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A review of the Diapheridae (Gastropoda: Eupulmonata: Streptaxoidea), with special emphasis on India and Myanmar

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Abstract. High-spired South and Southeast Asian Streptaxoidea has been classified mostly in the Diapheridae, and partly in the Streptaxidae, and the systematic position of several of them has not been resolved yet. The examination of conchological characters and the analysis of the homologies of apertural barriers revealed that some new genera must be introduced. *Parasinoennea* Z.-Y. Chen & Páll-Gergely, new genus, is erected to include a few species from Vietnam and southern China. *Platylennea* Páll-Gergely, new genus, and *Rowsonia* Páll-Gergely, new genus, include species from the Western Ghats of southern India. *Pupennea* Páll-Gergely, new genus, is erected for *Pupa planguncula* Benson, 1863, which inhabits central India. All these three are probably members of the Diapheridae. We list all Diapheridae species of India and Myanmar, and describe three new species from Myanmar as follows: *Diaphera polita* Páll-Gergely, new species; *Diaphera turbanophora* Páll-Gergely & Grego, new species; *Sinoennea montawana* Páll-Gergely & Hunyadi, new species. *Sinoennea longtanensis* S. Ouyang, X.-M. Liu & X.-P. Wu, 2012 is treated as a synonym of *Parasinoennea splendens* (Möllendorff, 1882).

Key words. taxonomy, systematics, hunter snail, conchology, shell, biogeography

INTRODUCTION

The genus *Sinoennea* Kobelt, 1904 (in Kobelt, 1904a) is widely distributed in Asia from the southwestern Himalaya region through the Chinese Sichuan and Hubei Provinces to Korean Peninsula and Japan, and to northern Borneo and Sumatra in the south (Yen, 1939; Zilch, 1961; Azuma, 1982; Maassen, 1999, 2001; Vermeulen, 2007; Ramakrishna et al., 2010; Budha et al., 2015; Tanmuangpak et al., 2015). The number of known species is at least eighty. *Diaphera* Albers, 1850 can readily be distinguished from *Sinoennea* by its last whorl that is detached from the penultimate whorl. The latter genus is most diverse in the Philippines, but a few species are known in continental Asia (Cambodia, Myanmar, Thailand, Vietnam) and Borneo (Blanford & Godwin-Austen, 1908; Zilch, 1961; Benthem Jutting, 1962; Vermeulen, 1990; Sutcharit et al., 2010; Schileyko, 2011).

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Sinoennea, together with *Diaphera*, has been moved from the family Streptaxidae (see Schileyko, 2000) to a separate family, Diapheridae Panha & Naggs in Sutcharit, Naggs, Wade, Fontanilla & Panha, 2010, based on molecular phylogenetic data as well as morphology of the shell and reproductive anatomy. A few additional genera probably also belong to the Diapheridae, although we lack phylogenetic and anatomic proof. The Bornean endemic genus *Bruggennea* Dance, 1972, containing three species, differs from *Sinoennea* in the smooth shell surface, the ovate shell shape, and the prominent varices (remaining expanded peristomes of juvenile shells) that are imperfectly arranged in two rows on opposite sides of the spire (Dance, 1972; Vermeulen, 2007). Another Bornean endemic, *Platycochlium* Laidlaw, 1950 possesses a low conical/discoidal shell, but similar to *Bruggennea* in the presence of varices and in general aperture shape. *Tonkinia* J. Mabille, 1887, known only from northern Vietnam, is similar to *Platycochlium*, differing from that genus by an aperture that is turned upwards (see Páll-Gergely & Neubauer, 2020). The most recently described diapherid genus is the monotypic *Laoennea* Páll-Gergely in Páll-Gergely, Reischütz, Maassen, Grego & Hunyadi, 2020 from Laos.

Sinoennea, in our present understanding, is an extensively large genus in terms of number of species and morphological variability, and the classification of some species was not in agreement among recent publications. For example, some Vietnamese *Sinoennea* species were classified in *Indoennea* Kobelt, 1904 (in Kobelt, 1904a; Schileyko, 2011), although Peile (1935) already synonymised *Indoennea* with *Sinoennea*. Furthermore, the Indian species that were traditionally classified in *Ennea* H. Adams & A. Adams, 1855 (Blanford,

1899; Blanford & Godwin-Austen, 1908), have been partly treated as *Ennea* or were moved to *Gulella* (*Huttonella*) L. Pfeiffer, 1856 (Ramakrishna et al., 2010). In contrast, the southern Indian species were all classified in *Sinoennea* recently by Raheem et al. (2014), who mostly followed the principles of Kobelt (1904b).

In the present paper, after the examination of specimens or illustrations of practically all species of *Sinoennea* sensu lato, we hypothesise the homologies of apertural barriers, which is essential in defining the genus *Sinoennea* and recognising the species that should be classified in separate genera. As a result, we separate some species inhabiting southern China and Northern Vietnam in the genus *Parasinoennea*, new genus, based on differences of the shell shape, sculpture, aperture shape, and aperture dentition. Furthermore, the examination of Diapheridae inhabiting India revealed that the ones from the Himalaya all belong to *Sinoennea*, but the ones inhabiting central and southern India should be classified in three different groups that are introduced here as new genera. Additionally, we describe a new species of *Sinoennea*, and two of *Diaphera*, from Myanmar.

No ethanol-preserved specimens are available, and the distinctness of the new genera should ideally be tested by independent lines of evidence, such as anatomy and molecular phylogeny. However, the biogeographical and morphological differences with clear homology statements provide clear indication of possibly monophyletic groups, and allow us to erect new genus-group taxa that are testable hypotheses (Páll-Gergely, 2017).

MATERIAL AND METHODS

In this paper we list the Diapheridae occurring in India and Myanmar only. The *Sinoennea* species of other Southeast Asian countries were examined (type specimens in museums or their original descriptions) to an extent that their position within *Sinoennea* could be confirmed. Locality data presented with the specimen examined data are cited verbatim from the specimen labels.

The counting of the shell whorls (to the closest 0.25 whorl) follows Kerney & Cameron (1979: 13). Ten to 30 photographs were taken of each shell using Keyence LHX5000 digital microscope and merged to create a single image using Photoshop.

In order to maintain consistency with MolluscaBase (2020), initials of first names are indicated in all cases where a given author shares the same family name with another malacologist (e.g., L. Pfeiffer, X.-P. Wu).

Homology analysis of aperture barriers. Two structures (genes, organs, any morphological features) are homologous when they are shared with those in a common ancestor. Taxonomists compare putatively homologous morphological structures. In modern biology, homology between structures can be hypothesised using multiple techniques, such as gene expression patterns. In case of morphological structures of gastropod shells, however, we have to rely on "classic" approaches defined by Remane (1952), who recognised three criteria: (1) the criterion of topological equivalence (similar relative position of structures); (2) the criterion of special quality of structures ("similarity"); and (3) the linkage by intermediate forms. The primary and most important of these three is the topology, because the recognition of special quality of structures and intermediate forms requires a primacy of the criterion of topological correspondence (Hennig, 1966; Rieppel & Kearney, 2002). Based on these principles, mostly topology, we name each apertural barrier of diapherid genera, and list the possible homologies (Fig. 1, Table 1) after careful comparisons highlighted below.

The hypotheses on homologous structures can be made by comparing each structure (in the present case apertural barriers) with those of other species. For example, the upper palatal tooth (UPT) is variable in shape and size, but it can be recognised based on its fixed position just below the sinulus on the palatal lip. That tooth is pointed in *S. moerchiana* (Fig. 17D–F, J), and blunt in *S. fartoidea* (Fig. 15D–I), but their relative position is identical, which makes them homologous. Another example is the lower parietal tooth (LPT), which is smaller than the UPT and pointed in *Sinoennea otostoma* Páll-Gergely, A. Reischütz & Maassen in Páll-Gergely, Reischütz, Maassen, Grego & Hunyadi, 2020 (Fig. 22I), and larger than the UPT and elongated in *S. woodthorpei* (Peile, 1929) (Figs. 19F–M, 22O), but they are homologous due to the identical relative position. Moreover, the UPL and the LPT are almost always connected to each other. Following similar step-by-step comparisons, both palatal teeth (UPT, LPT), the parietal lamella, and the columellar lamella could be recognised in almost all *Sinoennea* species based on their relative positions.

Difficulties start when apertural barriers are not in the same relative position in two species. For example, in *Rowsonia*, new genus, the palatal barriers other than the UPT are not in the same position, shape, and orientation as in *Sinoennea*. The palatal wall of *Rowsonia*, new genus, bears three horizontal (= parallel with the suture) folds in some distance from the palatal lip. The lowest two (lower palatal fold: LPF, and middle palatal fold: MPF) are situated in similar approximate position to the LPT of *Sinoennea*. However, none of the two (i.e., LPF and MPF) are connected with the UPT, which would be the case in most *Sinoennea* species. Moreover, the LPF and the MPF of *Rowsonia*, new genus, are horizontal (= parallel to the suture), whereas the LPT of *Sinoennea* is either pointed (= not elongated), or elongated and oblique. Consequently, the lower palatal folds of *Rowsonia*, new genus, cannot be directly hypothesised as homologous traits with the LPT of *Sinoennea*. Similar step-by-step comparisons revealed that some apertural barriers of *Platylennea*, new genus, *Pupennea*, new genus, and *Rowsonia*, new genus, are only putatively homologous structures with some apertural barriers of *Sinoennea* (Table 1).

The relative position of apertural barriers vary between species groups. As a result, it is sometimes difficult to

Table 1. Homologies of apertural barriers of the diapherid genera *Platylennea*, new genus, *Pupennea*, new genus, *Rowsonia*, new genus, *Sinoennea*, and *Gulella* (*Huttonella*). The parietal lamella is not indicated because it is situated in the same position in every diapherid genus. Question marks indicate that the homology of the two structures is questionable. Traits marked in bold correspond with the genus marked in bold in comparisons.

	***Gulella* (*Huttonella*)**	***Platylennea*, new genus**	***Rowsonia*, new genus**	***Pupennea*, new genus**
Platylennea, new genus	**BT** = LBD; **CL** = CL; **PT** = UPT?			
Rowsonia, new genus	**BT** = no homologous structure; **CL** = CL; **PT** = UPF or MPF?	**CD** = ICE; **CL** = CL; **LBD** = LPF?; **UBD** = UPF or MPF?; **UPT** = UPT		
Pupennea, new genus	**BT** = IBD; **CL** = CL?; **PT** = LPT?	**CD** = CD?; **CL** = CL?; **LBD** = IBD?; **UBD** = OBD?; **UPT** = UPT or UPT+LPT?	**CL** = CL?; **LPF** = OBD?; **MPF, UPF** = no homologous structure; **UPT** = UPT or UPT+LPT?	
Sinoennea	**BT** = no homologous structure in most species; **PT** = LPT?	**CD** = ICE; **CL** = CL; **LBD** = no homologous structure; **UBD** = LPT?; **UPT** = UPT	**CL** = CL; **LPF** = LPT?; **MPF** = inner part of UPT?; **UPF** = inner part of UPT?; **UPT** = UPT	**CD** = ICE?; **CL** = CL?; **LPT** = LPT?; **OBD, IBD** = no homologous structure in most species; **UPT** = UPT?

Supplementary notes (Abbreviations): BT, basal tooth; CD, columellar denticle; CL, columellar lamella; IBD, inner basal denticle; ICE, inner columellar edge; LBD, lower basal denticle; LPF, lower palatal fold; LPT, lower palatal tooth; MPF, middle palatal fold; OBD, outer basal denticle; PL, parietal lamella; PT, palatal tooth; UBD, upper basal denticle; UPF, upper palatal fold; UPT, upper palatal tooth.

hypothesise about the homologies between apertural barriers of different species groups. However, within each group the homologies are clear. Thus, we propose three new genera to distinguish the species groups defined by their unique arrangement of apertural barriers.

Abbreviations.
D: shell diameter
H: shell height
HA: Collection András Hunyadi (Budapest, Hungary)
HNHM: Hungarian Natural History Musem (Budapest, Hungary)
MNHN: Muséum National d'Histoire Naturelle (Paris, France)
NHM: The Natural History Museum (London, UK)
NHMUK: when citing specimens deposited in the NHM
NMW: National Museum Wales (Cardiff, UK)
NZSI: National Zoological Collection of the Zoological Survey of India (when citing specimens deposited in the ZSI)
SMF: Senckenberg Forschungsinstitut und Naturmuseum (Frankfurt am Main, Germany)
UMZC: University Museum of Zoology (Cambridge, United Kingdom)
ZSI: Zoological Survey of India (Kolkata, India)

Taxon names. The proposed new genus *Parasinoennea* is attributed to Zhe-Yu Chen and Barna Páll-Gergely, thus the authorship of this new taxon name should be cited as *Parasinoennea* Z.-Y. Chen & Páll-Gergely in Páll-Gergely, Hunyadi, Grego, Sajan, Tripathy & Chen, 2020.

The proposed new genera *Platylennea*, *Pupennea*, and *Rowsonia* are attributed to the first author Barna Páll-Gergely, thus the authorship of these new taxon names should be respectively cited as *Platylennea* Páll-Gergely in Páll-Gergely, Hunyadi, Grego, Sajan, Tripathy & Chen, 2020, *Pupennea* Páll-Gergely in Páll-Gergely, Hunyadi, Grego, Sajan, Tripathy & Chen, 2020, and *Rowsonia* Páll-Gergely in Páll-Gergely, Hunyadi, Grego, Sajan, Tripathy & Chen, 2020.

Descriptions of the new species proposed herein are attributed to different authors. Páll-Gergely is responsible for *Diaphera polita*, new species; Páll-Gergely and Grego for *Diaphera turbanophora*, and Páll-Gergely and Hunyadi for *Sinoennea montawana*.

Thus, complete citations of the authors are, respectively, *Diaphera polita* Páll-Gergely in Páll-Gergely, Hunyadi, Grego, Sajan, Tripathy & Chen, 2020; *Diaphera turbanophora* Páll-Gergely & Grego in Páll-Gergely, Hunyadi, Grego, Sajan, Tripathy & Chen, 2020, and *Sinoennea montawana* Páll-Gergely and Hunyadi in Páll-Gergely, Hunyadi, Grego, Sajan, Tripathy & Chen, 2020.

