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Breathing device of a new *Streptaulus* species from Vietnam extends understanding of the function and structure of respiratory tubes in cyclophoroids (Gastropoda: Caenogastropoda: Pupinidae)

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The operculum of the terrestrial caenogastropod superfamily Cyclophoroidea tightly seals the aperture when the animal withdraws the entire soft body into the shell. For at least most species the operculum presents a barrier to gas exchange. Many cyclophoroideans have resolved this problem by evolving shell devices that provide alternative routes for gas exchange. These modifications range from a simple slit- or groove-like channel to a snorkellike tube at the peristome (Rees, 1964). Elaborate examples are found among Asian members of the family Alycaeidae (Godwin-Austen, 1886; Páll-Gergely, Naggs & Asami, 2016). Their sutural tube has no direct external opening. Instead, many microtunnels extend down from the sutural tube towards their opening near the umbilicus of the body whorl. The sutural tube possesses a pore that opens internally behind the point at which the operculum seals the aperture, allowing gas exchange between the body of the snail through the sutural tube and microtunnels to the outside air.

Many genera of the cyclophoroid family Pupinidae also exhibit diverse breathing devices (Kobelt, 1902; Egorov, 2013; Páll-Gergely et al., 2014, 2015, 2016). Two of them, *Rhaphaulus* L. Pfeiffer, 1856 with 14 species distributed from northern Borneo to northeastern India and *Streptaulus* Benson, 1857 with three species from northeastern India, possess a relatively long and complex tube for gas exchange. [*Streptaulus* has been referred to as a synonym or subgenus of *Rhaphaulus*, or as an independent genus (Godwin-Austen, 1886, 1917; Kobelt, 1902; Gude, 1921; Egorov, 2013). The latest review (Páll-Gergely, Hunyadi & Maassen, 2014) left the question of the taxonomic status of *Streptaulus* open.] From an interior opening within the body whorl the tube runs internally under the suture before passing through the shell and continuing along the outside of the shell to an external opening. Thus, their tube device is constructed with inner and outer portions.

The breathing tube in *Rhaphaulus* has a characteristic outer portion that extends from the parieto-palatal junction of the aperture to the outer opening. The direction, shape and length of this outer portion are species-specific. In *Rhaphaulus tonkinensis* Páll-Gergely, Hunyadi & Maassen, 2014 this outer portion runs into the last whorl near the peristome and continues posteriorly under the

suture to its inner opening (Fig. 1A–E). The inner portion of the tube can be recognized externally as a narrower extension behind the outer tube (Fig. 1B: subsutural furrow). In *Streptaulus*, the external tube runs along the suture from its opening toward the peristome (Fig. 1F–I) and continues posteriorly to the inner opening under the suture, inside the last whorl (Fig. 2A). The outer tube bears several circular external holes along its length (Fig. 2B, C).

That such a range of structures is present in breathing tubes in Cyclophoroidea prompts several questions about the selective pressures that operated and why a number of evolutionary solutions have arisen. The volume-to-surface ratio dictates that the larger the individual the more difficult it becomes to gain sufficient air intake for respiration and, the smaller the individual, the rate of water loss becomes more challenging. Balancing these conflicting demands with structural arrangements providing protection against predators is hypothesized to be the main selective force driving the development of breathing devices. It appears that the opportunity for evolutionary novelties or the strength of selective pressures for developing breathing tubes is greater in small taxa. Both a narrow opening in a breathing device and a reduced shell-apertural cross section should contribute to reduction of body-water loss in the terrestrial environment (Gittenberger, 1996; Páll-Gergely et al., 2016). Both the outer and inner portions of the breathing tube in *Rhaphaulus* and *Streptaulus* are narrow and long, each as much as a quarter whorl in the completed shell of adults. The length of the inner portion in these genera demonstrates that they begin to form the inner opening, and thus can utilize the inner portion for breathing, as juveniles. We suspect that the outer tube is constructed after adult shell size is reached by adding that portion afterwards, further back from the peristome (Fig. 2C), although no direct observation on the ontogeny of the tube, or series of subadult shells, are available to support this. The combined outer and inner portions extend the total length, providing a single functional breathing device. This long elongated tube system confers on the animal protection from predators, including beetles (e.g. Carabidae) that have elongated heads and modified mandibles adapted for probing deep into prey. This antipredatory device depends on the diameter and length of the breathing tube and there is no obvious functional

