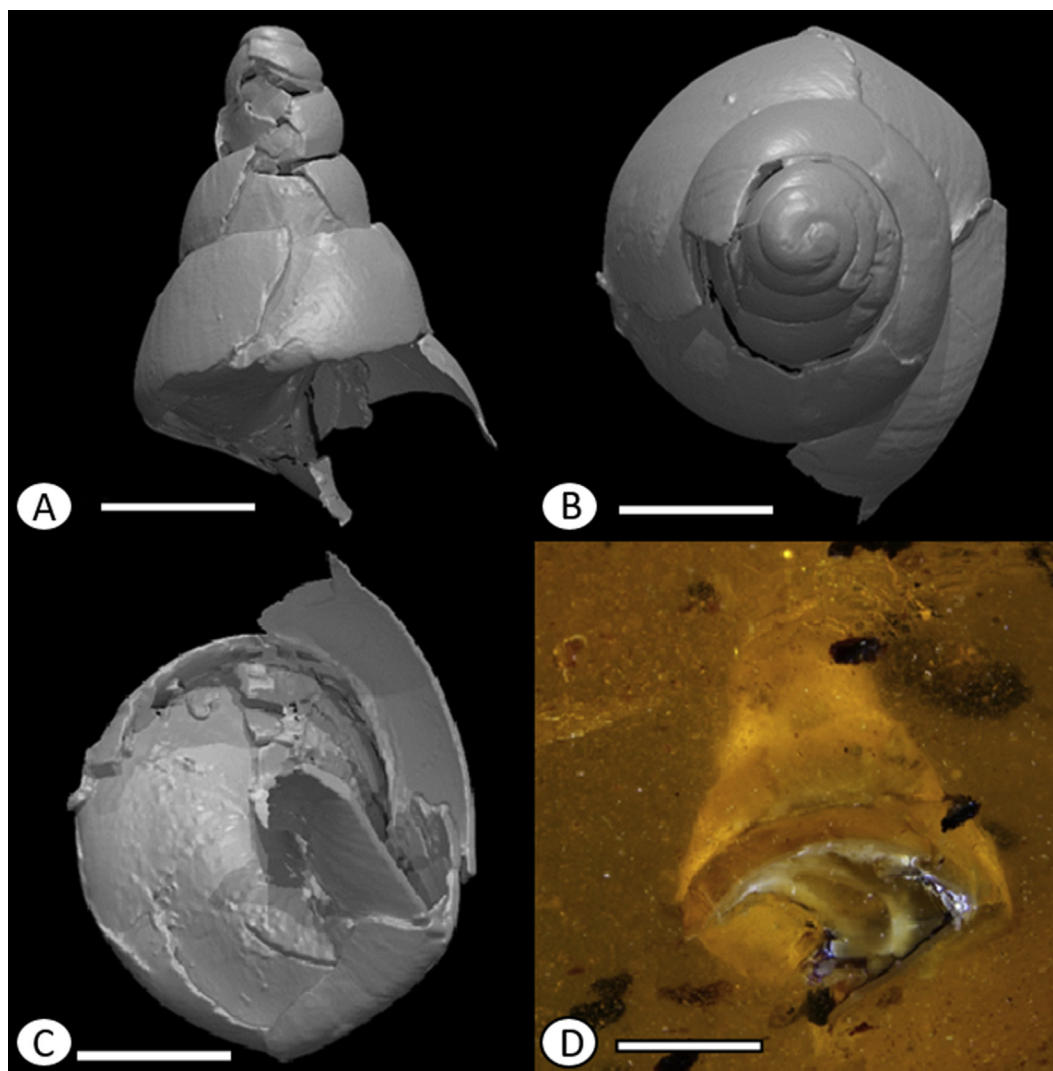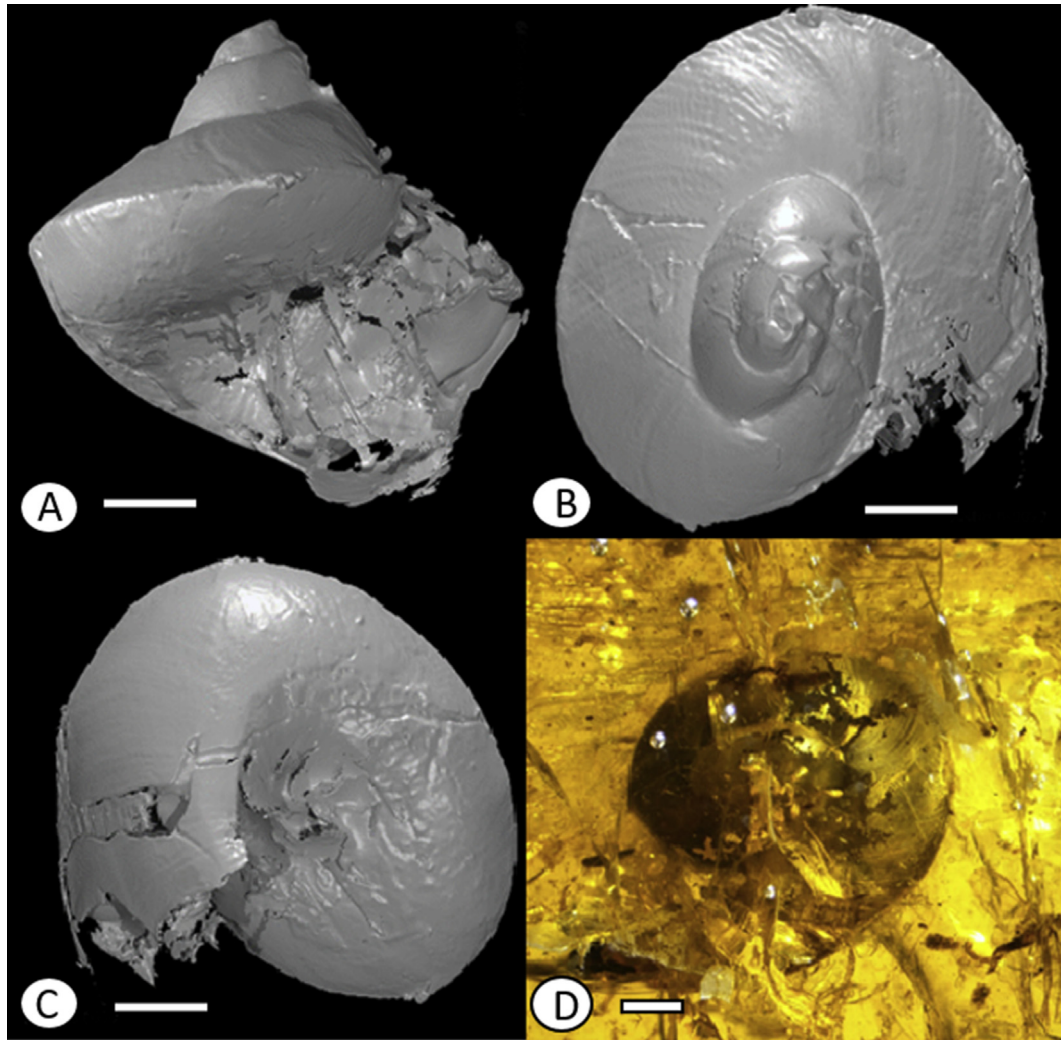
Fig. 11. Incertae sedis Species 5 from mid-Cretaceous Burmese amber (JZC Bu-538) MicroCT scans showing: **A**, apertural view; **B**, apical view; **C**, umbilical view; and **D**; *in situ* light micrograph. Scale bar = 1 mm.