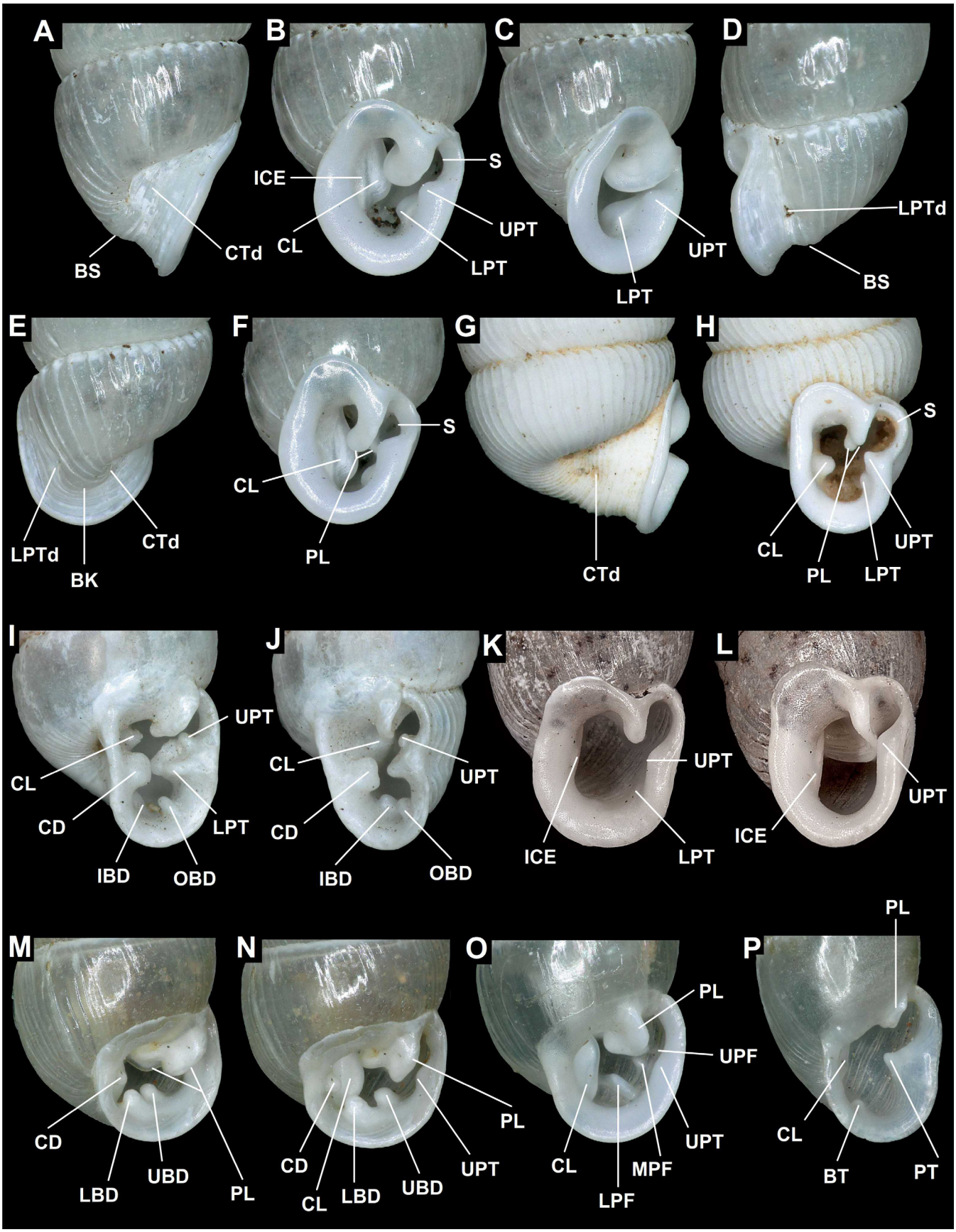

Fig. 1. Nomenclature of the apertural barriers. A–H, *Sinoennea*; I, J, *Pupennea*, new genus; K, L, *Sinoennea fartoidea*; M, N, *Platylennea*, new genus; O, *Rowsonia*, new genus; P, *Gulella* (*Huttonella*). Abbreviations: BK, basal keel; BS, basal swelling; BT, basal tooth; CD, columellar denticle; CL, columellar lamella; CTd, depression corresponding with the columellar lamella; IBD, inner basal denticle; ICE, inner columellar edge; LBD, lower basal denticle; LPF, lower palatal fold; LPT, lower palatal tooth; LPTd, depression corresponding with the lower palatal tooth; MPF, middle palatal fold; OBD, outer basal denticle; PL, parietal lamella; PT, palatal tooth; S, sinulus; UBD, upper basal denticle; UPF, upper palatal fold; UPT, upper palatal tooth.

RESULTS

Homology of diapherid apertural barriers. In almost all *Sinoennea* species (Fig. 1A–H, K, L) the apertural dentition is uniform, and the apertural barriers correspond with incisions of the outer shell surfaces. There are four main structures that are found in all *Sinoennea* species: parietal lamella, upper and lower palatal teeth, and columellar lamella. The parietal lamella is long, sometimes its inner end is not even visible. It is divided to internal and external portions that usually differ in orientation. The palatal wall is always with an upper palatal tooth that sits on the peristome edge and faces the tip of the outer end of the parietal lamella, and a lower palatal tooth that is situated deeper, and corresponds with an incision behind the palatal peristome. The lower palatal tooth shows a considerable variability in strength and position (close to the upper palatal tooth or very far from it). The upper and lower palatal teeth are often connected by a ridge. The columellar lamella is usually deeply situated, sometimes corresponding with a depression on the umbilical side. The only *Sinoennea* species lacking the columellar lamella is *S. fartoidea*. The slight thickening on the columella of that species (Fig. 1K, L) is probably homologous with the inner peristome edge of other *Sinoennea* species (Fig. 1B). A small basal tooth or other small denticles are sometimes present, for example in *S. angustistoma* Páll-Gergely, A. Reischütz & Maassen in Páll-Gergely, A. Reischütz, Maassen, Grego & Hunyadi, 2020, *S. ljudmilena* Páll-Gergely in Páll-Gergely, A. Reischütz, Maassen, Grego & Hunyadi, 2020, and *S. loeiensis* Tanmuangpak & S. Tumpeesuwan, 2015.

The peculiarities of *Pupennea*, new genus (Fig. 1I, J) are the following: (1) The palatal wall bears a bifurcated structure consisting of two parallel ridges entering the aperture from the peristome edge. The upper denticle of that structure is smaller, and it is probably homologous with the upper palatal tooth of *Sinoennea* species (which is the larger tooth of the two palatal teeth in that genus), whereas the lower denticle, which is larger in *Pupennea* than the upper one, is probably homologous with the lower palatal tooth of *Sinoennea*. (2) There are two denticles (inner basal denticle and outer basal denticle), which are absent in most *Sinoennea* species. (3) On the columellar side there are two teeth, one larger in the middle of the columella, and one smaller in the parieto-columellar corner. The homologies of these two teeth are questionable. The larger one is situated more anteriorly (closer to the peristome) than the columellar lamella of *Sinoennea*, whereas the smaller one is situated deeper, but higher in position (closer to the parietal wall). Thus, we hypothesise that the smaller, more upper situated tooth is homologous with the columellar lamella of *Sinoennea*.

Regarding the homology of the apertural barriers of *Platylennea*, new genus (Fig. 1M, N), we can have the following statements: (1) The thickening on the palatal lip is probably homologous with the upper palatal tooth of *Sinoennea* due to the same relative position and shape. The upper basal tooth of *Platylennea*, new genus, which is situated in a similar position as the lower palatal tooth of *Sinoennea*, may not be homologous with it, because in *Sinoennea* the upper and lower palatal teeth are usually in contact, whereas the upper basal denticle is in contact with the lower basal denticle in *Platylennea*. (2) The lower basal denticle has no homologous structure in most *Sinoennea* species, although some species in that genus have a basally situated tooth, which may be homologous with it. (3) The columellar denticle of *Platylennea*, new genus, is probably homologous with the denticle in the same position of some *Sinoennea* species, such as *Sinoennea bacca* Benthem Jutting, 1961, *Sinoennea chintamanensis* Tomlin, 1941 (see drawings in Benthem Jutting, 1961), and *S. loeiensis* (see Tanmuangpak et al., 2015). The columellar denticle is in the same position with that of *Pupennea*, new genus, but it is much larger in the latter genus.

Rowsonia, new genus (Fig. 1O) is obviously the closest relative of *Platylennea*, new genus, especially because of the geographic proximity. However, the homologies of the palatal barriers of those two genera are not self-explanatory. The open questions are the following: (1) Either the upper or the middle palatal fold of *Rowsonia*, new genus, may be homologous with the upper palatal tooth of *Sinoennea*. In the latter genus, the upper palatal tooth is usually short, and restricted to the peristome only, in some species it is elongated inside, and runs parallel with the parietal lamella. (2) The lower palatal fold of *Rowsonia*, new genus, may be homologous with lower palatal tooth of *Sinoennea*, and the lower or upper basal denticle of *Platylennea*, new genus. The uncertainty is caused by the different position of the two pairs. Namely, the upper and lower basal denticles of *Platylennea*, new genus, are situated closer to the columella than the lower and middle palatal folds of *Rowsonia*, new genus. In fact, the upper basal denticle of *Platylennea* sits in the same approximate position as the lower palatal fold of *Rowsonia*.

Gulella (*Huttonella*) (Fig. 1P) shares the following apertural barriers with diapherid genera: (1) The palatal tooth of *Gulella* (*Huttonella*) is the only tooth on the palatal wall of that genus. At first sight it looks similar to the upper palatal tooth of *Sinoennea*, which is the dominant (largest) palatal tooth of that genus. However, the palatal tooth of *Gulella* (*Huttonella*) is probably homologous with the lower palatal tooth of *Sinoennea*, because it is situated relatively far from the peristome edge, whereas the upper palatal tooth of *Sinoennea* sits exactly on the peristome edge. Moreover, the depression on the outer shell surface behind the peristome in *Sinoennea* corresponds with the lower palatal tooth. The homology of the palatal tooth of *Gulella* (*Huttonella*) in the genera *Platylennea*, new genus, and *Rowsonia*, new genus, is a matter of speculation (Table 1). (2) The basal tooth of *Gulella* (*Huttonella*) is probably homologous with the lower basal denticle of *Platylennea*, new genus, and with a lower probability the lower palatal fold of *Rowsonia*, new genus. The columellar lamella of *Gulella* (*Huttonella*) lies deep, away from the peristome, which suggests that it is homologous with the columellar lamella of diapherid genera.

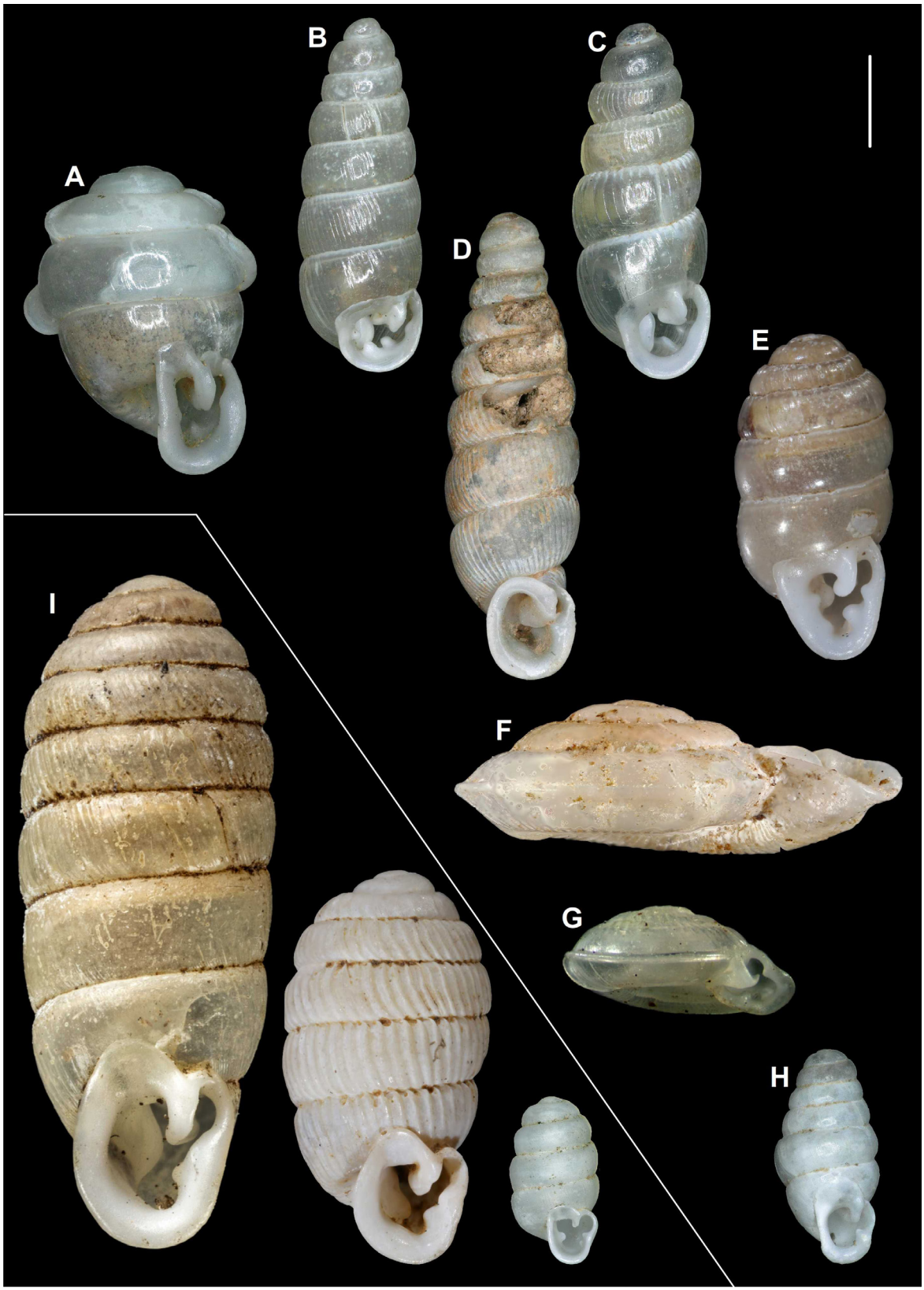

Fig. 2. Synoptic view of representatives of diapherid genera. A, *Bruggennea* Dance, 1972 (*Bruggennea* cf. *bongi* (Dance, 1970), NHMUK 20191106); B, *Platylennea* Páll-Gergely, new genus (*Platylennea subcostulata* (W.T. Blanford, 1881), NHMUK 1892.4.9.46–56); C, *Rowsonia* Páll-Gergely, new genus (*Rowsonia beddomei* (W.T. Blanford, 1881), NHMUK 1912.4.16.99); D, *Diaphera* Albers, 1850 (*Diaphera cylindrelloidea* (Stoliczka, 1871), NHMUK 1903.7.1.2856); E, *Parasinoennea* Z.-Y. Chen & Páll-Gergely, new genus (*Parasinoennea splendens* (Möllendorff, 1882) SMF 42775, lectotype); F, *Tonkinia* J. Mabille, 1887 (*Tonkinia mirabilis* Mabille, 1887, syntype, MNHN-IM-2000-30954); G, *Platycochlium* Laidlaw, 1950 (*Platycochlium saulae* Dance, 1970, NMW.Z.1970.001.00001); H, *Laoennea* Páll-Gergely in Páll-Gergely, Reischütz, Maassen, Grego & Hunyadi, 2020 (*Laoennea carychioides* Páll-Gergely, A. Reischütz & Maassen in Páll-Gergely et al., 2020, NHMW 113107, holotype); I, *Sinoennea* Kobelt, 1904 (*Sinoennea blanfordiana* Godwin-Austen, 1872, NHMUK 1903.7.1.2872, syntype, *Sinoennea strophiodes* (Gredler, 1881), SMF 42769, syntype, *Sinoennea infantilis* Páll-Gergely & Grego (HNHM 103485, holotype). Scale represents 1 mm.

