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Archaeospirostoma flinti gen. et sp. nov. from Late Cretaceous (Cenomanian) Kachin amber (Gastropoda: Caenogastropoda: Cyclophoridae)

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Abstract
Archaeospirostoma flinti Páll-Gergely, Yu & Szabó, sp. nov. is described from burmite (Kachin amber). This new species is characterized by long hairs on the widely-spaced ribs, being adherent to each other forming flat periostracal elements, and a conical, multispiral, scalariform operculum, reminiscent of that of the extant cyclophorid genus *Spirostoma* Heude, 1885. Based on these key characters a new genus (*Archaeospirostoma* Páll-Gergely, Yu & Szabó, gen. nov.) is described.

Key words Burmese amber, burmite, operculum, periostracum.

Introduction

Shell surface structure (Yoshimura & Sasaki 2026) and ornamentation of land snail shells (i.e., spiral striae, radial ribs, hairs, knobs, or wrinkles) is a frequent consequence of evolution (Giokas 2008). Structural details such as the periostracal (uppermost proteinaceous shell layer) hairs on shells are

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considered costly investments formed by the snail mantle via a complex process during shell growth (Allgaier, 2011). They are known in several modern land and marine snails (e.g., Iyengar et al. 2008). Homogenously hairy periostracum is known from members of all three large clades that invaded land (Vermeij & Watson-Zink 2022), such as Caenogastropoda (Lee et al. 2008), Neritimorpha (Richling, 2009) and Eupulmonata (Helicoidea: Welter-Schultes, 2012; Charopidae: Solem, 1988; Odontostomidae: Cuezzo et al., 2018; Polygyridae: Dourson, 2013), indicating that this trait has appeared multiple times independently across distantly related groups throughout land snail evolution (Pfenninger et al., 2005). However, in many groups, they do not uniformly cover the shell, but rather, are placed in single rows, most often along the margin (or keel) of snail shell whorls (e.g., Hirano et al., 2014, Páll-Gergely et al. 2026).

The earliest fossil occurrence of preserved periostracal hairs is known from cyclophorid snails, dating from Late Cretaceous amber of Myanmar (ca. 99 Ma) (Hirano et al., 2019; Neubauer et al. 2019, Bullis, et al. 2020, Bichain et al. 2022, Yu 2022). So far, the periostracal hairs of all species are either short (Bichain et al. 2022) or long (e.g., Neubauer et al. 2019, Hirano et al., 2019), straight, hair-like filaments, which are arranged along radial growth lines or ribs.

In this paper we describe a new genus and species (*Archaeospirostoma flinti* Páll-Gergely, Yu & Szabó, sp. nov.), which possesses long, flattened periostracal processes resulted by the adhesion of multiple hairs along the radial ribs.

Materials and Methods

The holotype was purchased from controlled commercial source. Regarding the paratypes and additional specimens, they were obtained from a former amber mine located near Noije Bum Village, Tanaing Township, in northernmost Myanmar.

Photos of the holotype of the new species were taken via a Nikon SMZ25 digital microscope with Nikon Nis-Elements software (HUN-REN ATK, Martonvásár), while the amber specimen was submerged in baby oil.

The samples were scanned using a Bruker SkyScan 2211 micro-CT system (SkyScan, Bruker, Belgium) equipped with a CCD camera. Measurements were performed at an X-ray tube voltage of 110 kV and a current of 800 µA, using a 0.25 mm aluminium filter, a rotation step of 0.1°, and frame averaging of five images per projection. The smallest achievable pixel size was selected according to the sample dimensions and ranged from 2 to 6 µm per pixel. Image reconstruction was performed using NRecon software (SkyScan, Bruker, Belgium), which employs the Feldkamp algorithm. The reconstructed images were 4032 × 2688 pixels in size. Corrections for beam hardening, ring artifacts, and misalignment were applied, and defective pixels were masked during reconstruction.

Abbreviations

NHMUS PAL Department of Palaeontology, Hungarian Natural History Museum (Budapest, Hungary)
NHMW Museum of Natural History of Vienna (Vienna, Austria)
NIGPAS (NIGP as part of inventory numbers) Palaeobiology and Stratigraphy, Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences (Nanjing, China)

Systematic Paleontology

Class: Gastropoda Cuvier, 1795
Subclass: Caenogastropoda Cox, 1960
Superfamily: Cyclophoroidea Gray, 1847
Family: Cyclophoridae Gray, 1847
Subfamily: Spirostomatinae Tielecke, 1940

Remarks: *Archaeospirostoma* gen. nov. is provisionally placed in the subfamily Spirostomatinae based on the conical operculum.

