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The first records of mollusks from mid-Cretaceous Hkamti amber (Myanmar), with the description of a land snail, *Euthema myanmarica* n. sp. (Caenogastropoda, Cyclophoroidea, Diplommatinidae)

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Abstract.—Five land snails and the borings of marine bivalves are reported from Hkamti (Khamti) amber whose age was recently uranium-lead dated to be ca. 110 Ma, in contrast to the nearby Kachin ('Burmese') amber considered to be ca. 99 Ma. Four of the snails belong to Cyclophoridae, and although their condition does not allow unambiguous identification or description of the species, one of them strongly resembles *Archaeocyclotus plicatula* Asato and Hirano in Hirano et al., 2019 from Kachin amber. The fifth snail, *Euthema myanmarica* n. sp. (Diplommatinidae), is a representative of a genus that was known exclusively from Kachin amber until now. The genus *Euthema* Yu, Wang, and Pan, 2018 is revised, with a new synonym, *Xenostoma* Bullis et al., 2020. The recently described '*Truncatellina dilatatus*' Yu, 2020 from Kachin amber is placed in *Euthema*. A comparison of the distinguishing characters of the eight *Euthema* species is provided. The borings of bivalves in Hkamti amber correspond to the ichnospecies *Teredolites clavatus* Leymerie, 1842, associated with the bivalve genus *Martesia* Sowerby, 1824 (Pholadidae), and are common in Kachin amber. Similarity of the malacofauna from Hkamti and Kachin ambers, as well as the presence of numerous, similar *Teredolites clavatus*, indicates that these ambers were formed in very similar paleoenvironments. This indication suggests that forests with very similar conditions existed throughout the entire Albian to the early Cenomanian, or that the dating of at least one of these amber deposits is incorrect. In the latter case, it would mean that Kachin amber is at least 110 Ma or older.

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Introduction

The little-known Hkamti amber from the Sagaing Region of northern Myanmar was recently uranium-lead (U-Pb) dated to be ca. 110 Ma of age (Xing and Qiu, 2020). Previously, it was thought to be the same age as Kachin (or 'Burmese') amber from the nearby Hukawng Valley in Kachin State, Myanmar (90 km from Hkamti). The age of Kachin amber was U-Pb dated to be ca. 99 Ma (Shi et al., 2012), a date considered to be supported by some fossils (Smith and Ross, 2018). Kachin amber is well-known for its extremely diverse and rich tropical paleobiota from the Cretaceous, with nearly 1,500 species currently described (Ross et al., 2010; Ross, 2019, 2020). Because amber mining began in Hkamti only recently, very few species have been reported (Jouault et al., 2020a, b; Olmi et al., 2020; Xing and Qiu, 2020), and its paleobiota is yet to be described and compared with that of Kachin amber.

Prior to the current study, there were no records of mollusks from Hkamti amber, but nearby Kachin amber is known to be rich in mollusks: 19 new species of land snails have been described since 2018 and numerous other molluskan inclusions have been reported (Yu et al., 2018; Hirano et al., 2019; Balashov, 2020; Balashov et al., 2020; Bullis et al., 2020; Yu, 2020). Kachin amber is much richer in mollusks than all other well-studied deposits of amber combined (Balashov, 2020). Only 11 species of land snails have been described from Eocene Baltic amber over 130 years of study (Stworzewicz and Pokryszko, 2006, 2015; Balashov and Perkovsky, 2020), and few specimens have been reported from Miocene Dominican amber (Poinar and Roth, 1991; Penney, 2010) and from Lower Cretaceous Lebanese amber (Roth et al., 1996) without species descriptions. The goals of this study are to describe the first mollusks from Hkamti amber, compare the species composition of this deposit to Kachin amber, and discuss the implications of the resulting comparisons.

Materials and methods

The amber was mined in Hkamti (sometimes spelled 'Khamti'), Hkamti District, Sagaing Region, northern Myanmar. Systematics follow Bouchet et al. (2017). The terminology used in the description of Diplommatinidae follows Neubert and Bouchet (2015) and Nurinsiyah and Hausdorf (2017).

Repository and institutional abbreviation.—Types, figures, and other specimens examined in this study are deposited in the collection of terrestrial mollusks of the I.I. Schmalhausen

Institute of Zoology NAS Ukraine, Kyiv, Ukraine (SIZK; the abbreviation IZAN is the same and also in use).

Systematic paleontology

Class Gastropoda Cuvier, 1795
Subclass Caenogastropoda Cox, 1960
Order Architaenioglossa Haller, 1892
Superfamily Cyclophoroidea Gray, 1847
Family Diplommatinidae Pfeiffer, 1856

Genus *Euthema* Yu, Wang, and Pan, 2018

2018 *Euthema* Yu et al., p. 255.
2019 *Euthema*; Hirano et al., p. 7.
2020 *Euthema*; Balashov, p. 2.
2020 *Paleodiplommatina* Bullis et al., p. 5.
2020 *Xenostoma* Bullis et al., p. 6 (n. syn.).

Type species.—Euthema naggsi Yu, Wang, and Pan, 2018.

Revised diagnosis.—Shell very small, dextral, nearly cylindrical, consisting of approximately six whorls. First two whorls irregularly tightly coiled. Constriction strong to almost reduced. Surface with prominent ribs. Aperture oval to circular or nearly heart-shaped. Peristome doubled. Umbilicus open, often with periumbilical keel.

Occurrence.—Only known from Kachin and Hkamti ambers (northern Myanmar), eight species; Albian–Cenomanian (mid-Cretaceous), ca. 110–99 Ma.

Size.—Height 1.7–3.25 mm; diameter 0.9–1.5 mm.

Remarks.—This genus has been previously revised (Balashov, 2020), but the addition of new specimens, including one described here, provide a more complete picture and require additional clarifications and arrangements.