TAXONOMY AND SYSTEMATICS

Superfamily Streptaxoidea Gray, 1860

Family Diapheridae Panha & Naggs in Sutcharit, Naggs, Wade, Fontanilla & Panha, 2010

Diapheridae Panha & Naggs in Sutcharit et al., 2010: 5.

Included genera. *Bruggennea* Dance, 1972, *Diaphera* Albers, 1850, *Laoennea* Páll-Gergely in Páll-Gergely et al., 2020, *Parasinoennea* Z.-Y. Chen & Páll-Gergely, new genus, *Platycochlium* Laidlaw, 1950, *Platylennea* Páll-Gergely, new genus, *Rowsonia* Páll-Gergely, new genus, *Sinoennea* Kobelt, 1904, *Tonkinia* J. Mabille, 1887 (see Fig. 2).

Remarks. Due to the lack of anatomical and molecular evidence, the inclusion of the genera other than *Diaphera* and *Sinoennea* in the Diapheridae is questionable (see Discussion).

Bruggennea Dance, 1972

Bruggennea Dance, 1972: 131.
Bruggennea — Richardson, 1988: 4.
Bruggennea — Schileyko, 2000: 800.

Type species. *Sinoennea laidlawi* Dance, 1970 by original designation.

Diagnosis. Shell ovoid or conical-ovoid, apertural dentition agree with that of *Sinoennea* (parietal lamella + columellar lamella, upper palatal tooth situated on peristome, lower palatal tooth situated deeper), varices (remaining expanded peristomes of juvenile shells) are imperfectly arranged in two rows on opposite side of the spire.

Distribution. Endemic to Borneo.

Remarks. The apertural dentition agrees with that of *Sinoennea*. Based on the original description (Dance, 1972), the distinction from *Sinoennea* is based on shell shape and sculpture, and the presence of varices. A more recent revision of this genus (Vermeulen, 2007) mentioned only the latter character as a distinctive feature. At the moment it is not possible to say more. *Bruggennea* is probably monophyletic due to the similar traits and geographic distribution, but the very diverse *Sinoennea* may not be monophyletic without *Bruggennea*. See Figs. 3 and 22G for comparison.

Diaphera Albers, 1850

Diaphera Albers, 1850: 210.
Diaphera — Zilch, 1960: 574.
Diaphera — Richardson, 1988: 5.
Diaphera — Schileyko, 2000: 800.

Type species. *Cylindrella cumingiana* L. Pfeiffer, 1845 (described in Philippi, 1845–1847) by monotypy.

Diagnosis. Shell shape variable (cylindrical to spindle-shaped and ovoid and elongate conical), last quarter to half whorl free (exceptionally not, see remarks), apertural dentition agree with that of *Sinoennea* (parietal lamella + columellar lamella, upper palatal tooth situated on peristome, lower palatal tooth situated deeper). See also remarks.

Distribution. Philippines, Borneo, northern Vietnam, South China (Guangxi), Cambodia, Thailand, southern Myanmar.

Remarks. This genus is recognised and defined on the basis of a free aperture and part of the last whorl, approximately a quarter to half whorl long. Given the patchy distribution of this genus, and the otherwise diverse shell characters, it is likely that the species classified here do not form a monophyletic group, and the free aperture has evolved multiple times independently (see also Discussion). *Diaphera turbanophora*, new species, does not have this character, but agrees with other *Diaphera* in other respects.

Other than the *Diaphera* species inhabiting Myanmar, the following species are known from the continent (= outside of the Philippines and Borneo): *D. densecostulata* (Möllendorff, 1901) (Vietnam), *D. prima* Panha in Sutcharit et al., 2010 (Thailand), *D. saurini* Benthem Jutting, 1962 (Cambodia). A new *Diaphera* species is being described from Chinese Guangxi Province (Z.-Y. Chen & Páll-Gergely, in press).

Diaphera brevicollis (W.T. Blanford, 1899)
(Fig. 4)

Ennea brevicollis W.T. Blanford, 1899: 768, pl. 50, figs. 23, 24.
Ennea (*Indoennea*) *brevicollis* — Kobelt, 1904b: 277, pl. 33, figs. 3, 4.
Ennea (*Diaphora*) *brevicollis* — W.T. Blanford & Godwin-Austen, 1908: 19, fig. 11.
Sinoennea brevicollis — Richardson, 1988: 155.

Type locality. "Ad Moulmein".

Material examined. Holotype (NHMUK 1888.12.4.590), Damathat, purchased from Theobald.

Remarks. The free last half whorl places this species in the genus *Diaphera*. The apertural barriers are similar to those of *D. cylindrelloidea*.

Diaphera cylindrelloidea (Stoliczka, 1871)
(Figs. 5, 6, 22F)

Ennea (*Huttonella*) *cylindrelloidea* Stoliczka, 1871: 171, pl. 7, fig. 4.
Ennea (*Huttonella*) *cylindrelloidea* — Nevill, 1878: 7.
Ennea (*Diaphora*) *cylindrelloidea* — Kobelt, 1904b: 122, pl. 18, fig. 3.
Ennea (*Diaphora*) *cylindrelloidea* — W.T. Blanford & Godwin-Austen, 1908: 18.
Diaphera cylindrelloidea — Richardson, 1988: 7.

Type locality. "Damotha, prope Moulmein; provincia Tenasserim".

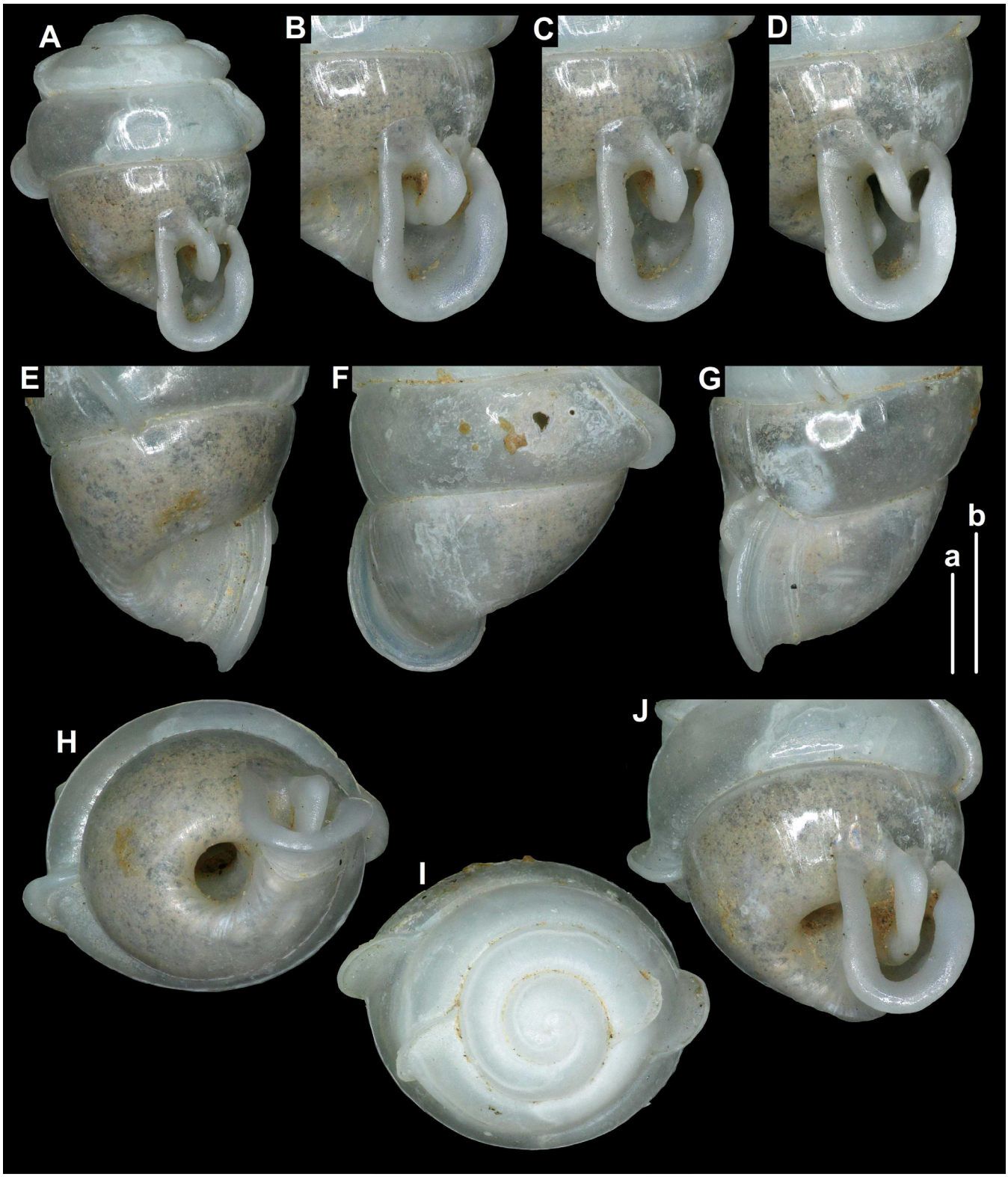

Fig. 3. Shell of *Bruggennea* cf. *bongi* (Dance, 1970). No locality, coll. Laidlaw, NHMUK 20191106. Both scales represent 1 mm; scale "a" refers to fig. A, scale "b" refers to figs. B–I.

Fig. 4. *Diaphera brevicollis* (W.T. Blanford, 1899) (Holotype, NHMUK 1888.12.4.590). Scale represents 1 mm. Photo: C. Sutcharit.

Material examined. Lectotype (hereby designated: 1 shell marked as "type", Fig. 5A–K) (NZSI M.16941/2), Damotha, Moulmain, coll. F. Stoliczka; 4 paralectotypes (3 adult + 1 juvenile shells [Fig. 5L–O]) (NZSI M.33966/9); 1 shell (NHMUK 1903.7.1.2856), Tenasserim, Moulmein, coll. Godwin-Austen (Fig. 6).

Remarks. Stoliczka (1871) stated in the original description that very few shells were found. Thus, although one shell in the ZSI was marked as type, it is not a holotype, but a syntype, as the other four shells deposited in the ZSI. The specimen we examined in the NHM may not be a type specimen, because the collector (Stoliczka) is not indicated, but it agrees with the syntypes *D. cylindrelloidea*, and it was collected at the type locality.

Nevill (1878) mentioned that the "type" of *E. cylindrelloidea* is deposited in the ZSI. However, this is not considered a valid lectotype designation.

Diaphera polita Páll-Gergely, new species
(Figs. 7, 22E)

Ennea (*Diaphora*) *cylindrelloidea* — W.T. Blanford & Godwin-Austen, 1908: 18.

Type material. Holotype (H: 4 mm, D: 1.3 mm) (NHMUK 1891.3.14.480), Damotha, Moulmein, coll. Hungerford.

Diagnosis. A small, smooth *Diaphera* species with relatively weak apertural barriers.

Description. Shell spindle-shaped, rather matte, colourless, although fresh specimens might have a light brownish colour, as indicated on the last whorl of the holotype. Shell wall slightly semi-transparent, nearly smooth, except for the last ca. half whorl. Some very fine spiral striation is visible on the teleoconch, although it does not consist of raised threads, but seemingly part of the lower shell layers. The last quarter whorl is very finely ribbed and free from the penultimate whorl. Ribs gradually disappearing towards the earlier whorls. Ribs low, fine, equally spaced, looking as if they were "pushed" backwards (= away from the aperture). Entire shell consisting of 7 whorls. Apex rounded, protoconch cylindrical, consisting of 3 whorls, smooth. Teleoconch gradually widening, the widest whorl being the penultimate one from standard apertural view. Therefore, the cylindrical protoconch is consciously narrower than the first and second teleoconch whorls. Suture somewhat deep, whorls rather bulging. Aperture subcircular with a rather wide sinulus. Apertural dentition 4-fold; parietal lamella moderately developed, moderately elevated, outer portion slightly bent in palatal direction, with a blunt end. Inner portion rather low, rounded, slightly bent towards columella. Sinulus rounded, opens slightly laterally, moderately isolated (tips of parietal lamella and upper palatal tooth situated rather far from each other). Palatal wall with a slight upper palatal tooth situated on the peristome, and a deeply situated, knob-like inner parietal tooth. There is seemingly no connection between the two parietal teeth. Columellar lamella situated rather close to the peristome, blunt, short, oblique to the shell axis. Peristome strongly thickened, expanded, and slightly reflected, weakest (thinnest) around the slightly laterally opening sinulus. Basal swelling not indicated. There is a small depression on the shell wall, behind the peristome, corresponding with the inner palatal tooth. Columellar lamella also corresponds with a slit-like, elongated depression that runs as a continuation of the umbilicus and stops before the peristome. Umbilicus absent due to the free last quarter whorl.

Differential diagnosis. *Diaphera seatoni* is far larger than the new species and has a strongly protruding aperture. Both *D. brevicollis* and *D. cylindrelloidea* are equally, strongly ribbed, whereas *S. polita*, new species, is smooth. Furthermore, *D. cylindrelloidea* has a more strongly protruding aperture, a more elevated parietal lamella, and a strong, sharp palatal ridge that connects the outer denticle, which is situated on the peristome, and the inner denticle.