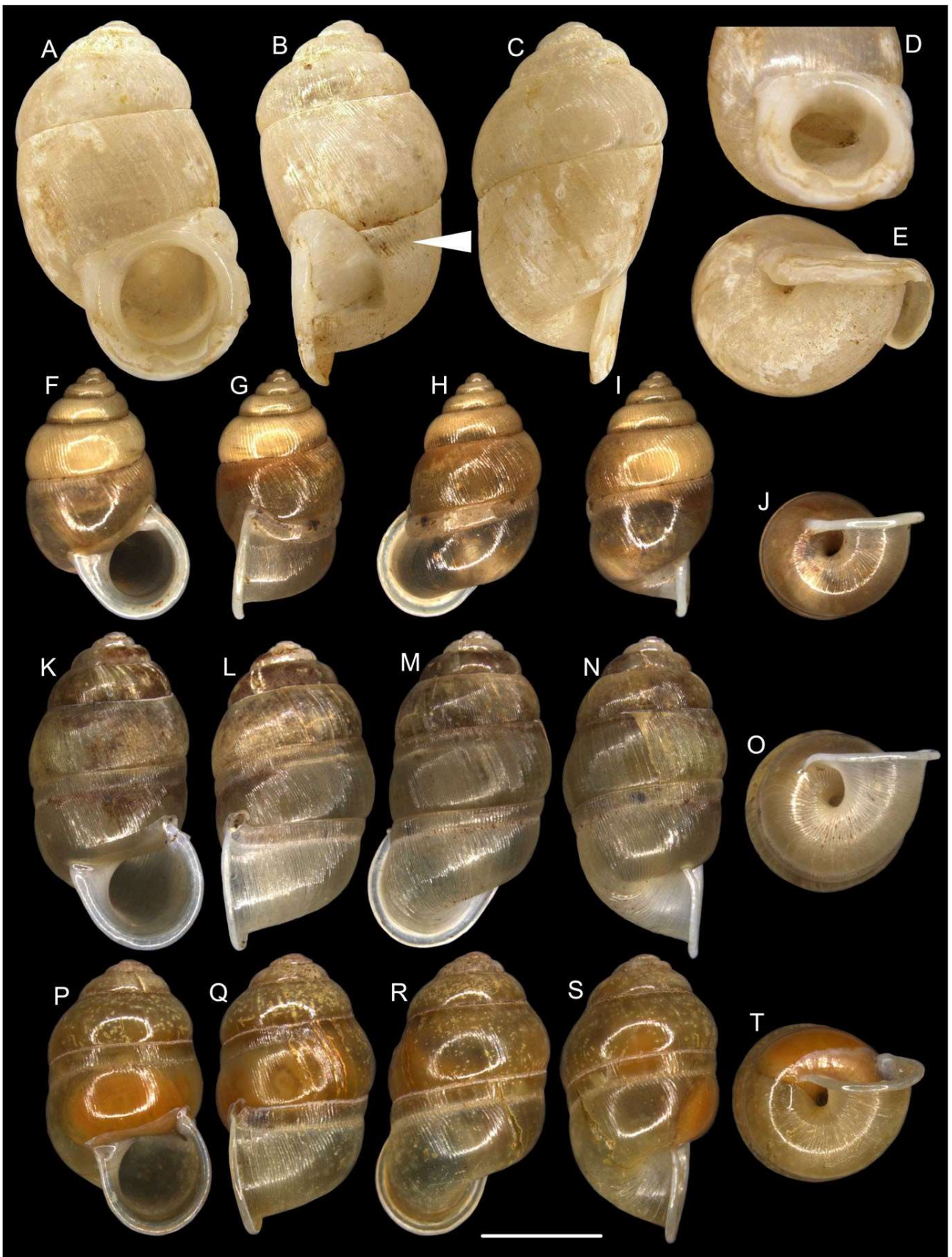
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advantage in possessing a combination of internal and external sutural tubes.