Genus *Archaeospirostoma* Páll-Gergely, T.-T. Yu & M. Szabó, gen. nov.
https://www.zoobank.org/urn:lsid:zoobank.org:pub:1890AE2F-ED7C-4830-92F1-AECAD668F8E5

Type species: *Archaeospirostoma flinti* sp. nov. (Figs 1–3)

Locality and age: Kachin Amber from Myanmar, ca. 99 MYA. We follow the statement of Shi et al. (2012), who mentioned Cenomanian age (98.79 ± 0.62 mya) based on U-Pb dating of zircons.

Diagnosis: A depressed cyclophoroidean genus with very widely-spaced ribs having large, triangular periostracal folds (formed by the concretion of multiple long hairs), and a conical, scalariform operculum.

Comparisons: There are three genera of Cyclophoridae from burmite having depressed shells: *Archaeocyclotus* Asato & T. Hirano, 2019 (type species: *A. plicatulus* Asato & T. Hirano, 2019), *Hirsuticyclus* Neubauer, L. Xing & Jochum, 2019 (type species: *H. electrum* Neubauer, L.D. Xing & Jochum, 2019) and *Perissocyclos* D. A. Bullis, Herhold, Czekanski-Moir, Grimaldi & Rundell, 2020 (type species: *P. kyrtostoma* D. A. Bullis, Herhold, Czekanski-Moir, Grimaldi & Rundell, 2020). Similarly to the new genus, *Archaeocyclotus* species (*A. plicatulus* and *A. brevivillosus* Bichain, Jochum, Pouillon & Neubauer, 2022) also have periostracal folds on their ribs, but those are shorter and narrower, do not attach to each other forming flat folds. No operculum of *Archaeocyclotus* is known so far. However, unpublished *Archaeocyclotus* specimens have opercula with concave outer surface (personal observations). The two species of *Hirsuticyclus* have different shell surfaces: *H. electrum* has long, straight periostracal hairs arranged along the dense ribs on the shell, whereas *H. canaliculatus* T.-T. Yu, 2022 (see also in Bichain et al. 2025) has prominent spiral keels, but lacks hairs. Nevertheless, those two species agree that their sculpture is dominated by spiral elements, whereas in *Archaeospirostoma* the radial elements are more prominent.

The operculum of *H. electrum* is similar to most Cyclophoridae by having the outer surface concave, although its fine structure cannot be seen (Yu 2022). The operculum of *H. canaliculatus* is flat, with approximately six whorls and a prominent nucleus (Bichain et al. 2025).

The peculiar operculum of *Archaeospirostoma* n. gen. (apex of the conical operculum points outside), is similarly to the extant genus *Spirostoma* Heude, 1885 (type species: *Spirostoma frinianum* Heude, 1885), which is nevertheless, a genus of hairless species (Fig. 4).

Etymology: From the prefix "archaeo-", meaning ancient, and the generic name *Spirostoma*, referring to the operculum similar in that genus.

***Archaeospirostoma flinti* Páll-Gergely, T.-T. Yu & Szabó, sp. nov.**
https://www.zoobank.org/urn:lsid:zoobank.org:pub:41B7968F-BD68-475F-923E-EEB1BF02B0AB
Figs 1–3

Type material:

Holotype
NHMUS PAL 2026.125.1. (Fig. 1).

Paratype
NIGP211604 (specimen no. 1248, 1 shell in transparent amber, Fig. 2): juvenile/subadult shell.

Additional specimens

NIGP211605 (specimen no. 1088 [juvenile], (Fig. 3A–B); NIGP211606 (specimen no. 1141 [juvenile], Fig. 3C–D); NIGP211607 (specimen no. 1229 [juvenile], (Fig. 3E).

Locality and age: Kachin Amber from Myanmar, ca. 99 MYA.

Diagnosis: As for the genus.

Description (based on the holotype and the paratype): Number of whorls approximately 4.25–4.75, although the protoconch is not clearly visible to allow exact determination of whorl numbers. Colour of specimen 1248 yellowish, with some hardly visible reddish zigzag colouration on the last quarter whorl. The colour of holotype is not visible clearly due to the strong yellow colour of the amber. Shell strongly depressed; spire only slightly elevated. Edge of body whorl not clearly visible, probably rounded or slightly keeled. Protoconch sculpture not visible. Teleoconch sculpture only visible on the last whorl, because preceding whorls are covered in mud. Ribs are situated very far from each other,