Etymology. This new species is named after its smooth shell, which distinguishes it from its congeners.

Remarks. The holotype specimen was mentioned under *D. cylindrelloidea* by Blanford & Godwin-Austen (1908). They recognised that it was a new species, but refrained from describing it.

Diaphera seatoni (Beddome, 1891)

Ennea (*Huttonella*) *seatoni* Beddome, 1891: 315, pl. 29, figs. 15–19.
Ennea (*Diaphora*) *seatoni* — Kobelt, 1904b: 122, pl. 18, fig. 5.
Ennea (*Diaphora*) *seatoni* — W.T. Blanford & Godwin-Austen, 1908: 19.
Diaphera seatoni — Richardson, 1988: 15.

Type locality. "Tenasserim, limestone rocks east of the Mooley-it mountain near the Siam frontier".

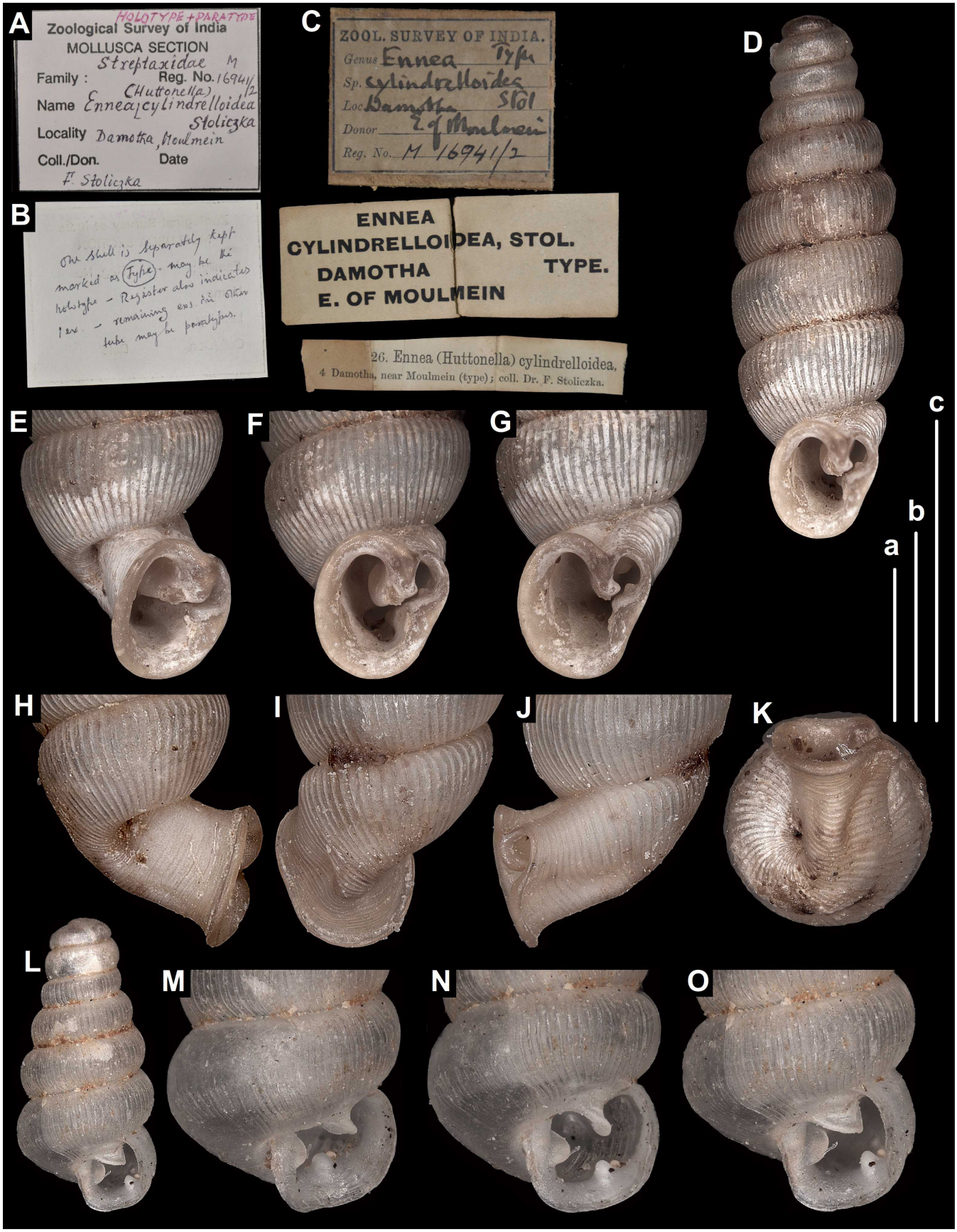

Fig. 5. Lectotype (D–K) and juvenile paralectotype (L–O) of *Diaphera cylindrelloidea* (Stoliczka, 1871) (NZSI M.16941/2). Scales represent 1 mm; scale "a" refers to figs. D and L, scale "b" refers to figs. E–K, and scale "c" refers to figs. M–O.

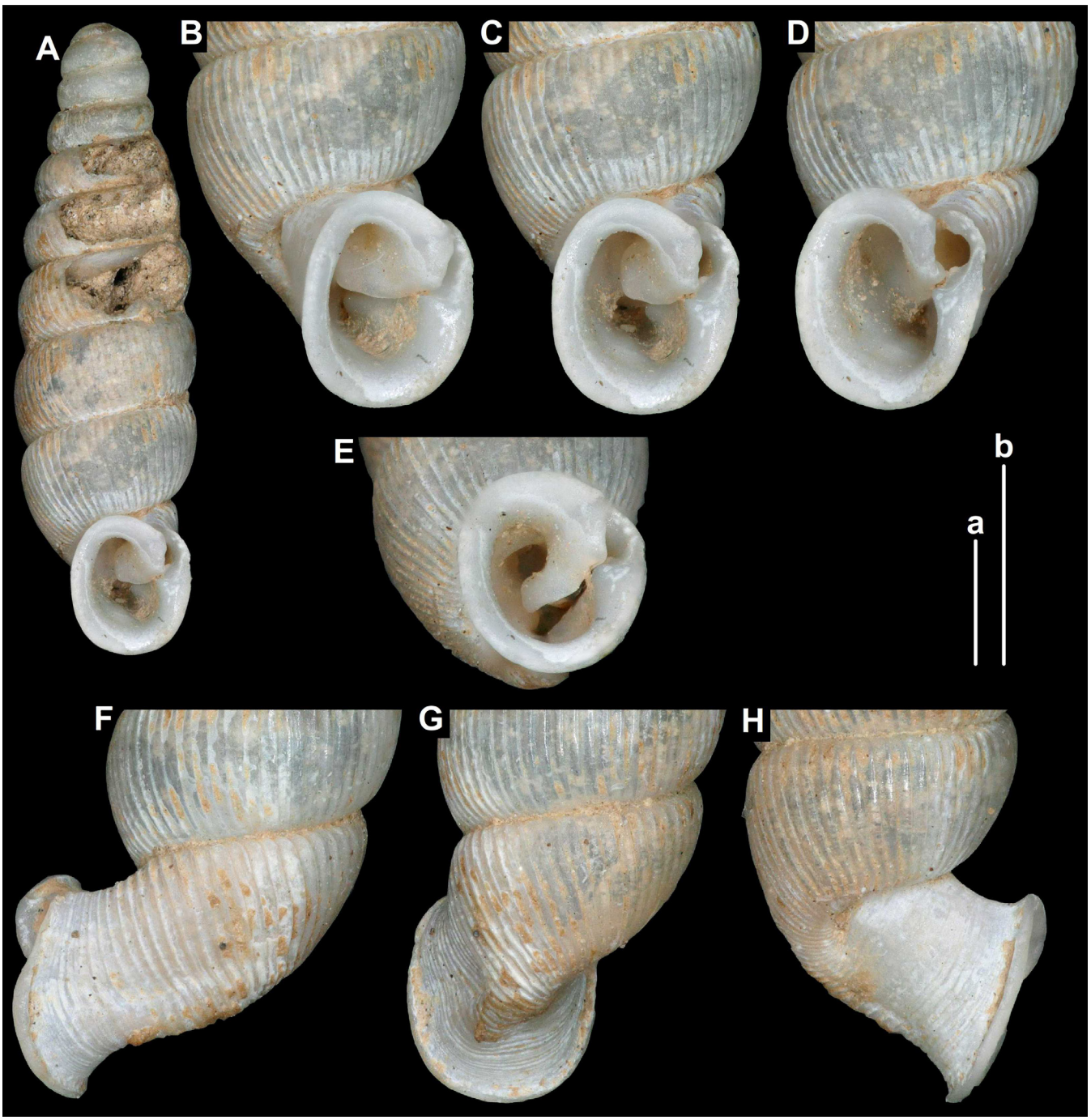

Fig. 6. *Diaphera cylindrelloidea* (Stoliczka, 1871), NHMUK 1903.7.1.2856.

Material examined. 1 shell, probable holotype (NHMUK 1912.4.16.102.), Mooley-it, foot of Tenasserim, coll. Beddome.

Remarks. The examined specimen is from the collection of its author and it is from the exact type locality. However, the other collector (Col. Seaton) is not mentioned on the label. Thus, it is considered to be a probable holotype (the description states that a single shell was available).

***Diaphera turbanophora* Páll-Gergely & Grego, new species**
(Fig. 8)

Material examined. Holotype (H: 3.9 mm, D: 1.3 mm) (HNHM 104436), Myanmar, Kayah State, Hpruso district, Maw Thi Do Village, Entrance of Phruno River Cave, 19°22.744′N, 97°2.570′E (locality code: JG102), coll. J. Grego, 12 December 2019.

Paratypes. 1 shell (H: 4.05 mm, D: 1.3 mm), same data as holotype; 2 apertural fragments (coll. JG), Myanmar, Kayah State, Hpruso district, Maw Thi Do, road towards Han Li Village, Rocks above bridge over Phruno River,

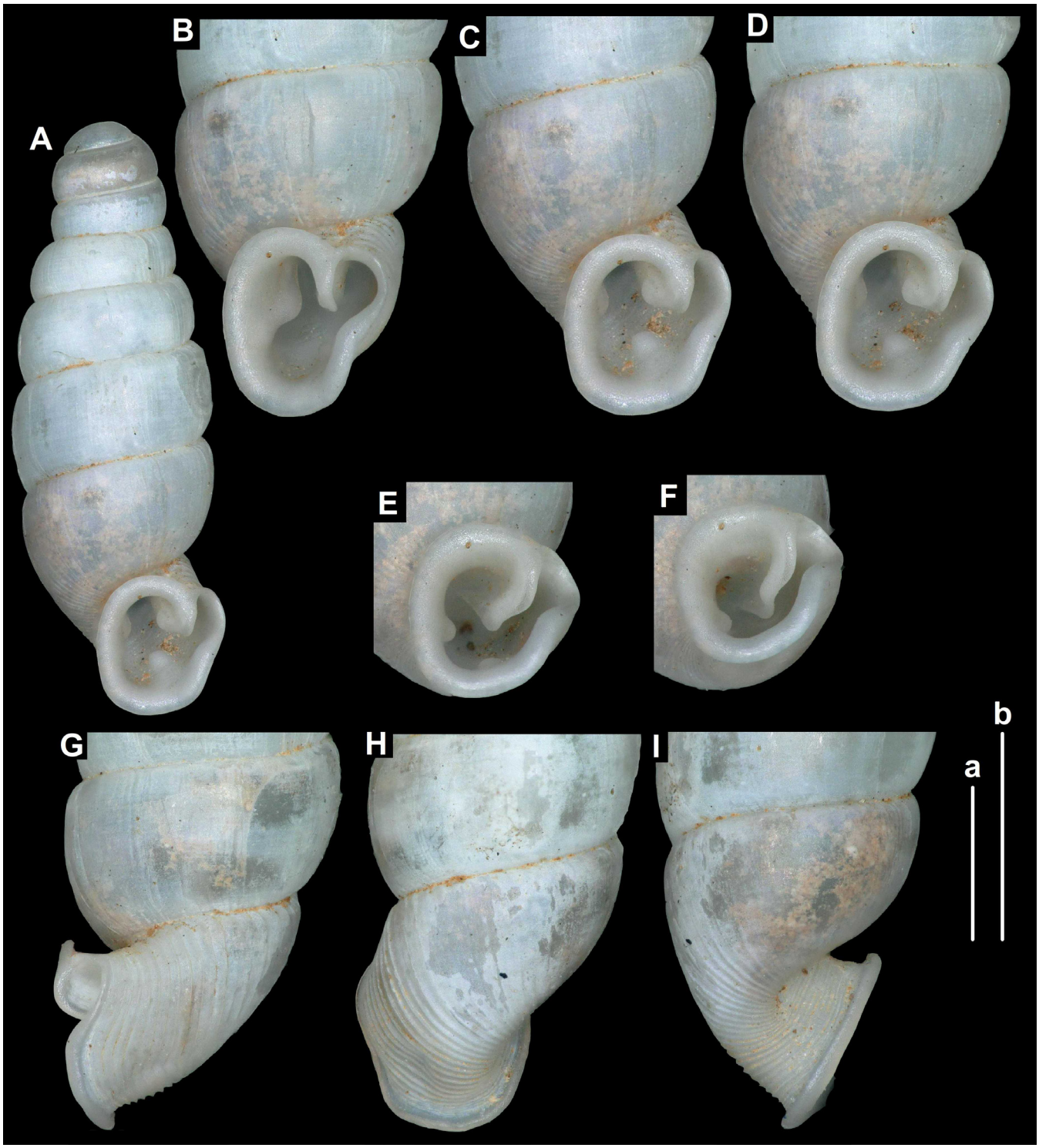

Fig. 7. *Diaphera polita* Páll-Gergely, new species, NHMUK 1891.3.14.480 (holotype).

19°23.011′N, 97°2.108′E (locality code: JG101), coll. J. Grego, 12 December 2019.

Diagnosis. A *Diaphera* species with a slender, finely ribbed, glossy shell, a constricted first whorl of teleoconch, a strong parietal lamella, a blade-like columellar tooth, a long upper palatal tooth, and a very small, deeply situated lower palatal denticle.