We have discovered a new pupinid species that builds a very long inner tube (Figs 1K–T, 2B, D–F, 3), but lacks an outer tube, resulting in a tube that is even longer than the combined length of

the inner and outer tube portions in other species of *Streptaulus* and *Rhaphaulus*. This long inner tube has an additional benefit: the earlier

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Figure 1. A–E. *Rhaphaulus tonkinensis* Páll-Gergely, Hunyadi & Maassen, 2014 (holotype HNHM 98757). F–J. *Streptaulus blanfordi* (NHMUK 20160319, specimen 1). K–T. *Streptaulus longituba* n. sp. (K–O, holotype; P–T, paratype 1). Arrow indicates subsutural furrow. Scale bar = 5 mm.

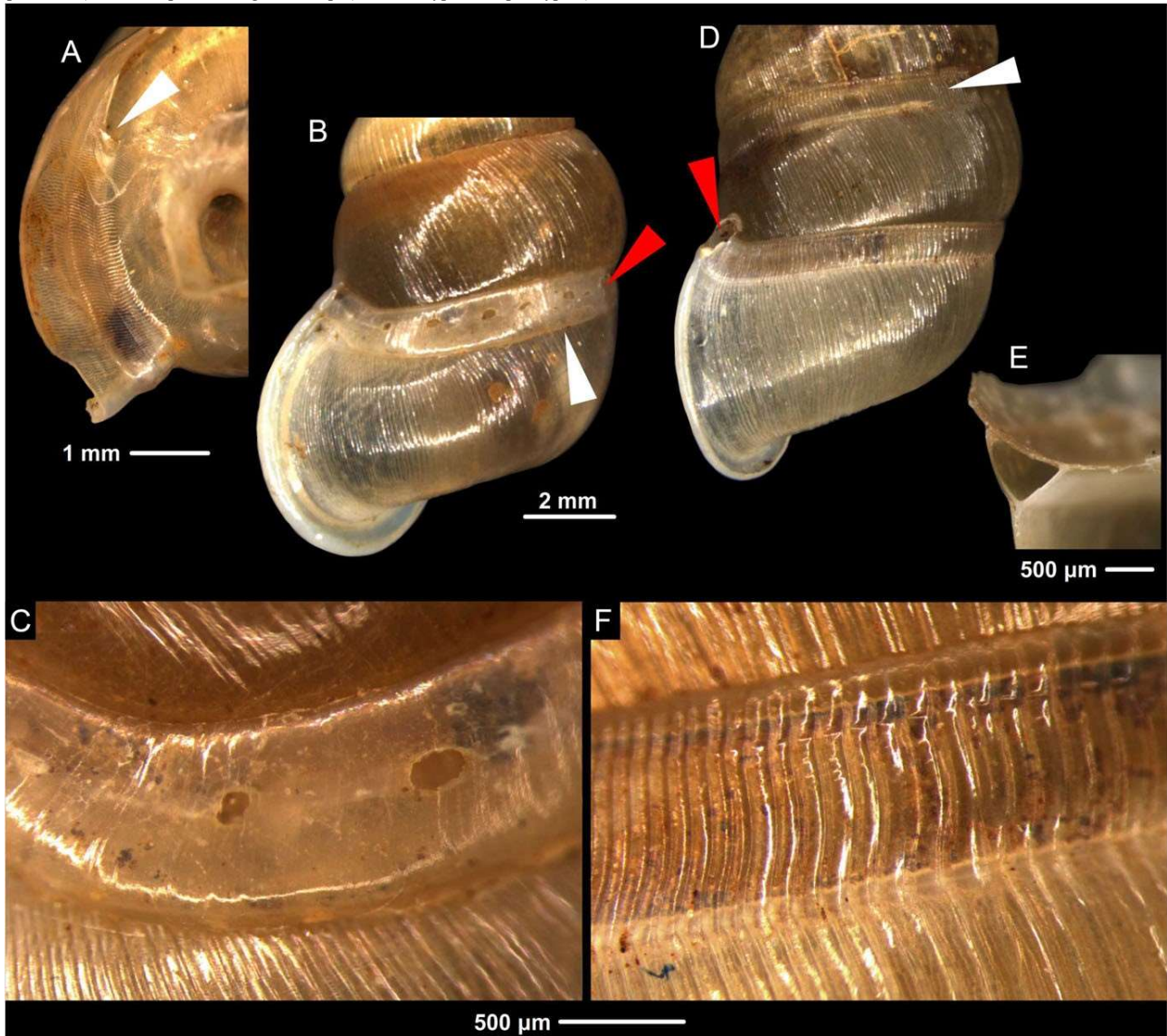


Figure 2. Structure of the breathing tube of *Streptaulus blanfordi* (A–C) and *Streptaulus longituba* n. sp. (D–F). A. Ventral view of inner tube (NHMUK 20160319, specimen 2). B. Outer tube (NHMUK 20160319). C. Outer tube surface (NHMUK 20160319, specimen 1). D. Inner tube (holotype). E. Cross sectional view of inner tube (paratype 1). F. Inner tube surface (holotype). Red arrows indicate place where breathing tube opens to outside, and white arrow position where inner tube opens to inside of whorl.

MNH
NHM
NHMUK

