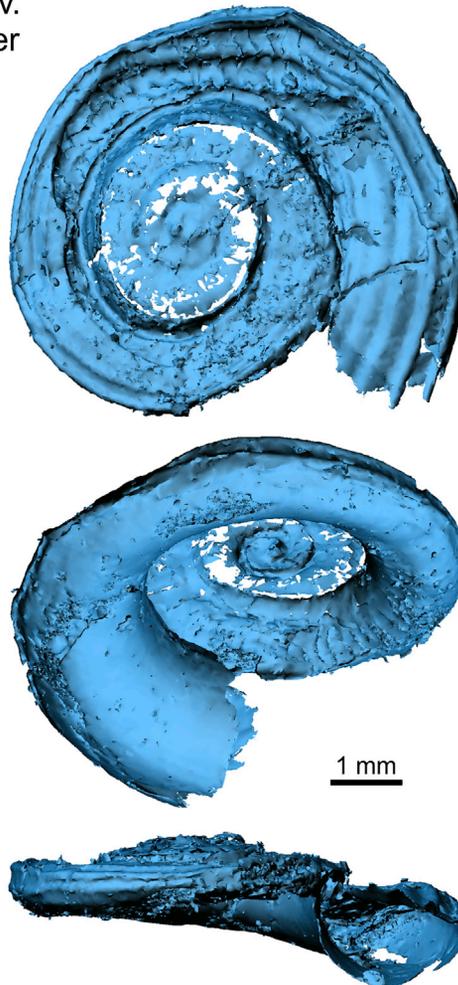
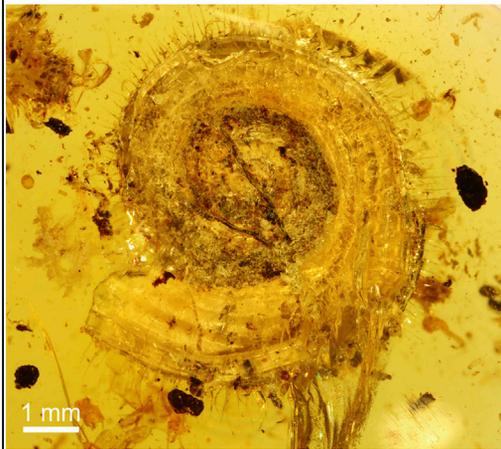


## Article

## Land Snail with Periostracal Hairs Preserved in Burmese Amber

*Hirsuticyclus electrum* gen. et sp. nov.  
from mid-Cretaceous Burmese amber



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**HIGHLIGHTS**

We document the oldest fossil record of a hairy land snail

The hairs are interpreted as adaptation to a tropical forest environment

Hairs are suggested to increase adhesion to plants during foraging

The adaptation was potentially caused by the coeval radiation of flowering plants

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## Article

## Land Snail with Periostracal Hairs Preserved in Burmese Amber

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## SUMMARY

Excellent preserved fossils often provide important insights into evolutionary histories and adaptations to environmental change in Earth's biogeologic record. Mid-Cretaceous Burmese amber, for example, is a proven reservoir for spectacular findings. Here we document the first record of a fossil land snail with periostracal hairs preserved in amber. We interpret the development of hairs as an adaptation to the tropical forest environment, serving as a mechanism to increase adhesion of the snail to plants during foraging while collecting and transporting seeds in the process. The present record coincides with a major global radiation of angiosperms, a main food resource for terrestrial snails. As such, the expansion of flowering plants likely triggered this evolutionary adaptation and, thus, the diversification of land snails in the Cretaceous.