Description. Shell slender, glossy, off-white (colourless), semitransparent. Ribs very faint, low, equally spaced. Shell consisting of 6.25–6.5 whorls. Apex acutely pointed, protoconch moderately glossy, rather matte, consisting of 1.5 whorls, boundary of protoconch and teleoconch sharp, teleoconch sculpture glossier, slightly ribbed, its first whorl is constricted, therefore the third whorl from apertural view is narrower than the preceding. Last two whorls are the widest from apertural view. Suture not deep, whorls moderately bulging. Aperture suboval. Parietal callus rounded, thick, not "smeared" onto preceding whorl and only slightly extending beyond the suture. Apertural dentition 5-fold. Parietal lamella strongly developed, elevated, outer portion slightly bent in

Fig. 8. *Diaphera turbanophora* Páll-Gergely & Grego, new species (holotype). Scale represents 1 mm.

palatal direction, with a triangular end, inner portion also elevated, rounded, slightly bent towards columella. Sinulus rounded, opens slightly laterally, well isolated (tips of parietal lamella and upper palatal tooth situated close to each other). Palatal wall with a strongly elongated, sharp ridge that corresponds with the parietal lamella, a small, blunt denticle that is situated in the lower edge of the sinulus, and a very slight, blunt denticle that is situated deep inside, at the inner end of the elongated ridge. Out of these three structures, the first two (elongated ridge and denticle inside the sinulus) are probably homologous with the upper palatal tooth, whereas the deeply situated denticle is homologous with the lower parietal tooth. Columellar lamella deeply situated, sharp, lamella-like, vertical (parallel with shell axis). There is a blunt, inconspicuous swelling on the basal side some distance inward from the peristome. Peristome strongly thickened and expanded, slightly reflected. Basal swelling slight, situated a relatively large distance from peristome. Depression anterior to basal swelling on the outer side relatively deep, slightly elongated (corresponding with an elongated ridge on the palatal side). Inner side without depression; umbilicus entirely closed.

Differential diagnosis. The most similar species is *Diaphera cylindrelloidea* (Stoliczka, 1871), which is larger and has a protruding, more circular aperture. The formation and arrangement of the apertural barriers of the two species are strikingly similar. The only difference we found was the parietal lamella, which is of equal height in *D. cylindrelloidea*, but slightly lowered just behind its outer end in the new species.

Diaphera seatoni Beddome, 1891 is much larger (ca. 1 cm in height), has a protruding aperture, much deeper suture, and different apertural barriers. Namely, anterior to the columellar tooth there is an oblique ridge that descends from near the columellar-parietal angle of the aperture towards the deep basal part, and consists of two elongated knobs.

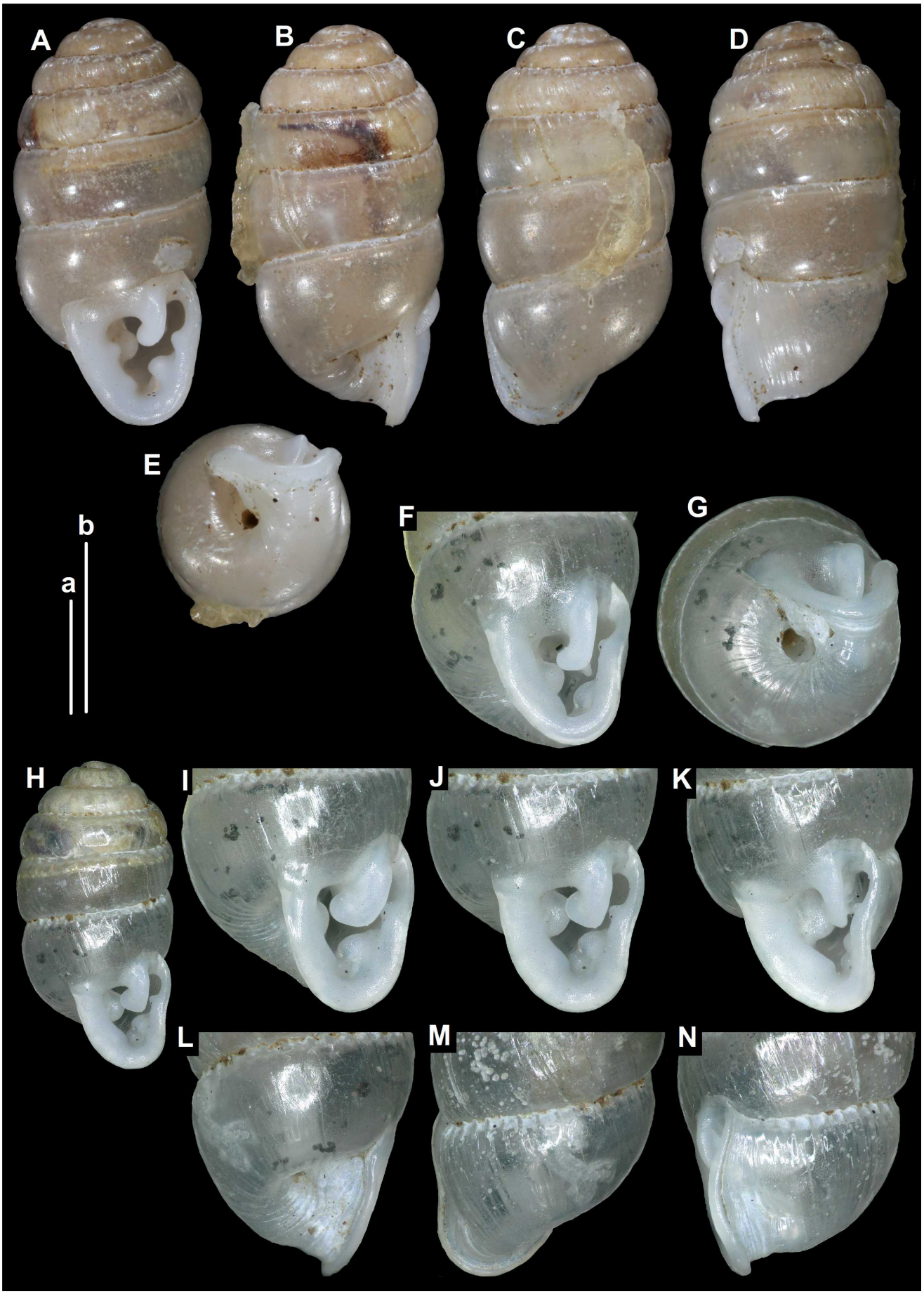

Fig. 9. Shells of *Parasinoennea*, new genus. A–E, *Parasinoennea splendens* (Möllendorff, 1882) SMF 42775 (lectotype); F–N, *Parasinoennea ovulum* (Bavay & Dautzenberg, 1912), MNHN-IM-2000-30970 (syntype). Both scales represent 1 mm; scale "a" refers to figs. A–E and H, scale "b" refers to figs. F–G and I–N.

Furthermore, the outer (upper) palatal tooth is not in contact with the deeply situated lower palatal tooth, which, in this case, consists of two small blunt knobs.

Sinoennea woodthorpei, which was described from Fort Stedman (= Maing Thauk), not far from the type locality of the new species, has elongate-ovoid shape with regular ribbing.

Etymology. The first whorl of the teleoconch is constricted compared with the protoconch. Therefore, the apex looks like a head wearing a turban.

Remarks. The *Diaphera* species of Myanmar have apertures that protrude straight ahead, and are not distorted downwards from apertural view, as in other *Diaphera* species. This suggests that the free last whorl has probably been developed more than once during the evolution of the Diapheridae, and the *Diaphera* species of Myanmar are likely closer relatives of *Sinoennea* of the region than the *Diaphera* species of the Philippines. However, until more solid evidence is provided, we maintain these taxa in *Diaphera*.

The body whorl of *Diaphera turbanophora*, new species, is not free from the penultimate whorl, but the species is classified in the genus *Diaphera* due to its similarity with other *Diaphera* species of Myanmar.

Laoennea Páll-Gergely in Páll-Gergely, Reischütz, Maassen, Grego & Hunyadi, 2020

Laoennea Páll-Gergely in Páll-Gergely et al., 2020: 2.

Type species. *Laoennea carychioides* Páll-Gergely, A. Reischütz & Maassen in Páll-Gergely, Reischütz, Maassen, Grego & Hunyadi, 2020, by original designation.

Diagnosis. Shell minute, elongate with wide penultimate and conspicuously narrow last whorl. Swelling behind peristome absent, parietal lamella nearly continuous, long. Palatal wall with a single pointed upper palatal tooth.

Distribution. Known only from Laos.

Platycochlium Laidlaw, 1950

Platycochlium Laidlaw, 1950: 370.
Platycochlium — Zilch, 1960: 560.
Platycochlium — Richardson, 1988: 243.
Platycochlium — Schileyko, 2000: 785.

Type species. *Platycochlium sarawakense* Laidlaw, 1950, by original designation.

Diagnosis. "Shell colourless, translucent when fresh, later white, low conical to almost discoidal in frontal view. Whorls with 4–5 varices next to the peristome (approximately one per ⅓–½ whorl in the last whorls), each varix preceded by a number of ribs, the ribs crossed by a fine, concentric striation. Umbilicus wide, orbicular to elliptic. Aperture subtriangular with the parietal side concave. Peristome reflected, with a knob-like thickening on the palatal side, above which is a shallow sinus. Teeth four: one angularis, a sinuous lamella starting deep inside and ending in a thick knob; one short basalis; two deeply set palatales, the upper one hidden behind the palatal swelling of the peristome." (Vermeulen, 1991).

Distribution. Endemic to Borneo.

Parasinoennea Z.-Y. Chen & Páll-Gergely, new genus

Type species. *Ennea splendens* Möllendorff, 1882 (Fig. 9A–E).

Diagnosis. Shell ovate, glossy; aperture triangular, adnate to the penultimate whorl.

Differential diagnosis. The shell shape of *Parasinoennea*, new genus, is oval, whereas it is usually elongated and cylindrical in *Sinoennea*. The teleoconch of *Parasinoennea* is usually smooth, sometimes ornamented by low, blunt ribs, but is always glossy. In contrast, the ribs of *Sinoennea* are usually sharp and elevated, and the shell has a less glossy appearance. The main difference is in the aperture shape, which is triangular (in some species the palato-basal part distorted laterally) in *Parasinoennea*, new genus, but elongated oval and cylindrical in *Sinoennea*. The aperture is adnate (i.e., the parietal callus is attached to the penultimate whorl) in *Parasinoennea*, new genus, and the parietal callus is always clearly separated from the penultimate whorl in *Sinoennea*. The apertural dentition is not clearly different, although *Parasinoennea*, new genus, often possesses two tubercles (denticles) on the columellar peristome (anterior to the columellar lamella), which has not been observed in any *Sinoennea* species to our knowledge. The upper denticle is probably homologous with the upper denticle of *Pupennea*, new genus, and *Platylennea*, new genus.

Included species. *Parasinoennea demangei* (Bavay & Dautzenberg, 1912) (northern Vietnam), *P. formica* (Bavay & Dautzenberg, 1912) (northern Vietnam), *P. splendens splendens* (Möllendorff, 1882) (Guangdong, China), *P. splendens hongkongensis* Möllendorff, 1885 (Hongkong, China), *P. ovulum* (Bavay & Dautzenberg, 1912) (northern Vietnam) (Figs. 9F–N, 22H).

Etymology. The Greek prefix para- (παρά, meaning beside, next to, against, etc.) is attached to *Sinoennea* to show that it is separated from that genus. Grammatical gender: feminine.

Distribution. South China (Guangxi, Guangdong, Hong Kong, Jiangxi) and northern Vietnam (Fig. 10).

Remarks. *Sinoennea longtanensis* S. Ouyang, X.-M. Liu & X.-P. Wu, 2012 does not differ from typical *P. splendens* (examined material: SMF 42775, lectotype, see Fig. 9A–E) in any traits. Therefore, we considered it a synonym of the latter.

Platylennea Páll-Gergely, new genus

Type species. *Ennea subcostulata* W.T. Blanford, 1881.

Diagnosis. Shell reminiscent of members of Aciculidae (glossy, elongate conical); umbilicus entirely closed. Peristome discontinuous, parietal callus only indicated as transparent calcareous layer. Parietal lamella well-developed, complex, long, running deep inside, its outer end bent towards the palatal wall, and also has a blunt projection in the other side, resulting in a bifurcated outer end. Palatal wall with a tiny upper parietal denticle that is situated on the peristome. There are two basal denticles (upper and lower basal denticle) of comparable size, sometimes connected with a ridge. Lower basal denticle situated on or very close to the peristome, whereas the upper basal denticle (the one situated closer to the palatal tooth) situated somewhat deeper. Columellar lamella well-developed, semilunar, sharp, blade-like, slightly oblique to the shell axis. There is an additional tiny, blunt denticle (columellar denticle) on the columellar lip. No deeply-situated folds or denticles present. See Fig. 1I, J for explanation.

Differential diagnosis. *Platylennea*, new genus, differs from *Ennea* based on the conical (not ovoid) shell shape, the long and complicated parietal lamella, the absence of deeply situated plicae and the strong columellar and basal/lower parietal barriers.

This new genus mainly differs from *Rowsonia*, new genus, in the arrangement of the apertural barriers. Namely, *Platylennea*, new genus, has two basal denticles situated close to the peristome edge, whereas *Rowsonia*, new genus, has three horizontal, deeply situated palatal folds (for information on their homologies, see Results and Table 1). Furthermore, *Platylennea* possesses a small columellar denticle anterior to the columellar lamella, and the prominent parietal lamella is bifurcated near/at its outer end.

Platylennea, new genus, has an elongate conical shell shape and a complicated, long parietal lamella, whereas the shell of *Pupennea*, new genus, is ovoid and its parietal lamella is short. Furthermore, the latter genus possesses a strongly developed, complex structure on the parietal side, in the position of the upper parietal tooth of *Platylennea*, new genus.

Sinoennea species are mostly elongate ovoid and cylindrical, with ovoid-rectangular aperture and well-developed callus. In *Sinoennea* there is an upper and lower palatal tooth which are in contact with each other. In contrast, *Platylennea*, new genus, has an upper palatal tooth and two basal denticles. The upper basal denticle of *Platylennea*, new genus, is probably homologous with the lower palatal denticle of *Sinoennea*. Furthermore, *Sinoennea* has a depression on the lateral side behind the reflected peristome corresponding with the lower palatal denticle. In the absence of a lower palatal denticle in corresponding position, there is no such depression behind the peristome of *Platylennea*, new genus.

Included species. *Platylennea exilis* (W.T. Blanford, 1881), *P. levis* (Peile, 1935), *P. macrodon* (W.T. Blanford, 1881), and *P. subcostulata* (W.T. Blanford, 1881).