Muséum National d'Histoire Naturelle (Paris)
Natural History Museum (London)
when citing NHM registered specimens.

SYSTEMATIC DESCRIPTION

Family PUPINIDAE L. Pfeiffer, 1853

Genus *Streptaulus* Benson, 1857

Type species: *Streptaulus blanfordi* Benson, 1857 by monotypy.

Recognized species: *Streptaulus blanfordi* Benson, 1857, *Streptaulus longituba* Páll-Gergely & Gargominy, n. sp., *Streptaulus luyorensis* Godwin-Austen, 1917, *Streptaulus miriensis* Godwin-Austen, 1917.

Remarks: In a previous review of *Rhaphaulus* and *Streptaulus* (Páll-Gergely et al., 2014) we left open the issue of the distinctness of the two genera. Based on our new information on the breathing tube

the juvenile starts developing the inner tube, the earlier the animal can utilize the tube for breathing. This new species is from southern Vietnam and is similar to the northeastern Indian genus *Streptaulus* in possessing a weak parietal callus. It differs from all *Streptaulus* and *Rhaphaulus* in possessing the inner tube, which runs along the suture for at least 1.2–1.3 whorls and opens inside the penultimate whorl, but entirely lacking the outer tube. This inner tube opens to the air outside just above the parieto-palatal junction of the peristome.