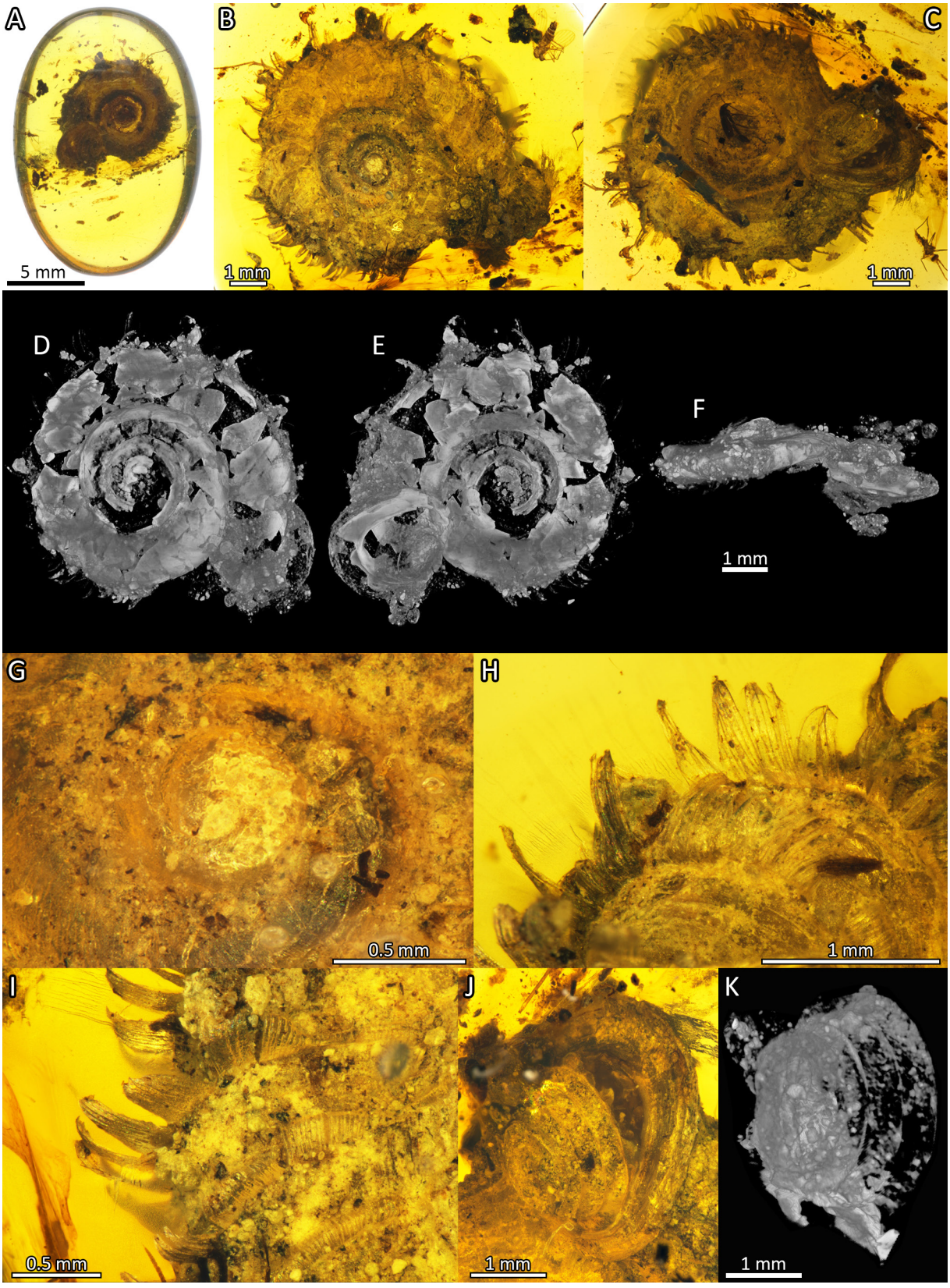


Figure 1. Holotype of *Archaeospirostoma flinti* Páll-Gergely, T.-T. Yu & Szabó, sp. nov. (NHMUS PAL 2026.125.1.). A: Burmite specimen containing the holotype of *A. flinti* gen. et sp. nov., under light microscope. B: Habitus in dorsal view; C: Habitus in ventral view; D–F: *A. flinti* gen. et sp. nov. as reconstructed by X-ray CT-scan; G: protoconch (under light microscope); H–I: periostracal folds (under light microscope); J: operculum (under light microscope); K: operculum (CT-scan), outer side pointing leftwards.