years for small shells, while large shells may only be slightly degraded after three years. Thus, our largest specimen (Incertae sedis Species 1), might have persisted in the environment for quite some time after death and before fossilization. However, the majority of our specimens likely could have lasted in the environment for less than three years before fossilization, given their very small body size and preservation. This suggests that these small-bodied species could have been preserved in amber soon after death or less than a few years after death. We also observed that one of our specimens might include body tissue (*Eotrichophorus kachin*), providing evidence that some snails might have been trapped alive in resin, while crawling on vegetation or in leaf litter. Live snails might have also co-mingled with leaf litter patches containing dead shells (as they do in modern rainforests; Pearce and Örstan, 2006).

The nature and origin of periostracal hairs in land snails is also of significant interest in helping us better understand the ecology of particular species during the mid-Cretaceous, and in increasing our understanding of evolution land snail shell adaptations generally. *Eotrichophorus kachin* (this study) very likely represents one of the earliest land snail fossils with periostracal hairs. Periostracal hairs have evolved several times independently in both marine snails (e.g., Capulidae, Cymatiidae) and in land snails (e.g., Assimineidae,

Charopidae, Helicidae, Hygromiidae and Polygyridae). In small (<2 cm) marine snails (e.g., *Trichotropis cancellata* Hinds, 1843), it has been suggested that the hairs aid in predator deterrence (Iyengar et al., 2008). More generally, the relative thickness of gastropod shells' periostracum has likely evolved in response to the threat of shell dissolution, which on land includes the acidic leaf litter or soil surrounding certain species (Solem, 1974). Based on this premise, periostracal hairs might provide further shell fortification against dissolution in leaf litter-dwelling land snails. Shell hairs are also thought to allow for easier maneuvering in wet or damp environments among leaf litter dwelling and herbaceous plant foraging snails since the hairs are hydrophobic (Suvorov, 1999). Pfenniger et al. (2005) showed that land snails with haired shells tend to occur in habitats with low evaporation and/or high precipitation, while non-hairy shells tended to occur in habitats with high evaporation and/or low precipitation. On a water-covered leaf surface hairy shells require a significantly higher force to overcome adhesion and thus are harder to knock off wet leaves (Pfenniger et al., 2005). It is very likely then that *Eotrichophorus kachin* was preserved in a forest with low evaporation and/or high precipitation, for which there is abundant direct evidence in the amber (e.g., presence of Onychophora, angiosperm leaves with

Fig. 12. Incertae sedis Species 6 from mid-Cretaceous Burmese amber (AMNH B-0099) MicroCT scans showing: **A**, apertural view; **B**, apical view; **C**, umbilical view; and **D**; *in situ* light micrograph. Scale bar = 1 mm.

drip tips, epiphytic bryophytes, etc: Grimaldi and Ross, 2017). It is also not unlikely that *E. kachin* in particular was a leaf litter dweller. Shell hairs are energetically costly to produce, and they form via a complex mechanism separate from the rest of the periostracum (Allgaier, 2011). Thus it is likely that shell hairs have some adaptive significance and can be indicative of a wet terrestrial habitat (Salvador and Rosser, 2017).

South-East Asia is currently a very diverse area for land snails (Solem, 1984; Vermeulen et al., 2015). As in many groups, the Cretaceous represents a time when biotas were becoming more similar to modern ecosystems in terms of their functional and taxonomic composition. It is likely that the K/Pg mass extinction exerted a large toll on land snail communities, and therefore many of the land snails from 100 Ma may not survived. Analysis of the survivorship of fossil marine genera across the Phanerozoic reveals an average age of 28 Ma with the distribution being heavily right-skewed (Raup, 1991). Recent studies confirm this particularly for tropical marine bivalves which have a median age of 26.2 Ma (Jablonski et al., 2013). Given the majority of land snails species (especially in the tropics) have very small range sizes (Lydeard et al., 2004) compared to tropical bivalves, their propensity for extinction is much higher. While some genera do last much longer in the fossil record, it is likely that many if not most land snail genera from the Cretaceous would not belong to an extant genus.

Finally, it is important to note that classifying land snails using shell morphology alone is challenging, in part due to convergence in teleoconch traits (Bandel and Geldmacher, 1996; Bandel and Frýda, 1996). Accurately identifying and describing these early land snail fossils is hampered by lack of soft tissue characters and occluded shell characters due to shell damage and other inclusions. Solem and Yochelson (1979) were able to identify Paleozoic land snail taxa to extant caenogastropod and stylommatophoran families based on internal and external shell morphology, but this has been questioned (Naggs, 1997). While fossil-calibrated estimates of the origin of the caenogastropods support a Paleozoic origin (Zapata et al., 2014), whether the taxa described here are representatives of extant caenogastropod lineages (i.e., Diplommatinidae and Cyclophoridae) is still up for debate (Naggs, 1997; Naggs and Raheem, 2005). Protoconch traits have been demonstrated to be more informative in diagnosing larger gastropod clades (Ponder and Lindberg, 2008), but these traits can very often be poorly preserved or occluded especially in oft-damaged amber specimens.

5. Conclusions

In this paper, 12 previously unidentified mid-Cretaceous Burmese amber land snails are described significantly increasing the number of species known from Burmese amber. The taxa described

likely represent 2–3 independent colonizations of the terrestrial realm. We also report the earliest land snail species with periostracal hairs, an adaptive trait supporting the wet terrestrial preservational environment of these fossils. Finally we show the majority of these shells are preserved after death and likely persist on the forest floor for a short period of time before being encased in amber. Extant land snails may rival both extant tetrapods and extant marine snails in diversity, but unlike these two groups, our understanding of this grade from the Mesozoic comes from just a few assemblages. This work represents a key jumping-off point for future studies in the diversity and diversification dynamics of this fascinating group.

Acknowledgements

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Appendix A. Supplementary data

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