## INTRODUCTION

Gastropods have conquered a wide range of global habitats and have evolved an extraordinary variety of life styles reflected in a broad spectrum of shell shapes and ornamentation types (Pyrön and Brown, 2015). Especially among several species of land snails, shells occasionally bear stubbly projections, casually referred to as "hairs" that sometimes produce a bristly texture of the periostracum, the protective outer organic layer of mollusk shells. Little is known about the selective advantage of having hairs, and hypotheses range from prevention or mitigation of predation to ease of movement by storing water for when it is needed and increased efficacy of surface adhesion (Pfenninger et al., 2005; Dourson, 2013). Although the evolutionary origin of hairs in gastropods is debatable (Pfenninger et al., 2005; Allgaier, 2011), support of any hypothesis is precluded by lack of fossil evidence due to rare preservation of the periostracum.

Here we report the first record of an exceptionally preserved land snail densely covered with periostracal hairs (Figure 1). The specimen derives from mid-Cretaceous amber deposits in Myanmar (early Cenomanian, c. 99 Ma; Shi et al., 2012). Burmese amber, or "burmite," is a unique lagerstätte providing a rich archive for understanding Mesozoic biota and paleoenvironments (Grimaldi et al., 2002; Ross et al., 2010; Wang et al., 2016b; Ross, 2019; Sokol, 2019). The deposits have yielded over a thousand species of fossils belonging to various animal and plant groups, including spectacular finds of well-preserved dinosaur remains (Xing et al., 2016a), birds (Xing et al., 2016b), reptiles (Xing et al., 2018a), insects (Cockerell, 1916; Borkent and Grimaldi, 2004; Poinar and Danforth, 2006; Kania et al., 2015), and even marine animals such as a marine ostracod (Xing et al., 2018b) and ammonites (Yu et al., 2019).

The amber containing the new fossil snail comes from the Angbamo site in northern Myanmar. High-resolution stacking microscopy and micro-computed tomography ( $\mu$ CT) images were produced to visualize periostracal shell structures, as well as to enable systematic classification of the snail.

## RESULTS AND DISCUSSION

## Systematic Paleontology

The higher systematic classification follows Bouchet et al. (2017).

Class Gastropoda Cuvier, 1795

Subclass Caenogastropoda Cox, 1960

Order Architaenioglossa Haller, 1890

Superfamily Cyclophoroidea Gray, 1847

Family Cyclophoridae Gray, 1847

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**Figure 1. Amber Slice from the Angbamo Site in Northern Myanmar Containing the Hairy Snail**

The specimen measures  $2.2 \times 1.6 \times 0.6$  cm and weighs 1.19 g. Scale bar, 5 mm.

†*Hirsuticyclus* gen. nov.

#### LSID

urn:lsid:zoobank.org:act:1D948C29-0D74-4832-9426-6C6848497E9D.

#### Type Species

†*Hirsuticyclus electrum* sp. nov., only known species.

#### Etymology

From Latin “hirsutus” (“hairy” or “bristly”); the ending *-cyclus* refers to the similarity to extant Cyclophoridae species.

#### Diagnosis

Broad, low turbinata, nearly discoid shell with wide umbilicus; aperture broadly elliptical; shell surface covered with densely spaced, thin periostracal hairs that emerge at growth line margins; hairs are long at shell periphery, but short and more numerous around the umbilical zone; marked spiral lirae occur on the apical side and upper part of the whorl flank, producing a cancellate pattern where they intersect growth lines.

†*Hirsuticyclus electrum* sp. nov.

#### LSID

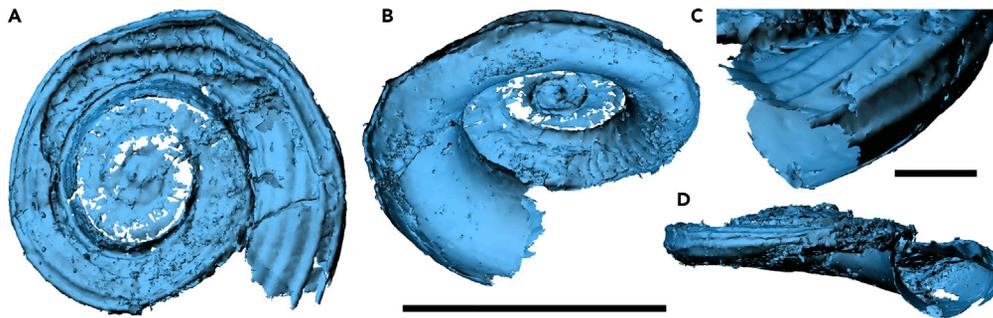
urn:lsid:zoobank.org:act:4112AE8E-9176-443E-B164-6EDB7D4B939B

#### Etymology

Latin for “amber” (from Greek ἤλεκτρον, *élektron*).