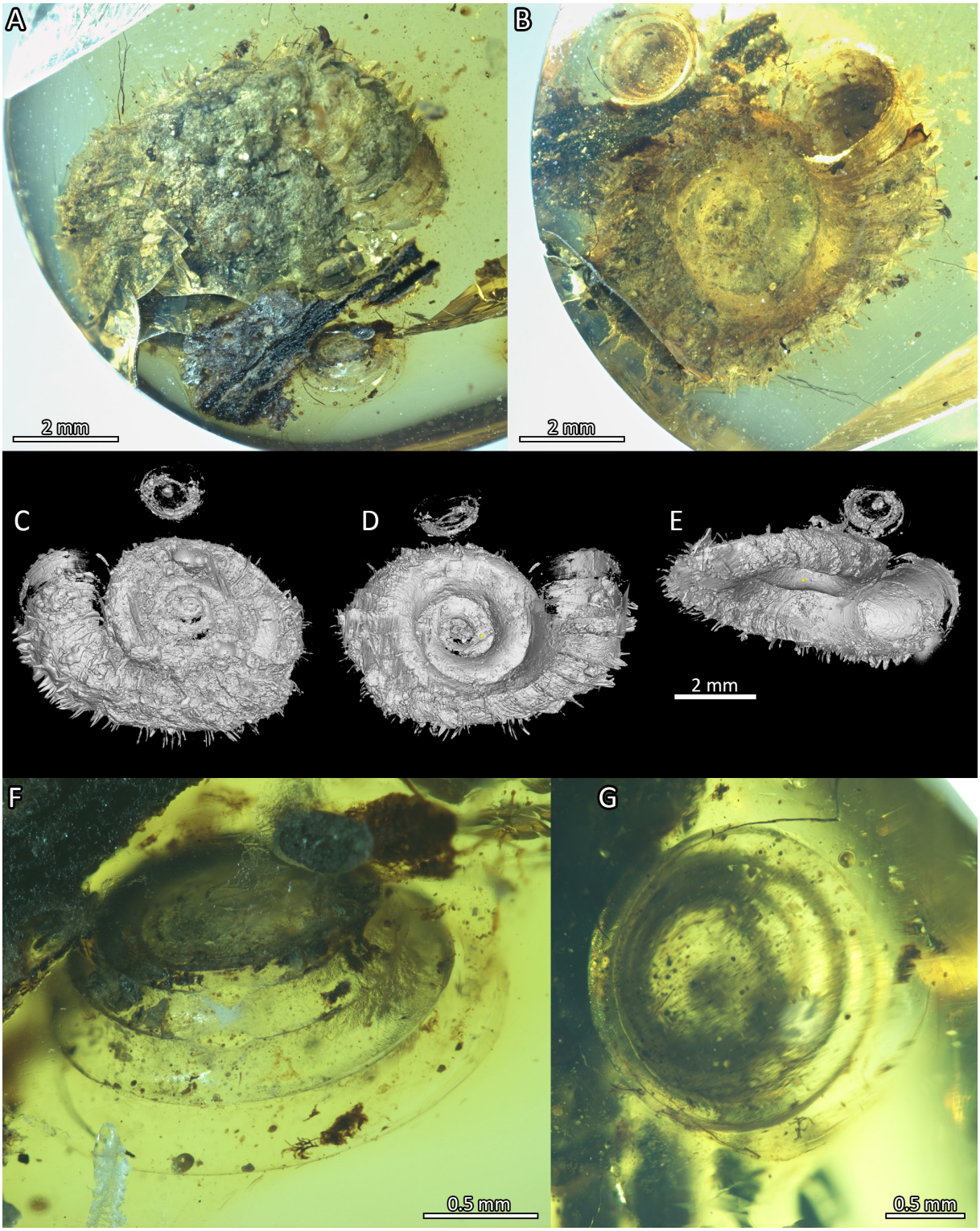


Figure 2. Paratype of *Archaeospirostoma flinti* Páll-Gergely, T.-T. Yu & Szabó, sp. nov. (specimen no. 1248, NIGP211604). A–B: shell in transparent amber (under light microscope); A: dorsal view; B: ventral view; C–E: specimen as reconstructed by X-ray CT-scan; C: dorsal view; D: ventral view; E: apertural view; F–G: Operculum under light microscope. F: lateral view of the operculum; G: inner view of the operculum.

they are reinforced with highly elevated, triangular periostracal folds. A series of these triangular folds are lining on the entire length of a rib from the umbilicus until the suture, but most prominently on the edge of body whorl. Rib density stable on the last whorl, and there are ca. 15 ribs on the last half whorl. Fine, dense spiral striation is visible between the ribs. Area between two ribs bears at least ten very fine

riblets. Aperture circular, strongly oblique to shell axis (i.e. strongly descending). Outer peristome strongly expanded in holotype. Umbilicus wide, wider than one third of shell width.