There are several significant characters that appear to be inherited from the ancestor of *Euthema* but are more or less reduced in some of the species. These characters are:

(1) In all *Euthema* spp., there is a constriction near the last quarter of the penultimate whorl and/or the first quarter of the last whorl, i.e., the diameter of the shell tube decreases, and the remaining part of last whorl continues with the same diameter as before the constriction. The constriction varies in *Euthema* spp. from strong to very weak (Table 1), but it is present in all specimens and is among the distinctive features of Diplommatinidae (Neubert and Bouchet, 2015; Nurinsiyah and Hausdorf, 2017).
(2) Largely because of the constriction, coiling of the two last whorls is more or less irregular in *Euthema*, and some part of the penultimate whorl is often appressed to the last whorl. This character has been described for *Euthema* spp. as 'penultimate whorl coiling tight' (Yu et al., 2018; Hirano et al., 2019; Balashov, 2020). This description means that, in abapertural view, the 'left' part of the penultimate whorl (last quarter) is usually irregularly lower than in the previous whorl. This is especially obvious in *E. naggsi* and *E. annae* Balashov, 2020 (see Yu et al., 2018, fig. 1A; Balashov, 2020, fig. 1B, D). However, if the constriction is oriented in a slightly different position, or if the shell is from a juvenile or subadult, then the same part of the penultimate whorl might be regularly higher than in the previous whorl, whereas the 'low part' might be displaced to the end of the penultimate whorl. This condition is particularly conspicuous in *E. hesoana* Asato and Hirano in Hirano et al., 2019 (see Hirano et al., 2019, fig. 4a–c). In some *Euthema* spp., this character is very weak, and the 'low part' can be displaced to the beginning of the last whorl; in such a case, the penultimate whorl coils almost regularly, but the last whorl does not.
(3) The first two whorls of *Euthema* are irregularly tightly coiled (oblique to the axis of the remaining shell and unproportioned in size), and in most species, they are also significantly narrower than the third and following whorls. Such coiling often forms a specific, slightly blunt and rounded shape of the upper part of the shell (first three whorls), which is especially conspicuous in *E. truncatellina* Balashov, Perkovsky, and Vasilenko, 2020 (see Balashov et al., 2020). This irregular coiling means that juveniles of some *Euthema* species with approximately three whorls have a relatively low shell, with the diameter exceeding the height, and this is perhaps beneficial to *Euthema* in its earlier life stages. Usually in species with a cylindrical or high-conical shell of three whorls, the shell is high already (but there are exceptions). This character seems to be especially important for generic delimitation because it does not occur in most extant Diplommatinidae. However, it is similar in *Notharinia* Vermeulen, Phung, and Truong, 2007 from Southeast Asia (Vermeulen et al., 2007, 2019; Maassen, 2008; Páll-Gergely and Hunyadi, 2018). Perhaps this means that *Notharinia* is distantly related to *Euthema*.
(4) A periumbilical keel is present only in some species of *Euthema*, and it largely reflects the shape of the constriction, e.g., it is probable that the keel initially formed as a result of a strong constriction. However, considering that a keel is also present in some species with a weak constriction and absent in some species with a moderate constriction (see Table 1), it appears to be an important independent character that should be especially useful for species delimitation in *Euthema*.

A comparison of distinguishing characters from all known Cretaceous species of Diplommatinidae (see Table 1) leads to the conclusion that members of this group are probably closely related and, therefore, should be viewed as a single genus. The implications suggest that *Xenostoma* should be considered a synonym of *Euthema*, as was previously concluded for *Paleodiplommatina* (see Balashov, 2020). *Xenostoma* was established for a single species from Kachin amber, *X. lophopleura* Bullis et al., 2020, and is characterized by the "very small elongate conical shell with penultimate whorl wider than body whorl, narrowly umbilicate, and uniquely oblique-ovate aperture with doubly expanded peristome" (Bullis et al., 2020, p. 6). All listed characters, except apertural shape, are common among *Euthema* spp. (see Table 1), and a slightly different shape of the aperture

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Table 1. A comparison of distinguishing characters in *Euthema* spp.

Characters/Species	*E. naggsi*	*E. hesoana*	*E. spelomphalos*	*E. lophopleura*	*E. dilatata* (juvenile)	*E. truncatellina*	*E. annae*	*E. myanmarica*
Height of shell (mm)	2.1	2	3.25	2.25	1.45	1.7	∼2	2
Diameter of shell (mm)	1.1	1	1.5*	1.25*	0.93	0.9	1–1.1	0.9
Number of whorls	6*	5–6 (6?)	6–7*	6.5*	5	6.5	6	6
Whorl convexity	strong	?	weak	strong	moderate	moderate	weak	moderate
Apertural shape	oval	oval	oval	oval, oblique	circular	circular	almost heart-shaped	oval
Ribs on the apertural half of penultimate whorl (approximate)	28	20	20	20	30	35	40	25
Constriction	moderate	strong	weak	moderate	moderate	weak	strong	weak
Penultimate whorl coiling tightly	yes	yes	no?	yes?	yes	no	yes	no
Umbilicus	narrow	wide, enormous	wide	narrow	narrow	narrow	narrow	wide
Periumbilical keel	none	very strong	weak	none or weak	none	none	weak	strong

*remeasured from the original photos

alone is not significant enough to distinguish genera. The whorls are relatively regularly coiled in *E. lophopleura* (see Bullis et al., 2020), but a weak constriction is present, and the first two whorls are coiled relatively irregularly and tightly. Other characters of *E. lophopleura* are like those of *E. naggsi*.

The nomenclatural acts by Bullis et al. (2020) should be addressed here because the publication date of the taxa being referred to is 2019 (Ross, 2020). The online version of the paper was first published in September 2019, but because the publication was not registered in ZooBank (Bullis et al., 2020), the requirements of Article 8.5 of the International Code of Zoological Nomenclature (ICZN, 1999, with amendments of 2012) were not met. Thus, the date of publication of the printed version (March 2020, day not specified) should be used.