#### Diagnosis

As for the genus.



**Figure 2.**  $\mu$ CT Reconstructions of †*Hirsuticyclus electrum* gen. et sp. nov.

(A) Top view with spiral lirae.

(B) Bottom view showing the wide umbilicus and distinct growth lines on the penultimate whorl.

(C) Close-up of the terminal part of the body whorl with distinct spiral lirae on whorl top and flank.

(D) Frontal view.

Scale bars, 5 mm (A, B, and D); 1 mm (C). See also [Figure S1](#) for an interactive 3D-plot.

#### Referred Material

Holotype only: Dexu Institute of Palaeontology, Guangdong, China; DIP-V-18111.

#### Locality

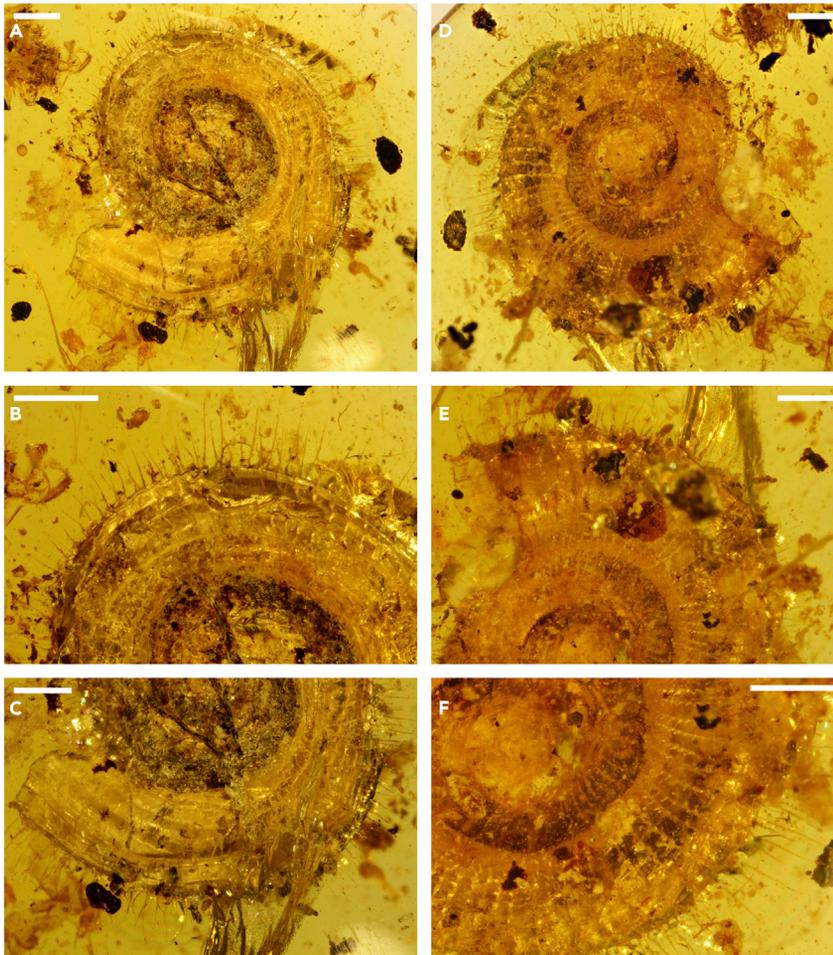
Early Late Cretaceous, early Cenomanian ( $98.8 \pm 0.6$  Ma); Angbamo site, Hukawng Valley, Tanaing Township, Myitkyina District, Kachin State, Myanmar.