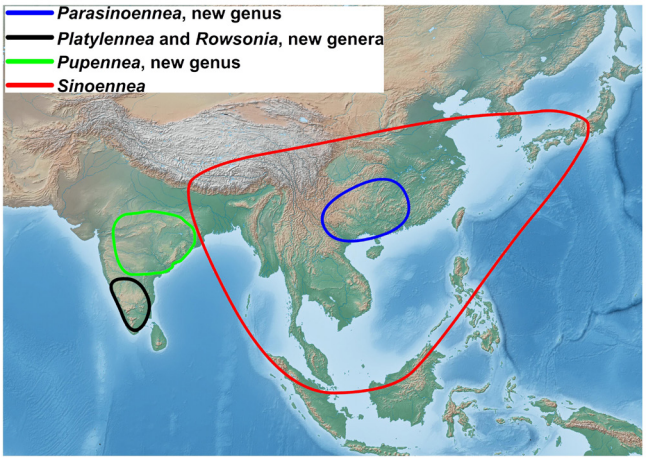

Fig. 10. Distribution of *Parasinoennea*, new genus, *Sinoennea* Kobelt, 1904, *Pupennea*, new genus, *Platylennea*, new genus, and *Rowsonia*, new genus.

Etymology. The name *Platylennea* is the combination of the generic names *Platyla* Moquin-Tandon, 1856, which the new genus resembles, and *Ennea* H. Adams & A. Adams, 1855, which is a generic name that used to be widely used for high-spired Streptaxidae. Grammatical gender: feminine.

Distribution. Southern India (Fig. 10).

Platylennea exilis (W.T. Blanford, 1881)

Ennea exilis W.T. Blanford, 1881: 207, pl. 2, fig. 14 (lower).
Ennea (*Sinoennea*) *exilis* — Kobelt, 1904b: 155, pl. 20, fig. 17.
Ennea (*Huttonella*) *exilis* — W.T. Blanford & Godwin-Austen, 1908: 22.
Gulella exilis — Richardson, 1988: 79.
Gulella (*Huttonella*) *exilis* — Ramakrishna et al., 2010: 193.
Sinoennea exilis — Raheem et al., 2014: 144, fig. 94A, B.

Type locality. "In montibus 'Balarangam' dictis provinciae Mysore in India Meridionali".

Material examined. Photos of the lectotype and a paralectotype were examined in Raheem et al. (2014).

Remarks. This species clearly fits in *Platylennea*, new genus, based on the general shell and aperture shape, the bifurcated parietal lamella, the two basal denticles situated close to the peristome edge, and the presence of a small columellar denticle anterior to the columellar lamella.

Platylennea levis (Peile, 1935)
(Fig. 11)

Sinoennea levis Peile, 1935: 382, fig. 1.
Sinoennea levis — Richardson, 1988: 160.

Type locality. "S. India".

Material examined. Adult holotype (mentioned as "the type" in the original description) + juvenile paratype (NHMUK 1935.7.10.1–2), S. India, coll. Fulton.

Fig. 11. A, *Platylennea levis* (Peile, 1935), NHMUK 1935.7.10.1–2 (holotype). Scale represents 1 mm.

Remarks. This species clearly fits in *Platylennea*, new genus, based on the general shell and aperture shape, the bifurcated parietal lamella, the two basal denticles situated close to the peristome edge, and the presence of a small columellar denticle anterior to the columellar lamella.

***Platylennea macrodon* (W.T. Blanford, 1881)**

Ennea macrodon W.T. Blanford, 1881: 205, pl. 2, fig. 15.
Ennea (*Indoennea*) *macrodon* — Kobelt, 1904b: 156, pl. 20, fig. 18.
Ennea (*Huttonella*) *macrodon* — W.T. Blanford & Godwin-Austen, 1908: 21.
Gulella macrodon — Richardson, 1988: 99.
Gulella (*Huttonella*) *macrodon* — Ramakrishna et al., 2010: 193.
Sinoennea macrodon — Raheem et al., 2014: 144, fig. 94C.

Type locality. "Apud Pykara in summos montes 'Nilgiri' dictos India Meridionalis".

Material examined. Lectotype, designated in Raheem et al. (2014) (NHMUK 1899.6.29.2), Nilgiris.

Remarks. This species clearly fits in *Platylennea*, new genus, based on the general shell and aperture shape, the bilobed parietal lamella (not as clearly bifurcated as in other *Platylennea* species), the two basal denticles connected with a ridge and situated relatively close to the peristome edge, and the indication of a columellar denticle anterior to the columellar lamella.

***Platylennea subcostulata* (W.T. Blanford, 1881)**
(Figs. 12A–I, 22C)

Ennea subcostulata W.T. Blanford, 1881: 206, pl. 2, fig. 14.
Ennea (*Indoennea*) *subcostulata* — Kobelt, 1904b: 159, pl. 20, fig. 16.
Ennea (*Huttonella*) *subcostulata* — W.T. Blanford & Godwin-Austen, 1908: 21.
Indoennea subcostulata — Peile, 1929a: fig. 4 (drawings show the dentate juvenile shell).
Gulella subcostulata — Richardson, 1988: 124.
Gulella (*Huttonella*) *subcostulata* — Ramakrishna et al., 2010: 194.
Sinoennea subcostulata — Raheem et al., 2014: 146, fig. 95E.

Type locality. "In montibus 'Shevrai' vel 'Shevroy' dictis, haud procul ad urbe Salem, Indiæ meridionalis."

Material examined. Lectotype, designated in Raheem et al. (2014) (NHMUK 1906.1.1.954), Shevroy Hills, coll. W. Blanford; 11 shells (NHMUK 1892.4.9.46–56), Shevaroy Hills, S. India, at 5,000', coll. Henderson.

Remarks. This species clearly fits in *Platylennea*, new genus, based on the general shell and aperture shape, the bifurcated parietal lamella, the two basal denticles situated close to the peristome edge, and the presence of a small columellar denticle anterior to the columellar lamella.

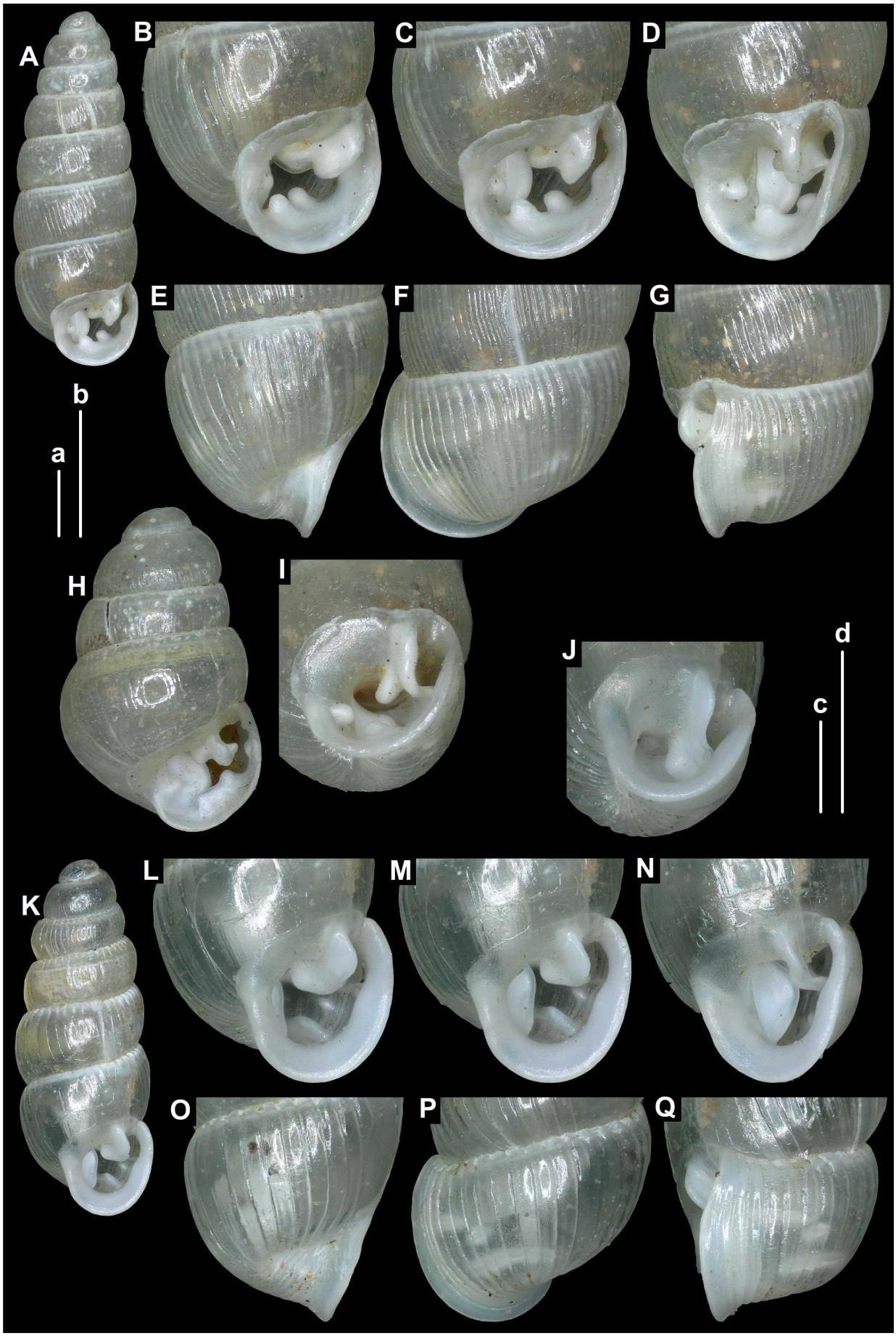

Fig. 12. A–G, *Platylennea subcostulata* (W.T. Blanford, 1881), NHMUK 1892.4.9.46–56, specimen1; H–I, NHMUK 1892.4.9.46–56, specimen2; J–Q, *Rowsonia beddomei* (W.T. Blanford, 1881), NHMUK 1912.4.16.99. All scales represent 1 mm; scale "a" refers to fig. A, scale "b" refers to figs. B–I, scale "c" refers to fig. K, scale "d" refers to figs. L–Q.

Pupennea Páll-Gergely, new genus

Type species. *Pupa planguncula* Benson, 1863.

Diagnosis. As in the type species.

Differential diagnosis. For homologies of apertural denticles, see Table 1. *Pupennea*, new genus, differs from all *Sinoennea* species by the short parietal lamella, which is long and consists of two portions even in small-shelled members of *Sinoennea*. The columellar lamella is pointed, small, and situated in the parieto-columellar corner. In contrast, most *Sinoennea* species have a deeply-situated, blade-like columellar lamella. Anterior of the columellar lamella there is a strongly developed columellar denticle, which is not present in *Sinoennea*. *Pupennea*, new genus, possesses an inner and outer basal denticle. In a few *Sinoennea* species one basal denticle is present, which is probably homologous with one of the basal denticles of *Pupennea*, new genus. The parietal callus is only indicated in *S. planguncula*, but well-developed in most *Sinoennea* species.

Platylennea, new genus, is similar to *Pupennea*, new genus, in possessing both a columellar lamella and a columellar denticle. Furthermore, two basally situated teeth are found in both genera. However, the homologies of the latter structures are questionable (see Table 1), because in *Platylennea* the lower basal denticle is situated closer to the columella and to the peristome, whereas in *Pupennea* the tooth situated closer to the columella (inner basal denticle) is the one, which is situated deeper in position. Further differences between the two genera are in the shell shape (ovoid in *Pupennea*, new genus, and elongate conical in *Platylennea*, new genus), the much shorter parietal lamella in *Pupennea*, and the more complex palatal teeth.

Rowsonia, new genus, has a well-developed parietal lamella, lacks a columellar denticle, and in the position of the upper palatal tooth there is only a slight thickening (a complex bilobed tooth in case of *Pupennea*, new genus). Furthermore, the deeply situated palatal folds of *Rowsonia* are absent in *Pupennea*.

The strongly developed upper parietal tooth, corresponding with a depression on the outer side of the palatal wall suggests that *S. planguncula* is related to *Sinoennea* instead of *Rowsonia*, new genus, and *Platylennea*, new genus.

Included species. *Pupennea planguncula* (Benson, 1863).

Etymology. The name *Pupennea* is the combination of the generic names *Pupa*, which was often used to be used for ovoid shells in the 19th century, and *Ennea* H. Adams & A. Adams, 1855, which is a generic name that used to be widely used for high-spired Streptaxidae. Grammatical gender: feminine.

Distribution. Central India (Fig. 10).

Pupennea planguncula (Benson, 1863)

(Figs. 13, 22D)

Pupa planguncula Benson, 1863: 426.
Ennea (*Huttonella*) *planguncula* — Nevill, 1878: 7.
Ennea stenostoma W.T. Blanford, 1881: 208, pl. 2, fig. 17.
Ennea stenostoma var. *minor* W.T. Blanford, 1881: 208, pl. 2, fig. 16.
Ennea (*Indoennea*?) *stenostoma* — Kobelt, 1904b: 157, pl. 20, fig. 19.
Ennea (*Huttonella*) *planguncula* — W.T. Blanford & Godwin-Austen, 1908: 23. (considered *Ennea stenostoma* as synonym)
Ennea planguncula — Richardson, 1988: 25.
Gulella (*Huttonella*) *planguncula* — Ramakrishna et al., 2010: 195.
Sinoennea planguncula — Raheem et al., 2014: 145, fig. 95A, B.

Type locality. "in regione Orissæ et prope fluvium Nerbuddæ" (*S. planguncula*); "In montibus 'Galconda' dictis, haut procul ad urbe Vizagapatam" (*S. stenostoma*); "In montibus haut procul ad urbe Karnul (Karnool) Indiæ meridionalis" (*S. stenostoma* var. *minor*).

Material examined. Lectotype (designated by Raheem et al. 2014, UMZC I.103310.B); 1 shell (NHMUK 1906.1.1.292), no locality, coll. W.T. Blanford, figured in FBI [Fauna of British India].

Diagnosis. Peristome discontinuous, parietal callus only indicated with a very slight calcareous layer. Basal swelling only slight. The depression on the outer side of the palatal wall is deep and corresponds with the large parietal tooth (lower parietal tooth). Parietal lamella elevated, well-developed, but short, with no inner and outer parts distinguishable. Palatal wall with a strongly developed bifurcated structure consisting of two parallel ridges entering the aperture from the peristome edge, and an incision between them which faces the tip of the parietal lamella. The upper denticle of this structure is probably homologous with the upper palatal tooth, whereas the lower is the lower palatal tooth. There is an additional, relatively slender, short, blunt tooth between the basal area and the complicated palatal tooth (outer basal denticle on Fig. 1). Another blunt basal tooth (inner basal tooth on Fig. 1) is situated in some distance from the lip, and relatively close to the columellar denticle. Columellar denticle large but blunt, situated on the columellar lip. Columellar lamella pointed, small, situated behind and little higher in position than the columellar denticle (in the parieto-columellar corner).