In the recent work of Yu (2020), three new shells of *Euthema* were reported from Kachin amber. Two were identified as *E. naggsi*, and the third was described as a new species, '*Truncatellina dilatatus*' Yu, 2020 of the extant genus *Truncatellina* Lowe, 1852 (Heterobranchia, Stylommatophora, Orthurethra). The latter genus belongs to a different subclass of gastropods than *Euthema*. There is absolutely no doubt that this shell is not a representative of pulmonate mollusks but belongs to Cyclophoroidea. The last whorl is constricted and slightly curved and irregularly coiled, which is a typical feature of Diplommatinidae (Nurinsiyah and Hausdorf, 2017) not found in Orthurethra. Some species of *Euthema* are indeed very similar to *Truncatellina*, so much so that together with the fact that I have collected and studied several thousands of the extant European snails of this genus, it has led me to naming one of the *Euthema* species after this genus, *E. truncatellina*, to acknowledge the convergence in the two lineages of land gastropods (Balashov et al., 2020).

An irregular character of shell coiling in *Euthema*, especially of the last whorl and of the first two whorls, is unmistakably different than in *Truncatellina*. As described above for *Euthema*, '*Truncatellina dilatatus*' has the first two whorls irregularly tightly coiled and significantly narrower than the third and following whorls. This condition is not found in *Truncatellina*, with all whorls coiling regularly. The shell coiling of '*Truncatellina dilatatus*' is identical to that of *E. naggsi*, *E. hesoana*, *E. truncatellina*, etc. Apparently, '*Truncatellina dilatatus*' is a juvenile *Euthema* with an incomplete aperture and a differently oriented constriction. From the main distinctive characters, '*Truncatellina dilatatus*' does not significantly differ from *E. naggsi*, except in being a little smaller and having fewer whorls and a circular aperture (see Table 1), all of which are expected differences for a juvenile *E. naggsi* with an unfinished shell. '*Truncatellina dilatatus*' could be conspecific with *E. naggsi* or could represent a separate species. Additional juvenile and subadult specimens of *Euthema* are required for clarification. Also problematic, the species name '*dilatatus*' is used in the masculine form, but both *Truncatellina* and *Euthema* are feminine; therefore, the ending should be changed to '*dilatata*' in agreement with gender.

One of the two other *Euthema* shells reported by Yu (2020, fig. 1A, B) apparently represents *E. naggsi* as it was identified, but the other (see Yu, 2020, fig. 1C, D) is clearly not a representative of this species. It is probably *E. hesoana* considering the enormous umbilicus resulting from the extremely strong constriction of the last whorl.

Therefore, eight species should be currently placed into *Euthema*: (1) *E. naggsi* Yu, Wang, and Pan, 2018 (additional specimen illustrated by Yu, 2020, fig. 1A, B); (2) *E. hesoana* Asato and Hirano in Hirano et al., 2019 (additional specimen illustrated by Yu, 2020, fig. 1C, D); (3) *E. spelomphalos* (Bullis et al., 2020); (4) *E. lophopleura* (Bullis et al., 2020); (5) *E. dilatata* (Yu, 2020); (6) *E. truncatellina* Balashov, Perkovsky, and Vasilenko, 2020; (7) *E. annae* Balashov, 2020; and (8) *E. myanmarica* n. sp.

Euthema myanmarica new species
Figure 1

Holotype.—SIZK GT 7178, single shell in a small piece of amber, 24 mm × 12 mm × 5 mm. No recognizable syninclusions.

Diagnosis.—Shell almost cylindrical; whorls moderately convex; aperture oval; constriction weak; penultimate whorl high, coiling almost regularly; umbilicus wide, with strong periumbilical keel.

Occurrence.—Hkamti, Sagaing Region, northern Myanmar; Albian (mid-Cretaceous), ca. 110 Ma.

Description.—Shell dextral, almost cylindrical, comprising six moderately convex whorls. Protoconch smooth. First two whorls irregularly tightly coiled, oblique, significantly narrower than third and following whorls. Penultimate whorl