Measurements: maximum diameter of shell, 6.94 mm; operculum, 2.41 mm (holotype); maximum diameter of the paratype (NIGP211604) is 7 mm. Measurements of the additional (juvenile) specimens: NIGP211605: 3.9 mm; NIGP211606: 3.2 mm; NIGP211607: 3.4 mm.

Operculum: Conical, multispiral, scalariform proteinaceous ("horny"), not calcareous. Apex of operculum sunken, each “whorl” deeply grooved between the sutures.

The operculum of the holotype is situated in its natural position, indicating that the apex of the operculum is pointing outside. The operculum of the holotype seems to be comparatively higher (more highly conical) than that of the paratype. This difference could reflect intraspecific variation or growth stage.

Comparisons: There are no other species known from burmite with similarly long hairs forming flat periostracal folds.

Compared with extant species, there are also no other depressed cyclophorids with flattened periostracal projections formed by multiple hairs. The operculum of *A. flinti* sp. nov. is lower conical than that of extant *Spirostoma* species, the apex of the operculum is sunken (blunt but pointed in *Spirostoma*, Fig. 4D–F), and the whorls of the operculum and more concave, grooved between the sutures.

Etymology: This new species is named after and dedicated to Keith Flint (1969–2019), English singer, a late member of the English music band The Prodigy. The periostracal folds of this new species are reminiscent of Flint's distinctive "Firestarter" hairstyle.

Remarks: The non-paratype specimens are juveniles, and lack an operculum. Therefore, questionably assigned to this species. Nevertheless, the most important sculptural elements (main ribs with triangular periostracal filaments, fine spiral striation) agree with the holotype.