#### Description

The shell seems to be slightly compressed. Also, the apical region is strongly corroded, which is why information on protoconch and early teleoconch whorls, as well as the exact number of whorls, is unknown. The shell is low turbinatae (Figure 2D), consists of c. 3.5–4 whorls, has a maximum diameter of 6.6 mm and a height of ca. 2.2 mm. Shell color is brownish and appears to be slightly darker on the umbilical side. The aperture seems to be originally broadly elliptical or round, but the apical region is depressed. Whorls are wider than high in cross-section. They bear five raised, broadly blunt spiral lirae on the apical side, whereas the outermost coincides with a distinct angle to the whorl flank; another strong lira appears on the flank below the outermost apical lira, and tendency of a second, lower one is visible on the last part of the body whorl (Figures 2A, 2C, 3A, and 3C). Lirae are separated by shallow concavities that are about two to three times as wide as a lira. The umbilical side is smooth, except for growth lines (Figure 2B). Whorls hardly overlap resulting in a very wide umbilicus. Growth lines are very distinct, orthocone, and more or less regularly and densely spaced; about seventy occur on the body whorl (Figures 3D–3F). Periostracal hairs emerge directly at growth lines; on the umbilical side, hairs are short (up to c. 150  $\mu$ m), thin (c. 25  $\mu$ m), numerous, and densely and regularly spaced (Figures 3D–3F); on the apical side and whorl flank, they are distinctly longer (up to 1.1 mm) and more widely spaced but equally thin (Figures 3A–3F). Despite being engulfed by resin, the long, thin hairs maintained an upright position, suggesting they are very sturdy and not brittle.

#### Remarks

The formation of the periostracal hairs along growth lines, trochoid shell shape, and spiral striation are typical for several species of tropical forest land snails in the family Cyclophoridae (Caenogastropoda). The slow, regular increase in whorl diameter and the wide umbilicus, in combination with the dense pelt-like layer of hairs, is, however, unknown in that family. Some species of the stylommatophoran family Plectopylidae superficially resemble †*Hirsuticyclus electrum*, but the perfectly rounded whorls and thin, long hairs are not found among plectopylids (Páll-Gergely and Asami, 2014). Also, the typically descending aperture known in plectopylids (Páll-Gergely and Asami, 2014) is not present. Another argument in favor of Cyclophoridae derives from the fossil record: several instances of cyclophoroid taxa have been described from Burmese amber deposits, whereas the oldest fossil plectopylid dates back to the Eocene (Páll-Gergely and Asami, 2014).



**Figure 3. Photos of †*Hirsuticyclus electrum* gen. et sp. nov.**

(A–C) Top (apical) view of the snail, showing long periostracal hairs at shell periphery and cross-section pattern between growth lines and spiral lirae; note that early whorls are corroded.

(D–F) Bottom (umbilical) view showing both long peripheral hairs and short hairs on the shell base.

Scale bars, 1 mm.

The new species is one of several species of Cyclophoroidea documented in Burmese amber (Yu et al., 2018; Neubauer et al., 2019; Xing et al., 2019). However, only a single and so far unnamed species of the family Cyclophoridae has so far been described from the deposits. Its hairless shell is similarly small (4.88 mm wide, 2.08 mm high) and has a broad turbinata shape and a circular aperture with reflexed peristome. No other described cyclophoroid species, neither from the mid-Cretaceous of Myanmar nor any other fossil deposit, resembles †*Hirsuticyclus electrum* gen. et sp. nov. The only other known worldwide Mesozoic Cyclophoroidea derive from the Late Jurassic to Early Cretaceous deposits of Germany and Switzerland (genera *Diplommoptychia* Maillard, 1884, *Loriolina* Huckriede, 1967, and *Maillardinus* Bandel, 1991) and the Late Cretaceous of Austria (genera *Cyclomastoma* Hrubesch, 1965, *Entypogyra* Hrubesch, 1965, *Pseudnicida* Hrubesch, 1965, and *Proelektrea* Hrubesch, 1965) (Bandel, 1991; Neubauer et al., 2019). All of these taxa differ clearly from †*Hirsuticyclus electrum* in their high-spired shells. *Pseudarinia* Yen, 1952 from the Cretaceous of Wyoming (United States), originally considered to be a cyclophorid, has been reclassified within Subulinidae (Raheem et al., 2018).