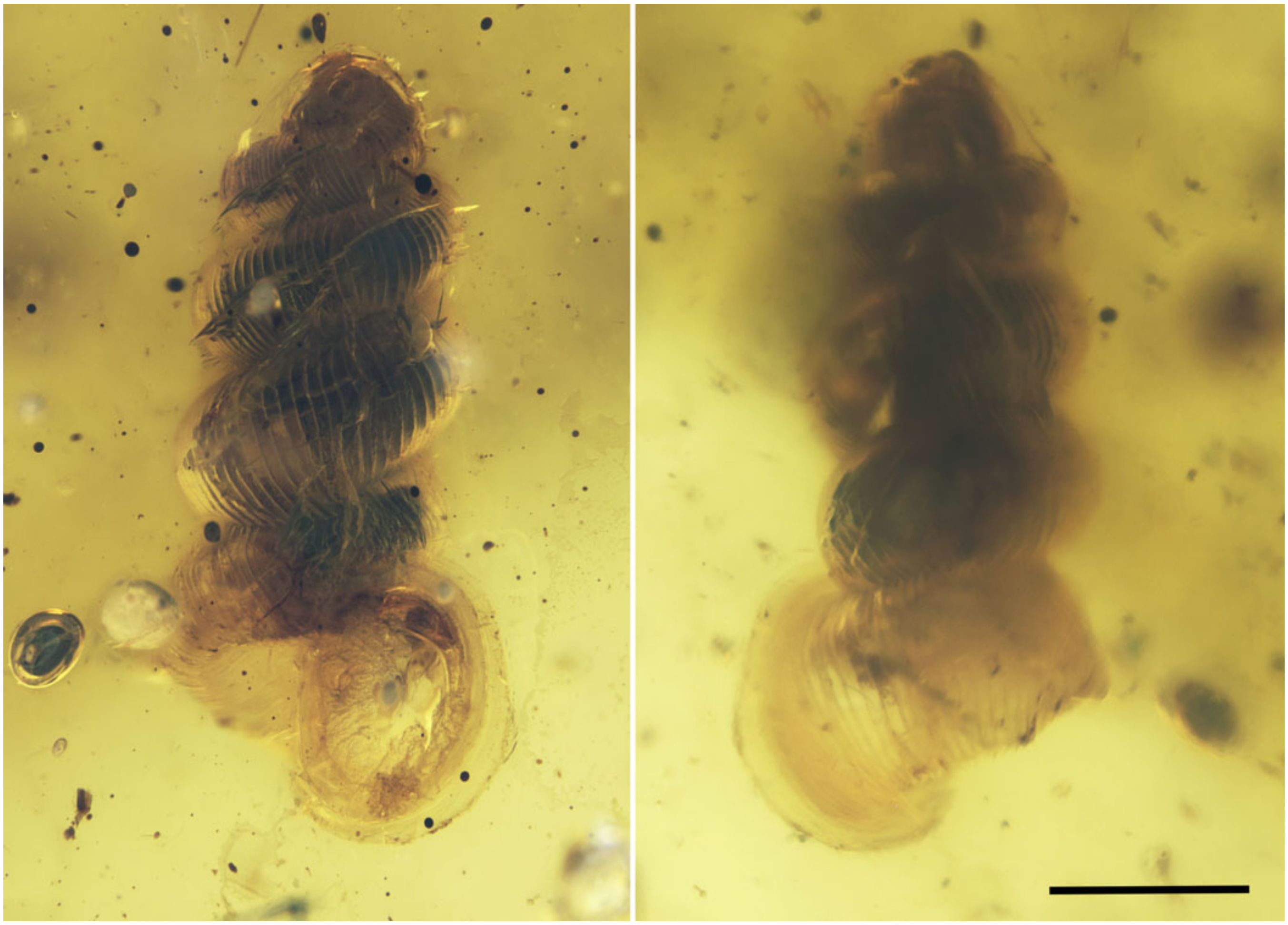

Figure 1. Holotype of *Euthema myanmarica* n. sp. in Hkamti amber, SIZK GT 7178, views from opposite sides of the amber stone. Scale bar = 0.5 mm.

relatively high, coiling almost regularly. Constriction weak, mainly on first quarter of last whorl. Sculpture of relatively straight regular ribs on entire teleoconch. Apertural half of penultimate whorl with ~25 ribs. Aperture oval, with no visible structures inside. Apertural height exceeding its width (ratio 1.25). Peristome doubled; inner peristome thickened; outer peristome thin, sharp, strongly expanded, slightly reflected. Umbilicus wide. Strong periumbilical keel on entire last whorl.

Etymology.—The species is named after the country of origin, Myanmar.

Size.—Shell height 2 mm, diameter 0.9 mm; apertural height 0.75 mm, width 0.6 mm; height of last whorl 0.9 mm, diameter without aperture 0.75 mm; height of visible part of penultimate whorl 0.5 mm, diameter 0.75 mm; height of visible part of fourth whorl 0.35 mm, diameter 0.7 mm; height of visible part of third whorl 0.25 mm, diameter 0.5 mm; height of visible part of second whorl 0.1 mm, diameter 0.3 mm.

Remarks.—This specimen clearly differs from most species of *Euthema* by the presence of the strong periumbilical keel (see Table 1). *Euthema spelomphalos* is much larger (height 3.25 mm) and has a columellar tooth and weaker periumbilical keel. The shells' proportions also differ: in *E. myanmarica* n. sp., the last 3 whorls make up more than four-fifths of the shell height, whereas in *E. spelomphalos*, the whorls make up only approximately two-thirds of the shell height. The first two whorls are not irregularly narrower than the third whorl in *E. spelomphalos*. In *E. hesoana*, the constriction is much stronger than that of *E. myanmarica* n. sp., resulting in the enormous umbilicus. In *E. myanmarica* n. sp., the umbilicus is wide but does not form a large cavity on the wall of the last whorl as in *E. hesoana.*

Family Cyclophoridae Gray, 1847

Genus *Archaeocyclotus* Asato and Hirano in Hirano et al., 2019

Type species.—*Archaeocyclotus plicatula* Asato and Hirano in Hirano et al., 2019.

Archaeocyclotus cf. *A. plicatula* Asato and Hirano in Hirano et al., 2019
Figure 2

Occurrence.—Hkamti, Sagaing Region, northern Myanmar; Albian (mid-Cretaceous), ca. 110 Ma.

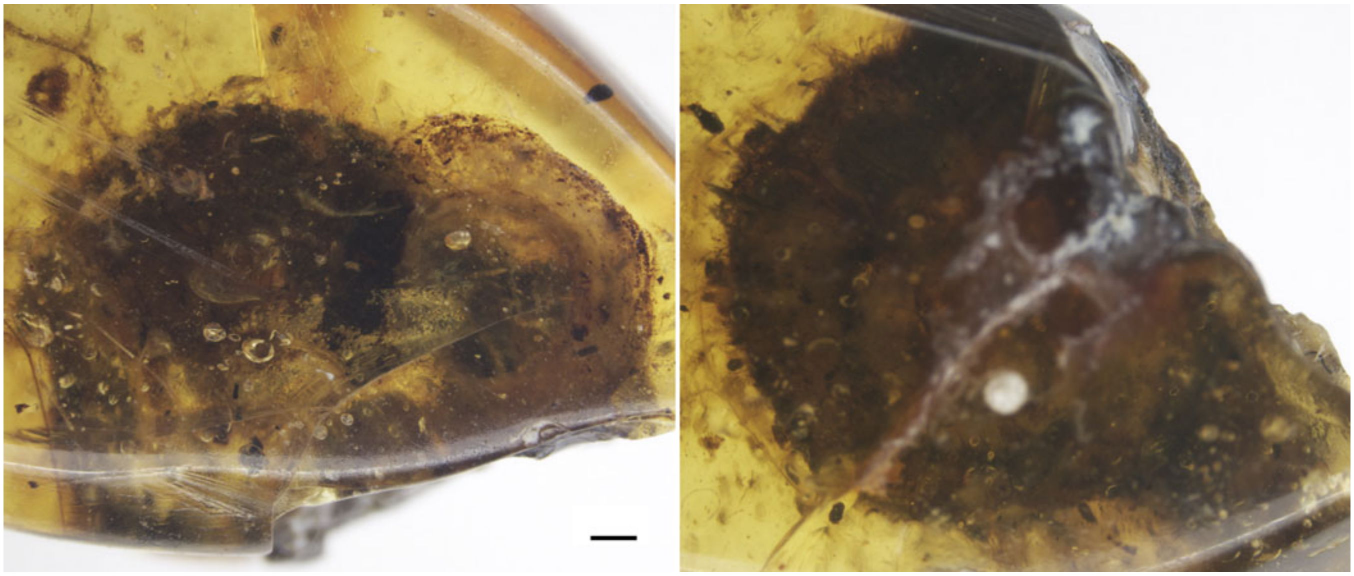

Figure 2. Shell of *Archaeocyclotus* cf. *A. plicatula* in Hkamti amber, SIZK GT 7179, views from opposite sides of the amber stone. Scale bar = 0.5 mm.