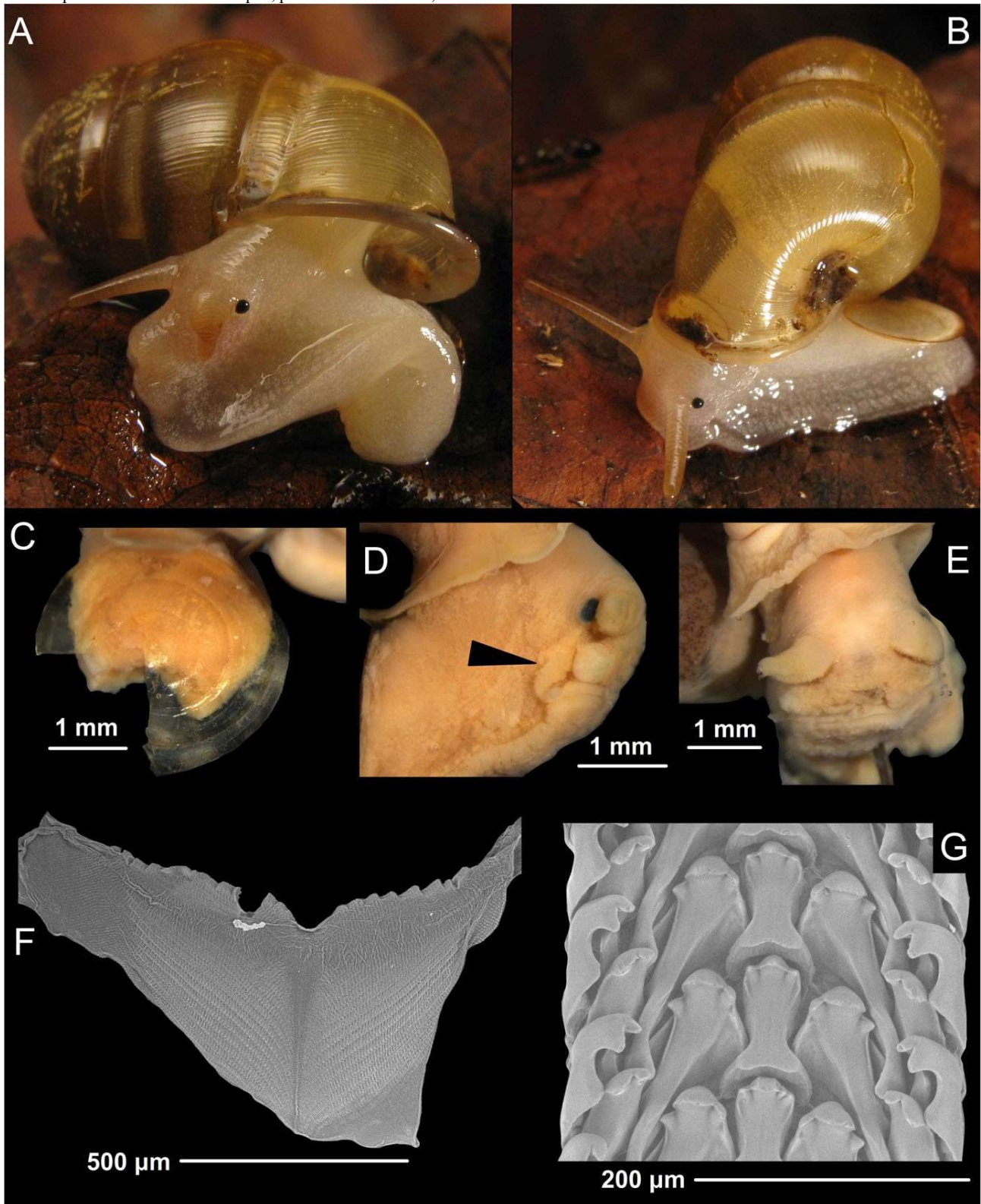
Abbreviations

HNHM Hungarian Natural History Museum (Budapest)

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and on peristome morphology of the new species, we reconsider this view and recognize the two genera. *Rhaphaulus* is diagnosed as follows: parietal callus well developed, peristome continuous; inner

tube short (of c. 0.25 whorl); outer tube varies in direction, without holes on side wall. *Streptaulus* is



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Figure 3. *Streptaulus longituba* n. sp. A, B. Living specimen (paratype 2). C–G. Anatomy (paratype 1). C. Operculum. D. Lateral view of soft body (arrow indicates penis). E. Head. F. Jaw. G. Radula.