Of the early Miocene Cyclophoridae described by Raheem et al. (2018) from northern Vietnam, *Alycaeus sonlaensis* superficially resembles the present species in terms of the low turbinata shell shape and the dense axial sculpture. The comparably narrow umbilicus and the smaller size (c. 4 mm wide, c. 2 mm high), however, distinguish the species from †*Hirsuticyclus electrum*.

### Implications for Land Snail Evolution

The present finding adds a striking new perspective to the evolution of periostracal hairiness in land snails. Hairiness is frequent across several unrelated families of land snails. It is known in stylommatophoran families, such as Hygromiidae, Helicidae, Plectopylidae, Camaenidae, and Polygyridae, as well as in the caenogastropod Cyclophoridae. Periostracal hairiness varies within families and even genera, suggesting that this feature has evolved several times independently (Pfenninger et al., 2005). Moreover, it has been suggested that hairiness is an ancestral state that was lost multiple times in evolutionary history, probably correlating with a shift from humid to arid conditions (Pfenninger et al., 2005). Fossil evidence supporting this claim has been scarce until now. Several fossil species of the families Eloniidae, Helicidae, and Hygromiidae expose the typical pattern of alternating pits on the surface that suggest the early presence of hairs (Kadolsky et al., 2016; Nordsieck, 2017). The oldest terrestrial representatives with confirmed hair pits date back to the Oligocene or perhaps the late Eocene (Kadolsky et al., 2016; Nordsieck, 2017). Hairs have also been reported for freshwater snails, where they occur in juvenile Viviparidae (Allgaier, 2011), as well as for marine taxa (Iyengar et al., 2008). Fossil evidence for those groups pre-dates the Cretaceous Burmese amber fossil, for example, species of Coelostylinidae from the Early Triassic of Pakistan (Kaim et al., 2013) and viviparids from the Early Cretaceous of France (Bandel, 1991). So far, however, †*Hirsuticyclus electrum* represents the only known record of preserved hair in a fossil gastropod.

Little is known about the ontogenetic formation of periostracal hairs, but the available evidence shows considerable variation across gastropod families. Thus, the casual term “hairs” should be used only in a broader sense. Hair formation in land helicoids occurs in the periostracal groove independently of the periostracum itself (Allgaier, 2011). After formation, hairs are attached to the shell margin, extracted from the mantle tissue, swiveled to the upper side of the periostracum, and fixed upright on the shell upon further growth of the periostracum (Allgaier, 2011). In contrast, hairs in freshwater Viviparidae, which occur on juvenile shell of some species, are secreted directly by the mantle processes at the edge of and toward the outside of the shell (Allgaier, 2011). The ontogenetic formation of hairs in Cyclophoridae (which, same as Viviparidae, belong to the Caenogastropoda) is not known, but the structures shown by †*Hirsuticyclus electrum*, as well as several extant species, can be best explained by the type of hair formation shown for viviparids. For example, *Cyathopoma pembense* from Zanzibar, Tanzania, bears radial lamellae along growth lines that are extended along the shell periphery into long hairs gathered into points or fringes (Rowson et al., 2010). Similarly, the thin hairs in *Cytora cytora* from New Zealand are aligned along growth lines (Marshall and Barker, 2007), and the same is found in the fossil †*Hirsuticyclus electrum*. Contrary to hairs in stylommatophoran land snails, the structures in cyclophorids appear as direct secretions at the mantle edge.