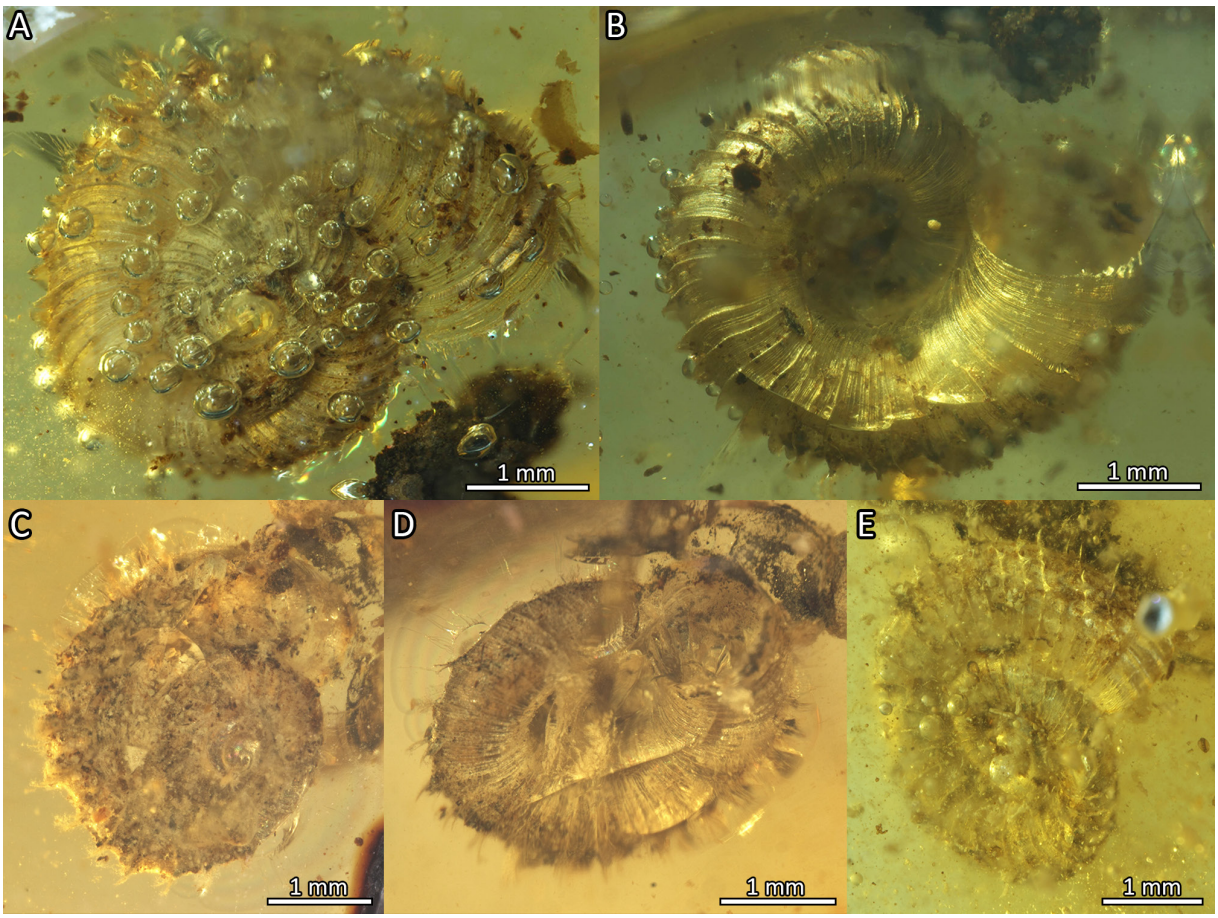


Figure 3. Juvenile specimens of *Archaeospirostoma* cf. *flinti* Páll-Gergely, T.-T. Yu & Szabó, sp. nov. (not paratypes). A–B: NIGP211605 (specimen no. 1088); A: dorsal view; B: ventral view; C–D: NIGP211606 (specimen no. 1141); C: dorsal view; D: apertural view; E: NIGP211607 (specimen no. 1229) (dorsal view).