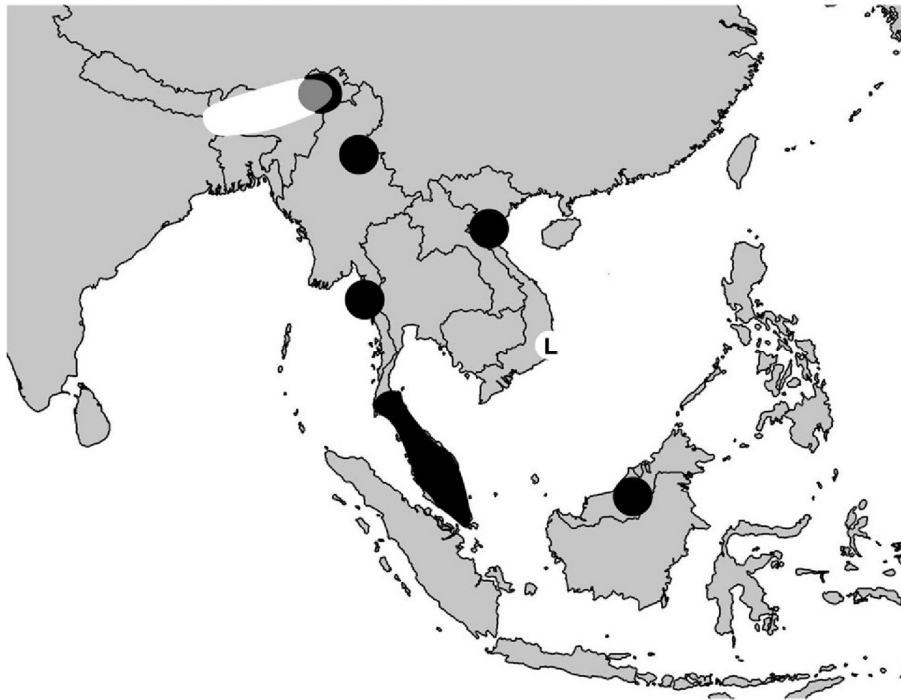


Figure 4. Distribution of *Rhaphaulus* (black) and *Streptaulus* (white) after Páll-Gergely et al. (2014). Locality of *Streptaulus longituba* n. sp. indicated with letter L.

diagnosed as follows: parietal callus weak, peristome interrupted; inner tube short to long (of c. 0.2–1.3 whorls); outer tube absent, or runs along suture, bearing several circular holes along its length.

Streptaulus longituba n. sp. might deserve its own genus based on the apparently stable differences between its tube and that of the other members of the genus. Furthermore, although there are common genera between the two geographic areas (i.e. northeastern India and central Vietnam), the distribution of the genus *Streptaulus* is notably disjunct. We postpone the description of a new genus for *S. longituba* n. sp. until more information (anatomy, radula, phylogeny) is available on this group.

Streptaulus longituba Páll-Gergely & Gargominy new species

Figures 1K–T, 2D–F, 3

Type material: Holotype: MNHN 2012-27162 (Figs 1K–O, 2D, F); Suoi Cat commune, Hon Ba Nature Reserve, Khanh Hoa Province, Vietnam, 690 m, 12.11458°N, 108.98192°E, leg. B. Fontaine & O. Gargominy, 18.11.2013; degraded forest among tumbled rocks in a valley. Paratype 1: MNHN 2012-27163 (Figs 1P–T, 2E, 3C–G; anatomically examined); road to Hon Ba, Suoi Cat commune, Hon Ba Nature Reserve, Khanh Hoa Province, Vietnam, 1270 m, 12.12736°N, 108.96331°E, leg. B. Fontaine & O. Gargominy, 17.11.2013; side of road in primary montane forest. Paratype 2: MNHN 2012-27164 (Fig. 3A, B); data as paratype 1; 1010 m, 12.12247°N, 108.96922°E.