Hairs form an exception in modern Cyclophoridae. Thus, the occurrence of a hirsute species in the mid-Cretaceous would support the hypothesis that hairs form an ancestral state (Pfenninger et al., 2005). However, the other co-occurring species of Cyclophoridae preserved in Burmese amber lacks hairs (Xing et al., 2019). Together, these fossils represent the oldest known members of the family, which is why the relevance of hairs as a potentially plesiomorphic character remains unresolved. The discovery of †*Hirsuticyclus electrum* provides significant evidence that the occurrence of hairs in Cyclophoridae has varied through evolutionary history.

Several theories have been proposed to explain the potential selective advantage of possessing a hairy periostracum, a biologically costly protein structure (Pfenninger et al., 2005). Since hairy snails are largely associated with moist environments, the presence of hairs in helicoids has been interpreted to increase adhesion onto plants while grazing (Pfenninger et al., 2005). Stronger adhesion would decrease the chance of falling off the leaf or stem, serving as a strategy to avoid the energy-intensive and time-consuming climb back up. Alternatively, hairs may hold and distribute water more uniformly across the shell, potentially facilitating movement over drier surfaces (Dourson, 2013). A hairy surface might also assist temperature regulation (Dourson, 2013). The hairs of some polygyrid and helicodiscid land snails from North America are known to collect forest debris, thought to help conceal the snail from possible predators like birds and salamanders (Dourson, 2013). A dense pelt of hairs might also prevent the snail from direct predation from insects, such as shell-boring beetle larvae (Baalbergen et al., 2014). In the marine capulid *Trichotropis*, the hairy periostracum is interpreted as a defense mechanism against predation from crabs and sea stars and as deterrent to the settlement of epibionts (Iyengar et al., 2008).

The fauna and flora buried in Burmese amber are indicative of a humid, tropical forest (Poinar et al., 2007; Yu et al., 2019; Xing et al., 2019). Although the amber is derived from conifer trees (Araucariaceae), which probably constituted a large part of the plant biodiversity back then, fossil evidence also includes early flowering plants (Poinar et al., 2007). Angiosperms date back to the Early Cretaceous, perhaps even to the Jurassic (Soltis et al., 2018), and they witnessed an explosive radiation in the mid-Cretaceous (Peralta-Medina and Falcon-Lang, 2012). This event coincides with the ample deposition of resin comprising the Burmese amber and the diversification of land snails in the mid-Cretaceous around 100 Ma (Yu et al., 2018; Neubauer et al., 2019; Xing et al., 2019). Land snails graze primarily on plant material (Speiser, 2001), and they likely preferred the soft-leaved angiosperms over the tough conifer needles.

The development of a hairy periostracum might be an adaptation to the increasingly angiosperm-dominated world of the mid-Cretaceous. The periostracal hairs facilitate attachment to the leaves of the angiosperms the snails feed on, minimizing the time- and energy-consuming process of re-ascending the plants after falling off. In the event of dropping to the forest floor, hairs might have limited potential damage to the shell by softening the impact. The bristly hairs perhaps additionally transported seeds much like a bee unintentionally transports pollen via body hairs from one blossom to another. During the mid-Cretaceous, average seed size was comparatively small (below 1 mm<sup>3</sup>; Eriksson et al., 2000), which might have facilitated dispersal by the small †*Hirsuticyclus electrum*. Alternatively, the hairs could have deterred predation as well as increased the snail's unpalatability while collecting soil debris as camouflage (Barker, 2001; Wang et al., 2016a). The exceptionally rich amber archive contains a variety of predators known today to prey upon land snails, such as beetles, ants, spiders, millipedes, lizards, and birds (Grimaldi et al., 2002; Ross et al., 2010; Wang et al., 2016b). In a predator-lurking, hostile environment, hairiness could have evolved as a survival strategy providing prickly armor for deterring predatory mid-Cretaceous birds by enabling the discoid snail to mimic the appearance of a curled up, unpalatable caterpillar. Many other snail predators access the shell via the aperture, and many extant land snails have developed narrow apertures or dentition to avoid predation (Barker, 2001). The aperture is only incompletely preserved in the Cretaceous snail, and we lack information about the shape and characteristics of the terminal part of the last whorl, as well as the arrangement of hairs around the peristome. Albeit missing, the snail likely had an operculum as member of the operculate land snail family Cyclophoridae, which might have served as an additional barrier against predation. Hairs may have additionally kept shell-boring predators at bay. They may have also shielded the shell from harmful phenolic compounds and tannins in the forest litter and from fungal pathogens in the soil. As has been proposed for extant hairy snail species (Dourson, 2013), a thick hairy periostracal layer could well have served as an insulating, thermal regulatory strategy in the steamy, tropical forested paleoenvironment.