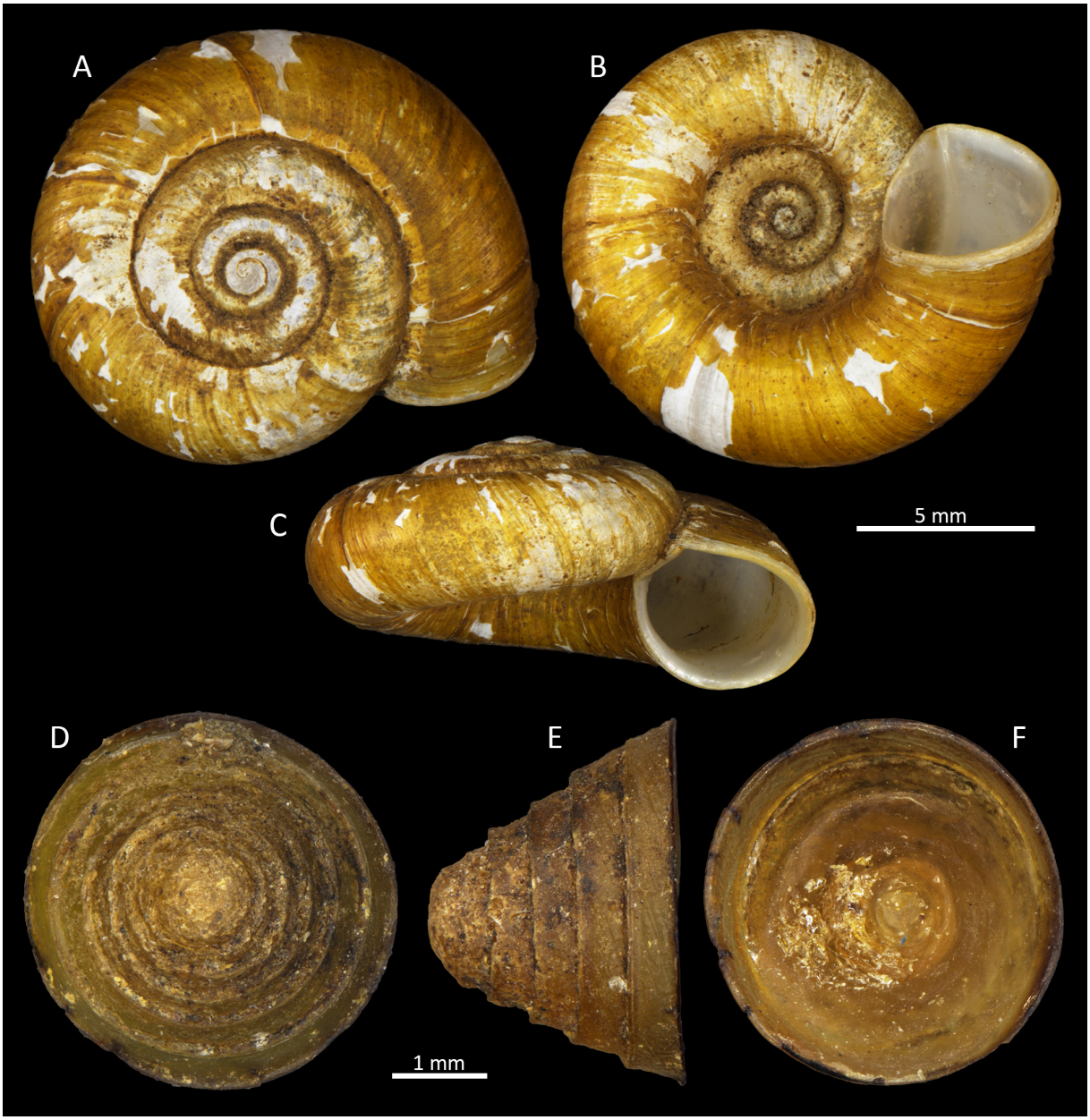


Figure 4. *Spirostoma japonicum* (A. Adams, 1867) (NHMW 5120). A: dorsal view; B: ventral (umbilical) view; C: apertural view; D: outer view of the operculum; E: lateral view of the operculum; F: inner view of the operculum.

Discussion

Together with the new species described herein, nine species of Cyclophoridae are known from burmite, being classified into six genera (Hirano et al. 2019, Neubauer et al. 2019, Bullis et al. 2020, Bichain et al. 2022, Yu 2022). Among them, 7 species possess hairs, while two are hairless. The newly described species, *Archaeospirostoma flinti* sp. nov. differs from all other depressed cyclophorid species known from burmite in the morphology of periostracal hairs. Namely, while all other species have short or long, single-standing straight hairs, those of *A. flinti* sp. nov. are congruent, forming flat periostracal folds. Most hairy shells in extant Cyclophoroidea are covered by single-standing, (short or long) straight hairs (e.g., Vermeulen & Junau 2007, Lee et al. 2008, Egorov 2009, Bhosale et al. 2025, Tran et al. 2026). However, congruent hairs similar to those in *A. flinti* sp. nov. have also appeared in a few genera, for example in *Mychopoma* W. T. Blanford, 1869 and *Craspedotropis* W. T. Blanford, 1864 (Raheem 2014, Fig. 5). In other cases, such as in the South African genus *Chondrocyclus* Ancey, 1898, there are

flattened periostracal flanges, but they are seemingly not formed by the concretion of multiple hairs (e.g., Cole 2019).