Description.—Shell discoidal, keeled, comprising 5.5 whorls. Suture deep. Protoconch smooth, comprising 2.5 whorls. Sculpture of sparse large axial ribs. Small periostracal hairs present. Aperture large, oval, with broadly reflected margins. Umbilicus open, wide, approximately one-third of shell diameter.

Materials.—SIZK GT 7179, single shell in a small piece of amber, 12 mm x 6 mm x 5 mm. No recognizable syninclusions.

Size.—Shell height ∼2.5–3 mm, diameter 6.8 mm.

Remarks.—This shell strongly resembles that of *Archaeocyclotus plicatula* (see Hirano et al., 2019), but it is larger and has strongly reflected apertural margins. This could indicate that the holotype of *A. plicatula* is a juvenile or subadult—it measures 5.2 mm at 5 whorls, whereas this shell is 6.8 mm at 5.5 whorls. Considering that the current specimen is presumably of a significantly different age than *A. plicatula*, it would be speculative to conclude that they are conspecific without having more specimens from both deposits.

The protoconch of this shell is not visible in photographs because of the amber's structure, but is fully observable by eye with distortion. The piece of amber is too small and the shell is too close to the surface for further polishing.

Cyclophoridae gen. indet. sp. indet. 1
Figure 3

Occurrence.—Hkamti, Sagaing Region, northern Myanmar; Albian (mid-Cretaceous), ca. 110 Ma.

Description.—Shell low-conical, slightly keeled, very thin-walled, comprising at least 3 whorls (protoconch unobservable). Last whorl very large, more than half of shell. Surface almost smooth, very weakly striated. Aperture very large, oval, with simple edges. Umbilicus closed or very narrow.

Materials.—SIZK GT 7180, single shell in a small piece of amber, 11 mm x 9 mm x 3.5 mm. No recognizable syninclusions.

Size.—Shell height ∼2.5 mm, diameter 5.9 mm.

Remarks.—This shell is likely from a juvenile and perhaps deformed.

Cyclophoridae gen. indet. sp. indet. 2
Figure 4

Occurrence.—Hkamti, Sagaing Region, northern Myanmar; Albian (mid-Cretaceous), ca. 110 Ma.

Description.—Shell low-conical, comprising at least two whorls (protoconch unobservable). Suture deep. Surface almost smooth, very weakly striated. Aperture large, oval, with simple edges. Umbilicus open, wide, approximately one-quarter of shell diameter.

Materials.—SIZK GT 7181, single shell in a small piece of amber, 21 mm x 17 mm x 7 mm. No recognizable syninclusions.

Size.—Shell height ∼0.5 mm, diameter 1.7 mm.

Remarks.—This shell is from a juvenile and slightly resembles that of *Perissocyclos kyrtostoma* Bullis et al., 2020 from Kachin amber, which is much larger. Perhaps this is a juvenile of *Perissocyclos* sp.

Cyclophoridae gen. indet. sp. indet. 3
Figure 5

Occurrence.—Hkamti, Sagaing Region, northern Myanmar; Albian (mid-Cretaceous), ca. 110 Ma.

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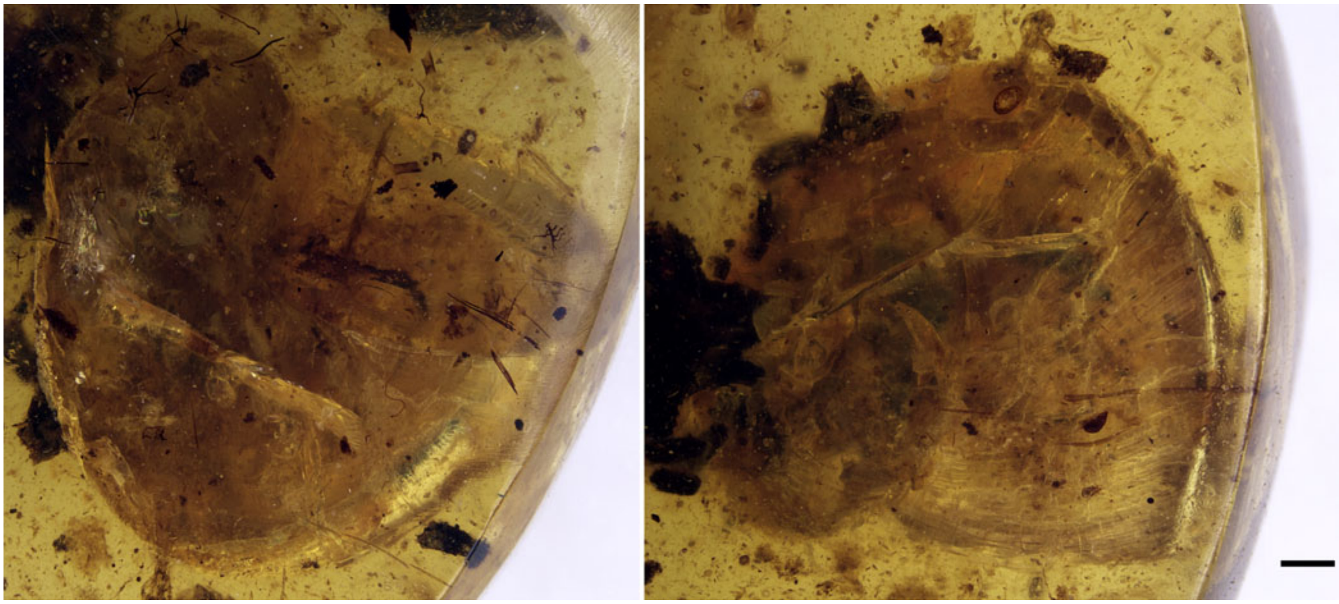

Figure 3. Shell of Cyclophoridae gen. indet. sp. indet. 1 in Hkamti amber, SIZK GT 7180, views from opposite sides of the amber stone. Scale bar = 0.5 mm.