### Limitations of the Study

The discussion offers a number of potential models to explain the advantage of having a hairy shell in a tropical mid-Cretaceous environment. However, despite the pros and cons discussed, the limited information available for both the shell (given its incomplete preservation) and the paleo-environment renders any conclusion premature. We thus advise to consider our interpretations as suggestions.

### METHODS

All methods can be found in the accompanying [Transparent Methods supplemental file](#).

### SUPPLEMENTAL INFORMATION

Supplemental Information can be found online at <https://doi.org/10.1016/j.isci.2019.09.034>.

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## AUTHOR CONTRIBUTIONS

T.A.N. and L.X.: concept design and writing the first draft; L.X.: material acquisition, photography, and CT scanning; T.A.N. and A.J.: morphological analysis, taxonomy, and evolutionary and ecological interpretation.

## DECLARATION OF INTERESTS

The authors declare no conflict of interest.

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**Supplemental Information**

**Land Snail with Periostracal**

**Hairs Preserved in Burmese Amber**

**Thomas A. Neubauer, Lida Xing, and Adrienne Jochum**

## **TRANSPARENT METHODS**

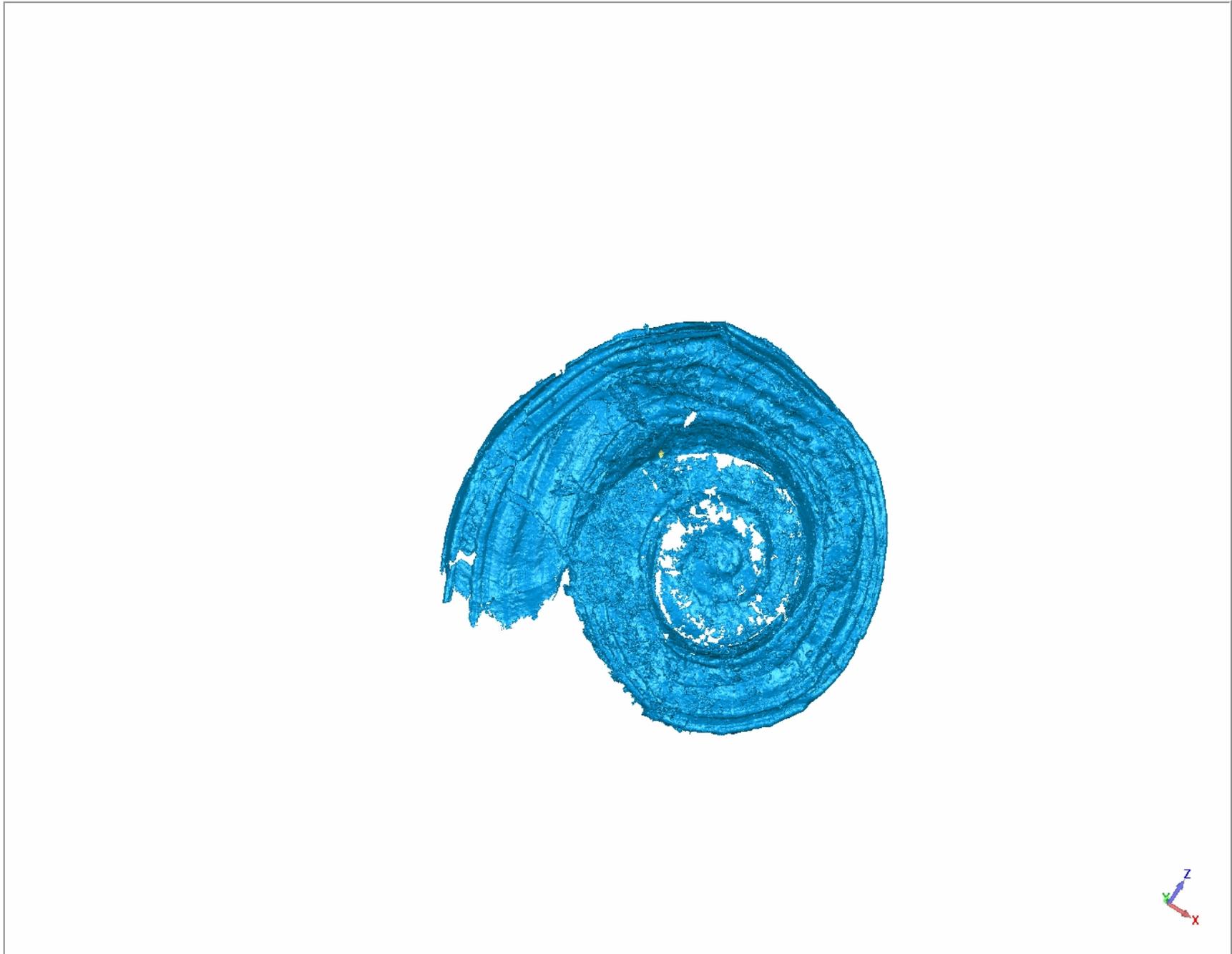