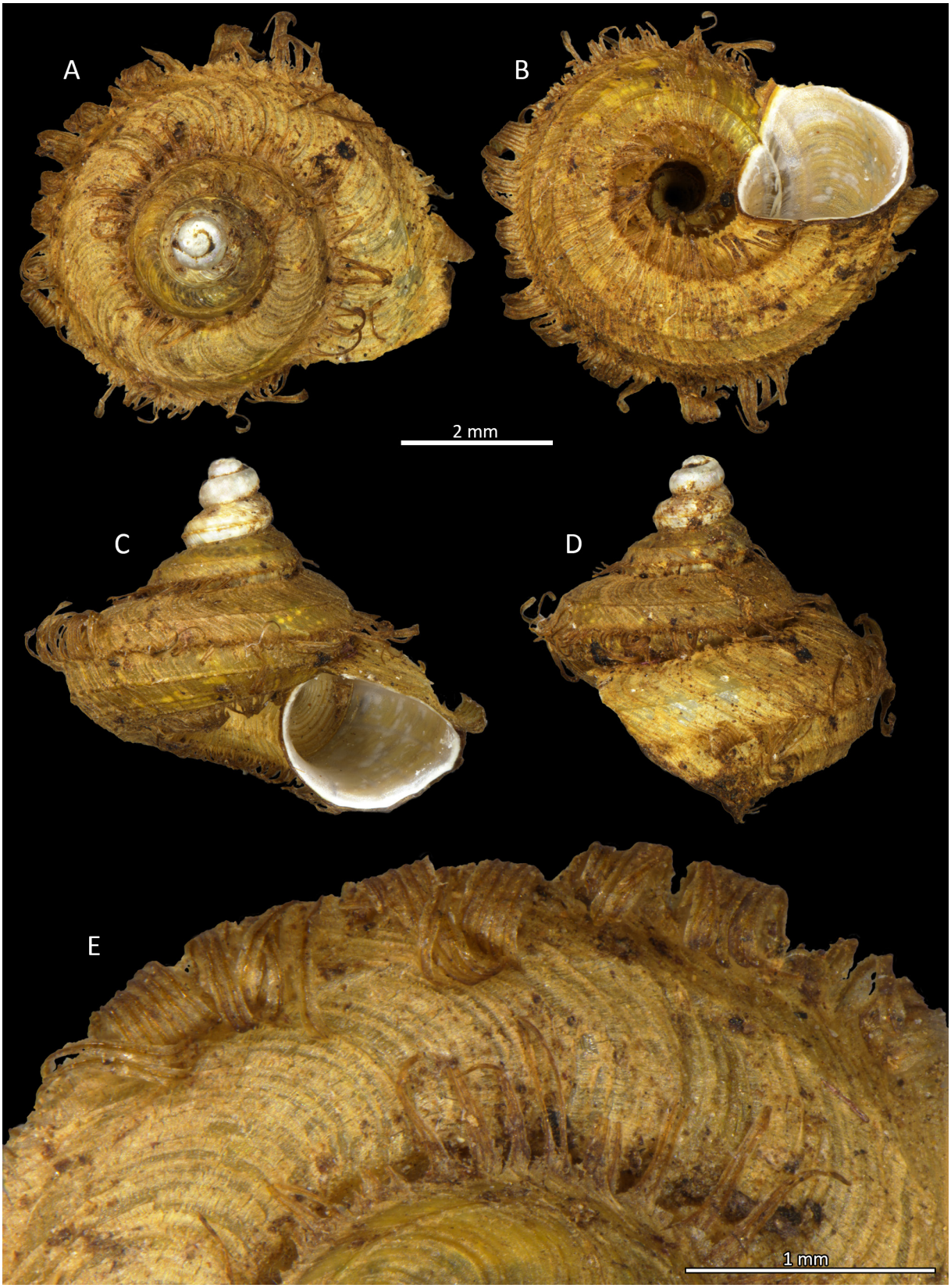


Figure 5. *Craspedotropis cuspidata* (W. H. Benson, 1851) (NHMW 2901). A: dorsal view; B: ventral (umbilical) view; C: apertural view; D: lateral view; E: close-up image of the body whorl showing the periostracal folds.

This finding shows that elongated periostracal sculptural elements already have reached a high morphological variability in the early evolution of Cyclophoridae. The function of hairs on snail shells have been investigated by multiple authors, but there is so far no agreement in the results, and there are more speculations than hard facts (Pfenninger et al. 2005, Holyoak & Holyoak 2012, Proćków et al. 2018, Suvorov 1999, Shvydka et al. 2020, Bichain et al. 2022). Although suggested for calcareous shell ornamentation instead of periostracal projections (Schilthuizen 2003), sexual selection can also not be excluded in the present case as a possible drive for the hairs' evolution.

Archaeospirostoma gen. nov. is classified in the Spirostomatinae together with the so far only extant genus, *Spirostoma*. *Spirostoma* species, however, lack periostracal hairs. Nevertheless, recent molecular phylogenetic analyses revealed that the closest relative of the extant Spirostomatinae is the Japoniinae K. Kuroda, 2026 (Kuroda & Nakano, 2026), many species of which are characterized by hairs of variable morphology (Kobelt 1902, Hwang 2015). If the assignment of *Archaeospirostoma* n. gen. to Spirostomatinae is correct, the presence of periostracal processes in *Archaeospirostoma* is consistent with the hypothesis of a hairy ancestor and subsequent loss in *Spirostoma*. Nevertheless, in the absence of additional fossil specimens bearing conical opercula between the Late Cretaceous and the present day, this scenario remains speculative.

The operculum of *Archaeospirostoma flinti* sp. nov. is peculiar among cyclophorids known from burmite due to its conical shape. The only similar operculum among terrestrial Caenogastropoda is known in the extant genus *Spirostoma* (Fig. 4D–F), the four species of which inhabit eastern and Southern China, Korea and Japan (Kobelt 1902, Pilsbry & Hirase 1908). *Spirostoma* is the only member of the cyclophorid subfamily Spirostomatinae, to which, due to the similar operculum morphology, *Archaeospirostoma* n. gen. is also classified.

Conical opercula are known in a few non-related aquatic gastropod groups, such as Architectonidae (*Heliacus* d'Orbigny, 1842, *Pseudotorinia* Sacco, 1892, *Spirolaxis* Monterosato, 1913), Vermetidae (*Dendropoma* Mörch, 1861), Siliquariidae (*Tenagodus* Guettard, 1770) and Hydrobiidae (*Gocea* Hadžišče, 1956). In the latter, freshwater genus the operculum is hollow, similar to that of *Archaeospirostoma* gen. n. and *Spirostoma* species. In contrast, all other genera are marine, and their opercula are solid, often with a peg that anchors it to the foot muscle (Bieler 1993). Not much is known about the function of the conical operculum. It was reported however, that siliquariids use their conical opercula as a plunger to quickly push water through the mantle cavity and shell slits (Bieler 2004). Similar function is highly unlikely in a terrestrial environment. One possible advantage might be that the hollow inner surface provides a larger area for the operculum to attach to the foot tissue.

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