Description.—Shell discoidal, irregularly coiled, comprising two whorls. Surface smooth. Aperture large, oval, with simple edges. Umbilicus open, wide, more than one-third of shell diameter.

Materials.—SIZK GT 7182, single shell in a small piece of amber, 18 mm x 8 mm x 4 mm. Syninclusions: two specimens of Scydmaeninae (Coleoptera, Staphylinidae).

Size.—Shell height ~1 mm, diameter 3.1 mm.

Remarks.—This shell is probably from a juvenile, notable by its specific irregular coiling.

Ichnofamily Gastrochaenolitidae Wisshak, Knaust and Bertling, 2019

Ichnogenus *Teredolites* Leymerie, 1842

Type ichnospecies.—*Teredolites clavatus* Leymerie, 1842.

Teredolites clavatus Leymerie, 1842
Figure 6

Holoype.—Unknown.

Occurrence.—Hkamti, Sagaing Region, northern Myanmar; Albian (mid-Cretaceous), 110 Ma.

Description.—Long, club-shaped structures with narrow distal end connected to surface of amber, more or less perpendicular to surface at point of connection. Diameter of structures gradually increases from narrow distal part to widest proximal part, continuing to rounded proximal end. Structures circular in cross section over whole length. Axis of structures more or less straight. Full length of structures approximately two or three times greater than maximum diameter.

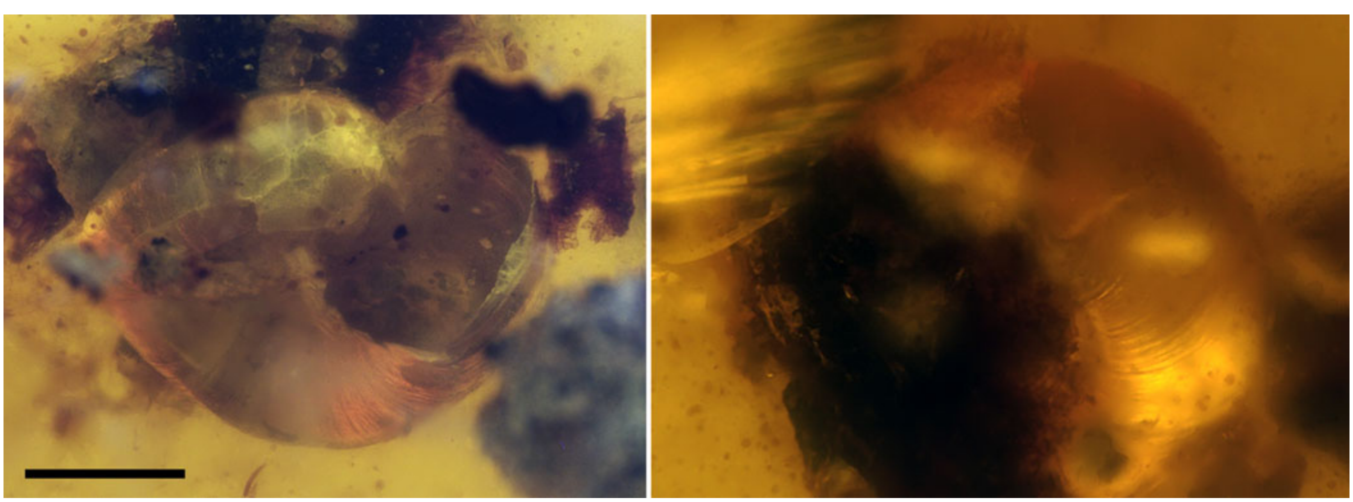

Figure 4. Shell of Cyclophoridae gen. indet. sp. indet. 2 in Hkamti amber, SIZK GT 7181, views from opposite sides of the amber stone. Scale bar = 0.5 mm.

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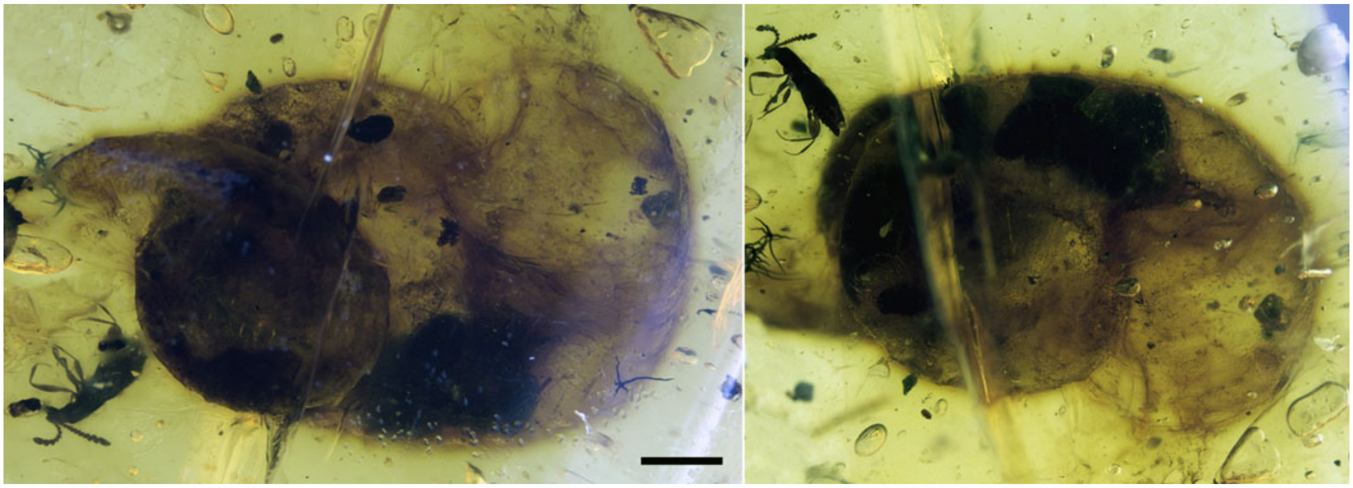

Figure 5. Shell of Cyclophoridae gen. indet. sp. indet. 3 and beetle (Scydmaeninae) in Hkamti amber, SIZK GT 7182, views from opposite sides of the amber stone. Scale bar = 0.5 mm.