Rowsonia Páll-Gergely, new genus

Type species. *Ennea beddomei* W.T. Blanford, 1881 (Fig. 12J–Q).

Diagnosis. Shell small to large, smooth to regularly ribbed, slender conical. Parietal callus well-developed to weak. Basal swelling not developed. Parietal lamella elongated inside, outer end usually straight, outer portion curves towards palatal wall. Inner portion curves towards columella. Palatal wall with an upper palatal tooth that faces the curved parietal lamella. There are two to three deeply situated, elongated additional folds (upper, middle, and lower palatal folds). Columellar lamella well-developed, sharp, oblique to shell axis. See Fig. 1O for explanation.

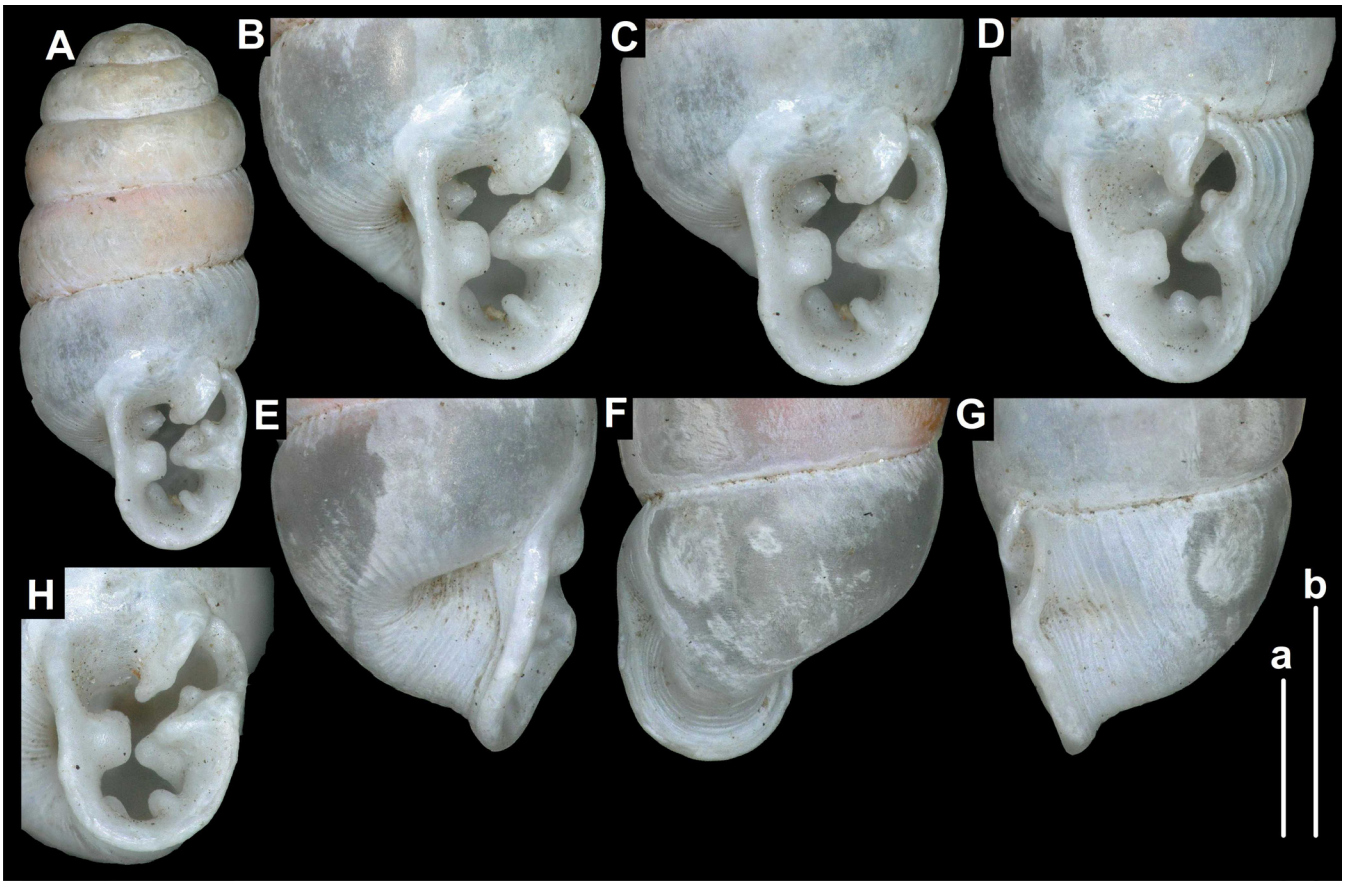

Fig. 13. *Pupennea planguncula* (Benson, 1863), NHMUK 1875.3.6.39. Both scales represent 1 mm; scale "a" refers to fig. A, scale "b" refers to figs. B–I.

Differential diagnosis. *Rowsonia*, new genus, differs from *Ennea* (compared only with the type species) in the following characters: the shell shape of the new genus is conical, whereas it is ovoid in *Ennea*; the parietal lamella is short in *Ennea*, inner and outer portions of different orientation cannot be recognised; columellar lamella of *Ennea* is weak, low, and not visible from straight view to the aperture; the deeply situated folds are much longer than those of *Rowsonia*, new genus, and they correspond with grooves on the dorsal ("neck") region.

Pupennea, new genus is ovoid, possesses two teeth on the columellar side (columellar lamella and denticle), has a shorter parietal lamella, has a complex structure consisting of the upper and lower parietal teeth, and lacks deeply situated palatal folds.

Sinoennea species are usually elongate ovoid and cylindrical in shell shape, lack any deeply situated parietal/basal folds, usually have a prominent basal swelling and there is a depression that corresponds with the upper palatal tooth. See under *Platylennea*, new genus.

Included species. *Rowsonia beddomei* (W.T. Blanford, 1881), *R. canarica* (W.T. Blanford, 1869), *R. pirriei* (L. Pfeiffer, 1855), *R. sculpta* (W.T. Blanford, 1869), and *R. turricula* (W.T. Blanford, 1899).

Etymology. This genus is dedicated to and named after Ben Rowson (National Museum of Wales), a specialist of the Streptaxoidea. Grammatical gender: feminine.

Distribution. Southern India (Fig. 10).

Remarks. The most closely related genus is probably *Platylennea*, new genus, which also inhabits southern India. The distinction of the two groups is clear, and thus, these two groups should be separated as distinct genera. However, the morphological diversity of *Sinoennea* is still larger than the difference between *Platylennea*, new genus and *Rowsonia*, new genus.

***Rowsonia beddomei* (W.T. Blanford, 1881)**
(Figs. 12J–Q, 22B)

Ennea beddomei W.T. Blanford, 1881: 210.
Ennea beddomii (sic) — W.T. Blanford, 1899: 770, pl. 50, figs. 20, 21.
Ennea (*Indoennea*) *beddomei* — Kobelt, 1904b: 161.
Ennea (*Huttonella*) *beddomii* (sic) — W.T. Blanford & Godwin-Austen, 1908: 23.
Sinoennea beddomei — Richardson, 1988: 154.
Gulella (*Huttonella*) *beddomei* — Ramakrishna et al., 2010: 192.
Sinoennea beddomei — Raheem et al., 2014: 143, fig. 93D, E.

Type locality. "In montibus 'Sivagiri' dictis Indiæ meridionalis."

Material examined. Lectotype, designated in Raheem et al. (2014) (NHMUK 1875.03.06.75/1) + 3 paralectotypes (NHMUK 1876.3.6.75), Sivagherry Hills, India; 2 syntypes of "var. *minima*" (NHMUK 1906.1.1.952), Sivagiri Hills, Tinevelly, 4,000'; 4 shells (NHMUK 1912.4.16.99), Sivagiri, Shevroys, S. India, coll. Col. R. Beddome.

Remarks. Aperture adnate, parietal callus indicated by a colourless calcareous layer. No swelling visible behind peristome. Outer part of parietal lamella slightly curved towards the palatal wall; deeper inside the curve is as strong as if it were broken at a right angle. On the other side of this strongly curved portion there is a slight projection into the other (parietal) direction. Columellar lamella blade-like. Palatal wall with three elongated folds: upper fold facing the curved parietal lamella, middle fold much shorter, situated deeper, slightly below the strongly curved part of the parietal lamella, lower fold stronger (more elevated) than the upper and middle ones, situated between the middle palatal fold and the columellar lamella.

Rowsonia canarica (W.T. Blanford, 1869)

Ennea canarica W.T. Blanford 1869: 142, pl. 16, fig. 11.
Ennea canarica — W.T. Blanford, 1881: 210.
Ennea canarica — W.T. Blanford, 1899: 770, pl. 50, fig. 25.
Ennea (*Indoennea*) *canarica* — Kobelt, 1904b: 161.
Ennea (*Huttonella*) *canarica* — W.T. Blanford & Godwin-Austen, 1908: 23.
Sinoennea canarica — Richardson, 1988: 155.
Gulella (*Huttonella*) *canarica* — Ramakrishna et al., 2010: 193.
Sinoennea canarica — Raheem et al., 2014: 144, fig. 93F.

Type locality. "In Provincia South Canara, haud procul a littore occidentali Indiæ."

Material examined. Holotype, (NHMUK 1875.03.06.74), South Canara, obtained by exchange with Lt. Col. Beddome; 4 shells (NHMUK 1912.4.16.98), S. Canara, coll. Beddome.

Remarks. Aperture adnate, parietal callus indicated by a colourless calcareous layer. No swelling visible behind peristome. Outer part of parietal lamella rather straight, inner part curved towards the parietal region. At the border of the outer and inner parts there is a small knob-like projection on the palatal side of the lamella. Palatal wall with three elongated folds: upper one facing the curved parietal lamella, middle one situated deeper, lower fold stronger (more elevated) than the upper and middle ones, situated between the middle palatal fold and the columellar lamella. Columellar lamella blade-like.

Rowsonia pirriei (L. Pfeiffer, 1855)

Pupa pirriei L. Pfeiffer, 1855: 295.
Ennea (*Huttonella*) *pirriei* — Nevill, 1878: 7.
Ennea (*Sinoennea*) *pirriei* — Kobelt, 1904b: 156, pl. 19, fig. 9.
Ennea (*Huttonella*) *pirriei* — W.T. Blanford & Godwin-Austen, 1908: 22.
Gulella pirriei — Richardson, 1988: 114.
Gulella (*Huttonella*) *pirriei* — Ramakrishna et al., 2010: 193.
Sinoennea pirriei — Raheem et al., 2014: 145, fig. 94D–F.

Type locality. "Koondah Mountains, near Calicut".

Material examined. Lectotype, designated by Raheem et al. (2014) (NHMUK 20110265/1) + 3 paralectotypes (NHMUK 20110265), Koondah [Kundah] Hills, near Calicut, coll. Mr. Pirrie, ex coll. Museum Cuming.

Remarks. Aperture oval with laterally strongly elongated, slender sinulus. Peristome continuous, smeared onto the penultimate whorl. Parietal callus rounded, reaching ca. ¼ of penultimate whorl. Parietal lamella prominent, elevated, sharp, rather straight, its middle part slightly bent to palatal direction. Palatal wall with a deeply situated low fold that is facing the bent part of the parietal lamella; two additional, very deeply situated, elongate folds are present on the palato-basal area. These are visible in straight view into the aperture. Columellar lamella strongly developed, its middle part with a sinulus, in which the inner end of the parietal lamella fits.

This species differs from all other species of this genus in its shell shape and size, but agree with the arrangement of the apertural barriers. Thus, at the moment we classify it in *Rowsonia*, new genus.

Rowsonia sculpta (W.T. Blanford, 1869)

Ennea sculpta W.T. Blanford, 1869: 141, pl. 16, fig. 10.
Ennea (*Huttonella*) *sculpta* — Nevill, 1878: 7.
Ennea (*Indoennea*) *sculpta* — Kobelt, 1904b: 158, pl. 20, fig. 20.
Ennea (*Huttonella*) *sculpta* — W.T. Blanford & Godwin-Austen, 1908: 22.
Gulella sculpta — Richardson, 1988: 120.
Gulella (*Huttonella*) *sculpta* — Ramakrishna et al., 2010: 194.
Sinoennea sculpta — Raheem et al., 2014: 145, fig. 95C, D.

Type locality. "In montibus Pulney, Indiæ meridionalis".

Material examined. Lectotype, designated in Raheem et al. (2014) (NHMUK 1906.03.03.80/1) + 8 paralectotypes (NHMUK 1906.03.03.80), "Palney Hills, S. India", "W.T. Blanford colln.".

Remarks. Apertural barriers are similar to those of *R. beddomei*.

Rowsonia turricula (W.T Blanford, 1899)

Ennea turricula W.T. Blanford, 1899: 768, pl. 50, figs. 16, 17.
Ennea (*Indoennea*) *sculpta* — Kobelt, 1904b: 276, pl. 32, figs. 15, 16.
Ennea (*Huttonella*) *turricula* — W.T. Blanford & Godwin-Austen, 1908: 22.
Ennea turricula — Richardson, 1988: 26.
Gulella (*Huttonella*) *turricula* — Ramakrishna et al., 2010: 194.
Sinoennea turricula — Raheem et al., 2014: 146, fig. 95F.

Type locality. "In montibus Animalai dictis, et in provincia Wynaad Indiæ meridionalis".