The Burmese amber specimen is stored at Dexu Institute of Palaeontology, Guangdong, China (inventory number DIP-V-18111) and measures 2.2 x 1.6 x 0.6 cm and weighs 1.19 g (Figure 1). The age of the material was estimated based on U-Pb dating of zircons from the volcanoclastic matrix that contains the amber at 99 Ma ( $98.8 \pm 0.6$  Ma), correlating into the earliest Cenomanian (Shi et al., 2012).

The specimen was investigated using a Leica MZ 12.5 dissecting microscope. Photographs were obtained with a Canon digital camera (5DS R III, MP-E 65mm f/2.8 1-5X) fitted to a macro rail (Cognisys) and processed in Helicon Focus 5.1. The scanning was performed with a Nikon Metrology XTH 225/320 LC dual source industrial micro-computed tomographic scanner, housed at the China University of Geosciences, Beijing, China. The specimen was scanned with beam strength of 120 kV and an absorption contrast with a spatial resolution of 5  $\mu$ m. The 3D-plot (Supplementary figure S1) was generated in Geomagic Studio 2013 (Haji Soft). Photos were cropped using Corel Photo Paint X8; the figure was assembled in Corel Draw X8.

This published work and the nomenclatural acts it contains have been registered in ZooBank, the online registration system for the International Code of Zoological Nomenclature. The corresponding Life Science Identifiers (LSIDs) are urn:lsid:zoobank.org:pub:95A49CDB-E074-4EA9-9E2F-9B0A556C61FB, urn:lsid:zoobank.org:act:1D948C29-0D74-4832-9426-6C6848497E9D, and urn:lsid:zoobank.org:act:4112AE8E-9176-443E-B164-6EDB7D4B939B.

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**Figure S1.** Interactive 3D-plot of the  $\mu$ CT scan. Related to Figure 2.