Materials.—Eight pieces of amber: (1) SIZK GT 7183, 3 borings in a stone measuring 16 x 8 x 3 mm (Fig. 6); (2) SIZK GT 7184, 5 borings in a stone measuring 23 x 17 x 7 mm; (3) SIZK GT 7185, 15 borings in a stone measuring 22 x 13 x 4 mm; (4) SIZK GT 7186, 16 borings in a stone measuring 19 x 15 x 9 mm; (5) SIZK GT 7187, 13 borings in a stone measuring 15 x 15 x 7 mm; (6) SIZK GT 7188, 6 borings in a stone measuring 17 x 14 x 4 mm; (7) SIZK GT 7189, 2 borings in a stone measuring 16 x 8 x 5 mm; (8) SIZK GT 7190, 4 borings in a stone measuring 16 x 12 x 6 mm. Syninclusions: various Diptera.

Size.—Length 1.9–6.5 mm, diameter at widest place of proximal part 0.7–2.9 mm, minimum diameter at narrowest place of distal part 0.2 mm.

Remarks.—Most of the structures are incomplete because significant parts have been chafed away with part of the

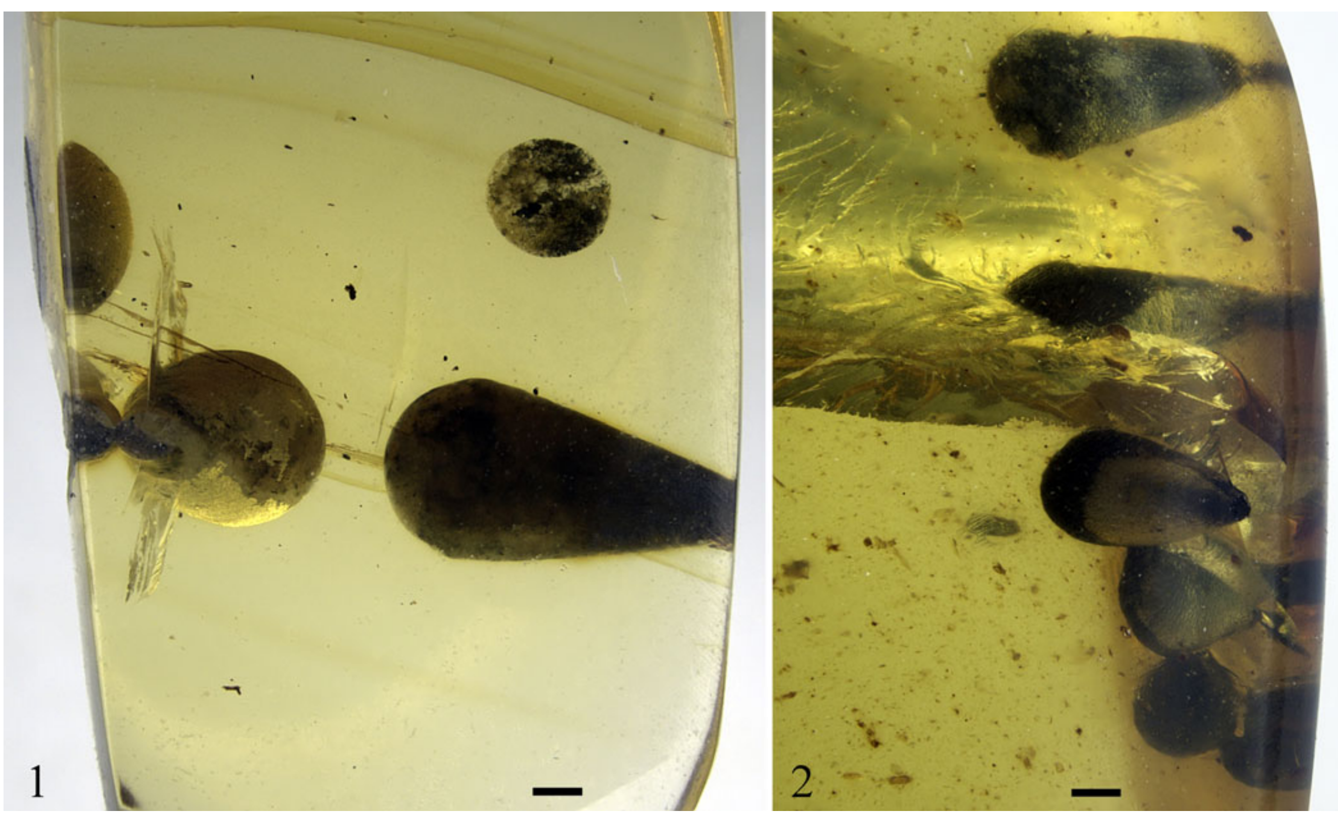

Figure 6. Ichnospecies *Teredolites clavatus*, the borings of pholadid bivalves, in Hkamti amber: (**1**) SIZK GT 7183; (**2**) SIZK GT 7184. Scale bars = 0.5 mm.

amber, naturally or during primary treatment of the amber after mining. Often, only the proximal part of the structure remains, or even only a proximal tip.