ZooBank registration: urn:lsid:zoobank.org:act:558AFB9F-FE0B-4E9FBEEA-696681229837

Etymology: The specific epithet *longituba* (long tube, Latin) refers to the long inner sutural tube.

Diagnosis: A *Streptaulus* species with long (c. 1.2–1.3 whorl) inner tube and no outer tube.

Shell (Figs 1K–T, 2D–F): Shell medium sized, yellowish horn-coloured, translucent, ovoid, of 5.5–6.75 slightly bulging whorls, separated by shallow suture; whole shell surface glossy with fine growth wrinkles (stronger in holotype and somewhat weaker in paratypes); some spiral structure discernible in first 3–4 whorls, but this belongs to shell layers beneath uppermost ostracum layer; aperture relatively wide, its margin expanded (especially in direction of umbilicus) and reflexed, but no distinct parietal callus visible; in position of parietal callus only very weak additional calcified layer discernible, which does not differ in colour from rest of shell, although in a very small area around opening of tube the shell is slightly whitish due to an additional calcareous layer; umbilicus slightly open but very deep, probably reaching ventral side of protoconch; breathing tube consists of an inner tube, which only opens to outside just above palatal-parietal angle of aperture and continues along suture for about 1.2 whorls, opening at end of tube to inside of penultimate whorl; ribs on whorls are slightly oblique to shell axis, and continue on sutural tube as well, where they are at right angles to axis (consequently, the portions of the rib on whorl and tube join at a slight angle). Measurements: holotype: shell height (SH) 13.4 mm, shell width (SW) 6.8 mm, apertural height (AH) 5.5 mm, apertural width (AW) 5.7 mm; paratype 1: SH 11.8 mm, SW 6.9 mm, AH 5.5 mm, AW 5.0 mm; paratype 2: SH 10.6 mm, SW 6.2 mm, AH 4.9 mm, AW 4.8 mm.

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Operculum (Fig. 3C): Only outer surface of operculum of a paratype could be examined. Operculum horny, translucent, not calcified, outer side slightly concave, glossy, nearly smooth, multispiral.

Body (Fig. 3A–E): Whole body light in colour, whitish or light grey; tentacles yellowish; sole short, seemingly holopod, uniformly whitish; tentacles short, cylindrical when extended, conical when slightly retracted, papilla-like, blunt in preserved animal; penis (examined in one paratype) situated below right tentacle, pointed, short, vermiform.

Jaw and radula (Fig. 3F–G): Jaw concave kite-shaped (deltoid), showing pattern of small parallelograms placed side by side in oblique rows. Radula long, elongated, teeth arranged in V-shaped rows of formula of 2–1–1–1–2; central tooth strongly narrowed in middle part, 3 main blunt cusps, but in some cases additional minor cusps between 3 main ones; lateral teeth asymmetric, with wide main cusps and 2 narrower ectocones, additional minor cusps can again be present; first marginal teeth with 2 cusps, second marginal with 3 cusps, ectocone of second marginals separated from 2 endocones by deep bay.

Distribution (Fig. 4): *Streptaulus longituba* n. sp. is only known from three specimens from three nearby localities (within a 1.3 km radius) in Hon Ba Nature Reserve, Khanh Hoa Province, southern Vietnam.

Remarks: Members of the genus *Rhaphaulus* have a well-developed parietal callus, which results in a round and continuous peristome. In contrast, the callus of *S. longituba* n. sp. is barely developed, resulting in a discontinuous peristome. Furthermore, *Rhaphaulus* species have a short inner tube and a short or moderately long outer tube, which is variable in direction. The breathing tube of the other three *Streptaulus* species has both an inner (inner tube) and an outer (outer tube) portion, each of about one quarter of a whorl.

The holotype differs from both the paratypes by having stronger sculpture and a larger shell. This might be genetic, environmental or sexual variation.

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