Discussion

All five snails found in Hkamti amber are representatives of the superfamily Cyclophoroidea, which is also the case for nearly all known land snails from Kachin amber, except one rather semi-aquatic species (Balashov, 2020). Cyclophoroidea is the second-most speciose lineage of extant land gastropods after Eupulmonata (Kobelt, 1902; Wenz, 1938–1939; Haas, 1961; Boeters et al., 1989; Emberton, 2002; Vermeulen et al., 2007, 2019; Maassen, 2008; Yamazaki et al., 2013, 2015a, b; Páll-Gergely et al., 2014, 2015, 2017a, b, 2019, 2020; Balashov and Griffiths, 2015; Neubert and Bouchet, 2015; Budha et al., 2017; Minton et al., 2017; Nurinsiyah and Hausdorf, 2017; Páll-Gergely and Hunyadi, 2018, and others). In the fossil record of the Palaeozoic and Mesozoic, excluding Kachin amber, a relatively small portion of land snails have been considered to belong to Cyclophoroidea (Bandel, 1993; Pan and Zhu, 2007; Raheem et al., 2017) and most have been interpreted as representatives of the superorder Eupulmonata (Huckriede, 1967; Solem, 1978; Solem and Yochelson, 1979; Roth et al., 1996; Roth, 2000; Pan and Zhu, 2007; Stworzewicz et al., 2009; Isaji, 2010; Nordsieck, 2014; Cameron, 2016; Cabrera and Martínez, 2017, Jochum et al., 2019, and others). The taxonomic placement of many such snails might be questionable, especially those placed in the order Stylommatophora (Bandel, 1993; Cameron, 2016; Balashov, 2020), as also indicated above by the erroneous description of a cyclophoroid snail in the stylommatophoran genus *Truncatellina* (Yu, 2020). However, there is significant evidence that snails of the order Ellobiida, or their extinct relatives, existed much earlier than the formation of Kachin and Hkamti ambers (Huckriede, 1967; Stworzewicz et al., 2009; Isaji, 2010; Dayrat et al., 2011; Cameron, 2016; Jochum et al., 2019). Therefore, the predominance of Cyclophoroidea and the absence of Eupulmonata indicate the close similarity of the malacofauna of Hkamti and Kachin amber.

Two identified snails from Hkamti amber, *Euthema myanmarica* n. sp. and *Archaeocyclotus* cf. *A. plicatula*, are representatives of genera that previously were only recorded from Kachin amber. In the latter case, the snail could be conspecific with true *A. plicatula* from Kachin amber. *Euthema myanmarica* n. sp. appears to be closely related to *E. hesoana*. Therefore, *E. myanmarica* n. sp. is probably more closely related to some species from Kachin amber than some of these species are related to each other. The representatives of *Archaeocyclotus* and *Euthema* appear to be among the most common gastropods in Kachin amber (Balashov, 2020). The fact that both genera are represented among the first five snails reported from Hkamti amber suggests that *Archaeocyclotus* and *Euthema* are probably not rare in this deposit either. These findings indicate that the Hkamti and Kachin amber deposits have a similar taxonomic composition of mollusks, and representatives of the same two genera appear to be among the most common snails in each deposit.

The ichnospecies *Teredolites clavatus*, reported above from Hkamti amber, is also present in various other ambers of different ages, first appearing in Lower Cretaceous Lebanese amber (Smith and Ross, 2018; Mayoral et al., 2020). *Teredolites clavatus* is considered to result from bivalve mollusks of the genus *Martesia* Sowerby, 1824 (Pholadidae) drilling into the amber or dry resin on the sea floor to make a crypt (Smith and Ross, 2018; Mayoral et al., 2020). Thus, formation of the borings could have occurred significantly later than formation of the resin, in some cases perhaps millions of years. Because some pholadid bivalves have been found in Kachin amber, both inside and outside of the borings, the borings have been considered of the same age as the amber (Smith and Ross, 2018). This consideration supports the U-Pb dating of Kachin amber to be ca. 99 Ma because it means that the resin was often washed into the sea shortly after formation. Because rocks that bear Kachin amber were formed on the sea floor and amber is a product of trees, it is disputable whether amber could be redeposited in these rocks long after its formation. The presence of pholadids suggests that the occurrence of fresh resin on the sea floor was probably common, and no additional geological processes required for the presence of the amber there (Smith and Ross, 2018).

Specimens of *Teredolites clavatus* from Hkamti amber are similar in size to those recorded from Kachin amber. All values strongly overlap, with only some slightly exceeding the known size values from Kachin amber (Smith and Ross, 2018; Mayoral et al., 2020). Specimens of *Teredolites clavatus* from Lebanese (early Barremian, Lower Cretaceous) and Mexican (Miocene–Oligocene) ambers are much longer, and their values do not overlap those presented here. The measurements here partially overlap those of specimens from Spanish and French ambers (both Albian, mid-Cretaceous; Mayoral et al., 2020).

It appears that *Teredolites clavatus* is very common in Hkamti amber, which is also the case for Kachin amber (Smith and Ross, 2018), suggesting that amber from both deposits has spent significant time on the sea floor. Most *Teredolites clavatus* from Hkamti amber are very incomplete and represented only by the proximal part of the structure that is naturally placed deeper in amber. This suggests that pieces of amber with these ichnofossils have spent a lot of time in the sea being polished by the other stones in the water. However, the incompleteness could also result from the primary treatment of the amber after mining. The similar size and the large numbers of *Teredolites clavatus* in Hkamti and Kachin ambers indicate closeness in age, but this is not significant enough for conclusions regarding precise dating.

Consequently, similarity of the malacofauna from Hkamti and Kachin ambers, as well as the presence of numerous, similar *Teredolites clavatus* in each, indicates that these ambers were formed in very similar paleoenvironments. Perhaps coastal forests with very similar conditions and very similar malacofauna existed for over ten million years, throughout the Albian to the early Cenomanian, or even longer. These numerous aforementioned similarities between the two ambers, especially the taxonomic composition of cyclophoroids at the generic level, raise some doubts regarding the current dating of the Hkamti and Kachin ambers. The U-Pb dating is based on zircons from the stone matrix next to the amber, not from the amber itself (Shi et al., 2012; Xing and Qiu, 2020) and, therefore, it is possible that the amber was redeposited in these rocks long after

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formation. The fact that Kachin amber could be directly deposited on the sea floor does not prove that it could not be redeposited into another marine deposit later. The U-Pb dating only provides solid evidence of the minimal age of the amber deposit. Therefore, assuming that Hkamti and Kachin ambers are of similar age and that the U-Pb dating is only the minimal age, Kachin amber could be 110 Ma or even older.

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