Material examined. Lectotype, designated in Raheem et al. (2014) (NHMUK 1899.07.04.12), Anamalais, Col. Beddome,

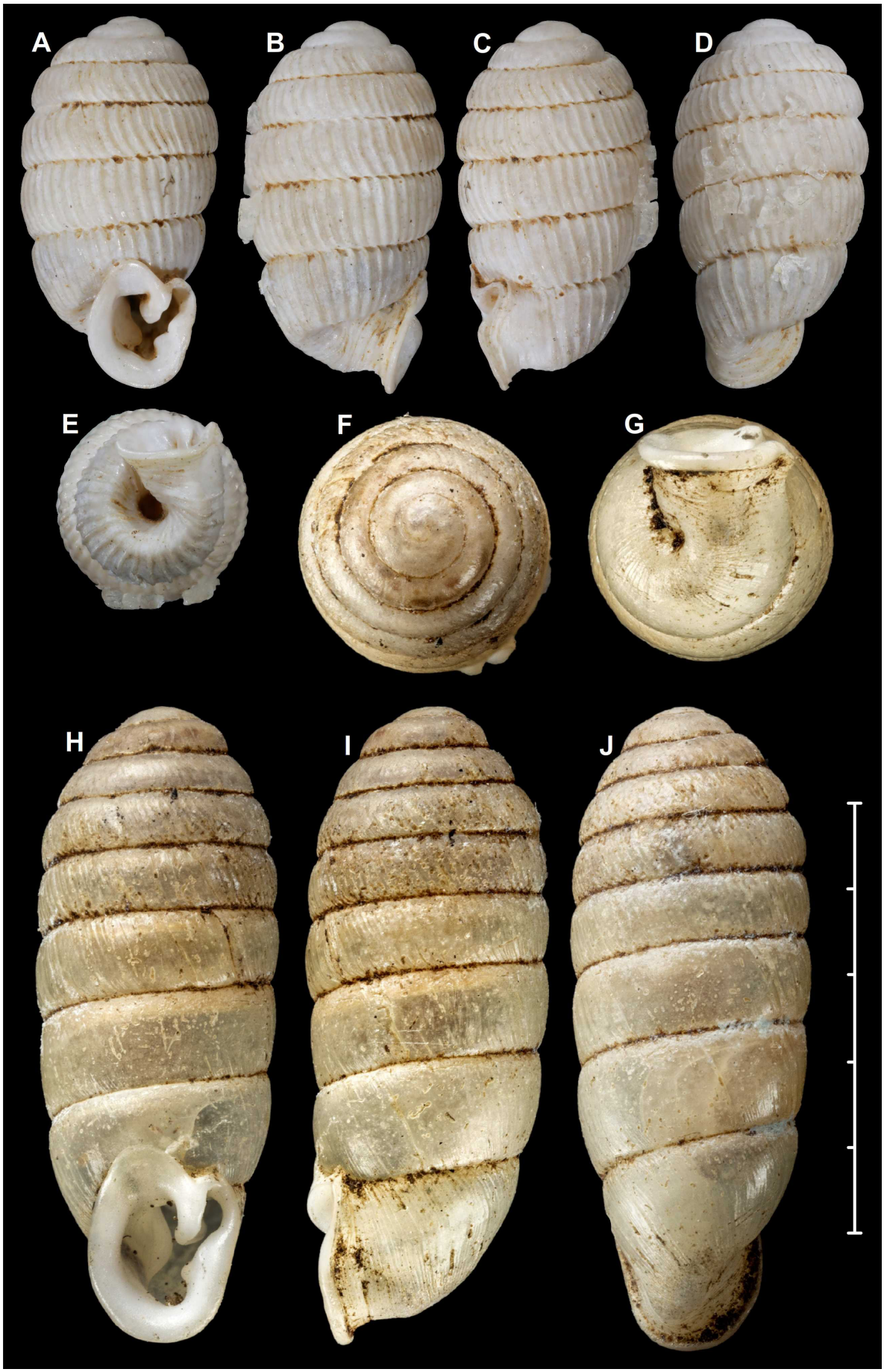

Fig. 14. Shells of *Sinoennea* species. A–E, *Ennea strophiodes* Gredler, 1881 (type species of *Sinoennea* Kobelt, 1904), SMF 42769 (syntype); *Sinoennea blanfordiana* Godwin-Austen, 1872 (type species of *Indoennea* Kobelt, 1904), NHMUK 1903.7.1.2872 (syntype). Scale represents 5 mm.

Pres.d by Colonel Beddome; 3 adult + 1 juvenile shells (NHMUK 1935.10.24.49–52), S. Canara, S. India.

Remarks. Apertural barriers are similar to those of *R. beddomei*.

Sinoennea Kobelt, 1904

Ennea (*Sinoennea*) Kobelt, 1904a: 27.
Indoennea Kobelt, 1904a: 28.
Sinoennea — Peile, 1935: 382. (synonymised *Indoennea* with *Sinoennea*)
Sinoennea — Zilch, 1960: 573. (including the subgenera *Indoennea* and *Sinoennea*)
Sinoennea — Richardson, 1988: 154.
Indoennea — Schileyko, 2000: 799.
Sinoennea — Schileyko, 2000: 800.

Type species. *Ennea strophiodes* Gredler, 1881 (Fig. 14A–E), by original designation.

Diagnosis. Shell usually elongate ovoid and cylindrical, glossy, and regularly ribbed. Apex usually domed. Basal swelling behind peristome usually present. Parietal lamella long, well-developed, divided to internal and external portions that usually differ in orientation. Palatal wall with an upper palatal tooth that sits on the peristome edge and faces the parietal lamella, and a lower palatal tooth that is situated deeper and corresponds with a depression behind the peristome. Small basal tooth sometimes present. Columellar lamella usually deeply situated, sometimes corresponding with a depression on the umbilical side (Fig. 1). Umbilicus open or closed, periumbilical keel might be present.

Differential diagnosis. *Bruggennea* agrees with *Sinoennea* in terms of apertural dentition, but possesses varices (remaining expanded peristomes of juvenile shells) that are imperfectly arranged in two rows on opposite sides of the spire. *Parasinoennea*, new genus, differs from *Sinoennea* mostly in the triangular aperture shape and the adnate parietal callus; other differences listed under the genus. *Platylennea*, new genus, differs from *Sinoennea* in the general shell shape (aciculid-like, elongate conical), the weak parietal callus, and the differently arranged apertural barriers (see under the genus). *Rowsonia*, new genus, differs from *Sinoennea* in the slender conical shell shape, the presence of deeply situated parietal/basal folds, and the basal swelling and the depression corresponding with the lower palatal tooth are absent. *Pupennea*, new genus, mostly differs from *Sinoennea* species by the short parietal lamella, the pointed, small columellar lamella, the well-developed columellar denticle, and the weak parietal callus.

Distribution. From northern India to northern Borneo in the south and Japan in the east (Fig. 10).

Remarks. This genus consists of over 80 species with diverse shell characters (shell size, sculpture, aperture formation). Still, at present we see no possibility to subdivide it in a useful way based on shell characters.

Indoennea was described by Kobelt (1904a, published on 22 February), and was later (Kobelt, 1904b, published in May) again declared new. The type species (*Ennea blanfordiana* Godwin-Austen, 1872, Fig. 14F–J), was designated to be the type species in the latter publication. Thus, the type species of *Indoennea* is fixed by subsequent designation.

Sinoennea austeni (Peile, 1929)

Indoennea austeni Peile, 1929b: 271, fig. 3.
Sinoennea austeni — Richardson, 1988: 154.

Type locality. "Burrail Range, Naga Hills".

Material examined. Holotype + 9 paratypes (NHMUK 1903.07.01.779), Burrail Range, coll. Godwin-Austen.

Remarks. The original description states that the only live-collected specimen (which is the largest among the others) is the type (= holotype). The shell shape and apertural dentition agrees with other *Sinoennea* species.

Sinoennea blanfordiana (Godwin-Austen, 1872)
(Fig. 14F–J)

Ennea blanfordiana Godwin-Austen, 1872: 515, pl. 30, fig. 4.
Ennea (*Huttonella*) *blanfordi* (sic) — Nevill, 1878: 7.
Ennea (*Sinoennea*) *blanfordiana* — Kobelt, 1904b: 154, pl. 20, fig. 21.
Ennea blanfordiana — W.T. Blanford & Godwin-Austen, 1908: 17.
Indoennea blanfordiana — Peile, 1929a: fig. 6 (drawings showing the dentate juvenile shell).
Sinoennea blanfordiana — Richardson, 1988: 155.
Ennea blanfordiana — Ramakrishna et al., 2010: 190.

Type locality. "Máhádeo Peak, near Asálú, North Cachar hills, among rocks at 5700 feet".

Material examined. 1 shell separated + 19 shells in another vial (probably syntypes) (NHMUK 1903.7.1.2872), Mahadeo Peak, Asalu, North Cachar; 8 probable syntypes (NHMUK 1903.7.1.2872a), Mahadeo Peak, Asalu, N. Cachar, coll. Godwin-Austen.

Remarks. Aperture subovoid, parietal callus well-developed, rounded, almost reaching half of penultimate whorl. Basal swelling situated close to the peristome. Parietal lamella well-developed, long, outer portion bent slightly towards columella, inner portion bent slightly towards the palatal wall. Columellar lamella relatively small, rounded but sharp, blade-like. Upper palatal tooth situated on the peristome edge, lower palatal tooth slightly elongated inside, the two sometimes connected with a ridge. Based on the key traits, this species is classified in *Sinoennea*.

Sinoennea fartoidea (Theobald, 1870), new combination
(Figs. 1K, L, 15, 22P)

Pupa fartoidea Theobald, 1870: 400.
Ennea (*Huttonella*) *fartoides* (sic) — Nevill, 1878: 7.

Fig. 15. Syntype of *Sinoennea fartoidea* (Theobald, 1870) (NZSI M.33964/9).

Pupa (*Ennea*) *fartoides* (sic) — Hanley & Theobald, 1876: 40, pl. 100, fig. 5.
Ennea (*Indoennea*) *fartoidea* — Kobelt, 1904b: 278, pl. 20, fig. 21.
Ennea fartoidea — W.T. Blanford & Godwin-Austen, 1908: 18.
Gulella fartoidea — Richardson, 1988: 81.

Type locality. "Shan States".

Material examined. 1 shell, probable syntype (NZSI M.33964/9), Shan States, coll. W. Theobald; 2 shells in separate vials (probably syntypes) (NHMUK 1888.12.04.491–2), Upper Salwin valley.

Remarks. Shell shape elongate ovoid with cylindrical sides and domed dorsal side. Upper whorls and last quarter whorl regularly ribbed, remaining ca. 2 last whorls with weak growth lines. Aperture subrectangular. Parietal callus distinct, not "smeared" onto preceding whorl, does not reach the middle of the preceding whorl. Apertural dentition 3-fold. Parietal lamella strong, elevated, straight, its inner end is not visible in oblique view to the aperture. Sinulus teardrop-shaped, opens slightly laterally, relatively small, and not conspicuously isolated due to the relatively weak palatal tooth. Palatal wall with two denticles. Upper one strong but blunt, situated on the peristome edge, lower one lower in position and deeper, very weak, only slightly indicated. No structure that would be homologous with the columellar lamella of other *Sinoennea* species is visible in oblique view to the aperture. The slight thickening on the columellar edge is homologous with the inner columellar edge of other *Sinoennea* species, and probably not homologous with the columellar lamella of other *Sinoennea* species (see Fig. 1B, K). Peristome strongly thickened and expanded, not reflected, relatively weak around the sinulus. Basal swelling very slight, situated very close to peristome. There is a slight depression just behind the peristome on the outer side (corresponds with the upper palatal tooth). Inner (umbilical) side very short, without depression. Umbilical development not visible. Periumbilical keel moderate, but relatively clearly visible from umbilical view, especially due to the slight furrow on the outer side.

Most shell characters of the general shell shape and the apertural barriers agree with other *Sinoennea* species, therefore this species is moved to that genus. The absence of the columellar lamella (Fig. 1K, L) is surprising, and was not found in any other *Sinoennea* species.

Sinoennea latens Peile, 1935
(Fig. 16A)

Sinoennea latens Peile, 1935: 383, fig. 2.
Sinoennea latens — Richardson, 1988: 159.

Type locality. "Khasi and Naga Hills".

Material examined. Holotype + one *S. stenopylis* specimen for comparison (NHMUK 1935.7.10.3–4), Khasi or Naga Hills.

Remarks. The differences compared with *S. stenopylis* are very minor. Both species belong to *Sinoennea*.

The description was based on a single specimen. The cardboard box containing the holotype of *S. latens* also contained a shell of *S. stenopylis* for comparison. This was clearly indicated by handwriting on the base of the cardboard box ("*Sinoennea latens* Peile, Type/+ *stenopylis* Bs. For comparison/Khasi or Naga Hills/Pr. Malac. Soc. 1935/H.C. Fulton Esq./1935.7.10.3–4").

Sinoennea (?) *milium* (Godwin-Austen, 1876), new combination
(Fig. 16C)

Ennea milium Godwin-Austen, 1876: 317, pl. 8, fig. 11.
Ennea milium — W.T. Blanford, 1899: 769, pl. 50, figs. 18, 19.
Ennea (*Indoennea*) *milium* — Kobelt, 1904b: 160, pl. 21, fig. 7.
Ennea milium — W.T. Blanford & Godwin-Austen, 1908: 18.
Gulella milium — Richardson, 1988: 103.
Ennea milium — Ramakrishna et al., 2010: 191.

Type locality. "Shengorh Peak, 7000 ft".

Material examined. Holotype (NHMUK 1903.7.1.2884), Dafla Hills, Toruputu Peak, 5,000', coll. Godwin-Austen.

Remarks. Peristome adnate, parietal callus indicated only as a thin transparent calcareous layer. Swelling behind peristome not indicated. Parietal lamella elevated but short, outer portion slightly bent towards columella, inner portion bent slightly in palatal direction; palatal wall with an upper palatal tooth that is situated on the peristome. Lower palatal tooth of similar size, situated lower and deeper than the upper palatal tooth; columellar lamella blade-like, sharp, oblique. There is an additional, low basal denticle. The arrangement of the apertural barriers places this species in *Sinoennea*.

The original description was based on a single shell (holotype).

Sinoennea moerchiana (Nevill, 1881), new combination
(Fig. 17)

Ennea (*Huttonella*) *moerchiana* Nevill, 1881: 130.
Ennea (*Huttonella*) *moerchiana* — Kobelt, 1904b: 139.
Ennea (*Huttonella*) *moerchiana* — W.T. Blanford & Godwin-Austen, 1908: 24, fig. 15.
Gulella moerchiana — Richardson, 1988: 106.
Gulella (*Huttonella*) *moerchiana* — Ramakrishna et al., 2010: 194.

Type locality. "Centre of Great Nicobar".

Material examined. Holotype (NZSI M.16940/2), Nicobar, coll. F.A. Do (sic) Roepstorff.

Remarks. Parietal callus strong, does not reach half of the preceding whorl. Parietal lamella strong, elevated, outer portion strongly bent towards columella, inner portion weaker, thinner, bent in palatal direction; palatal wall with a short upper palatal tooth that is situated on the peristome.

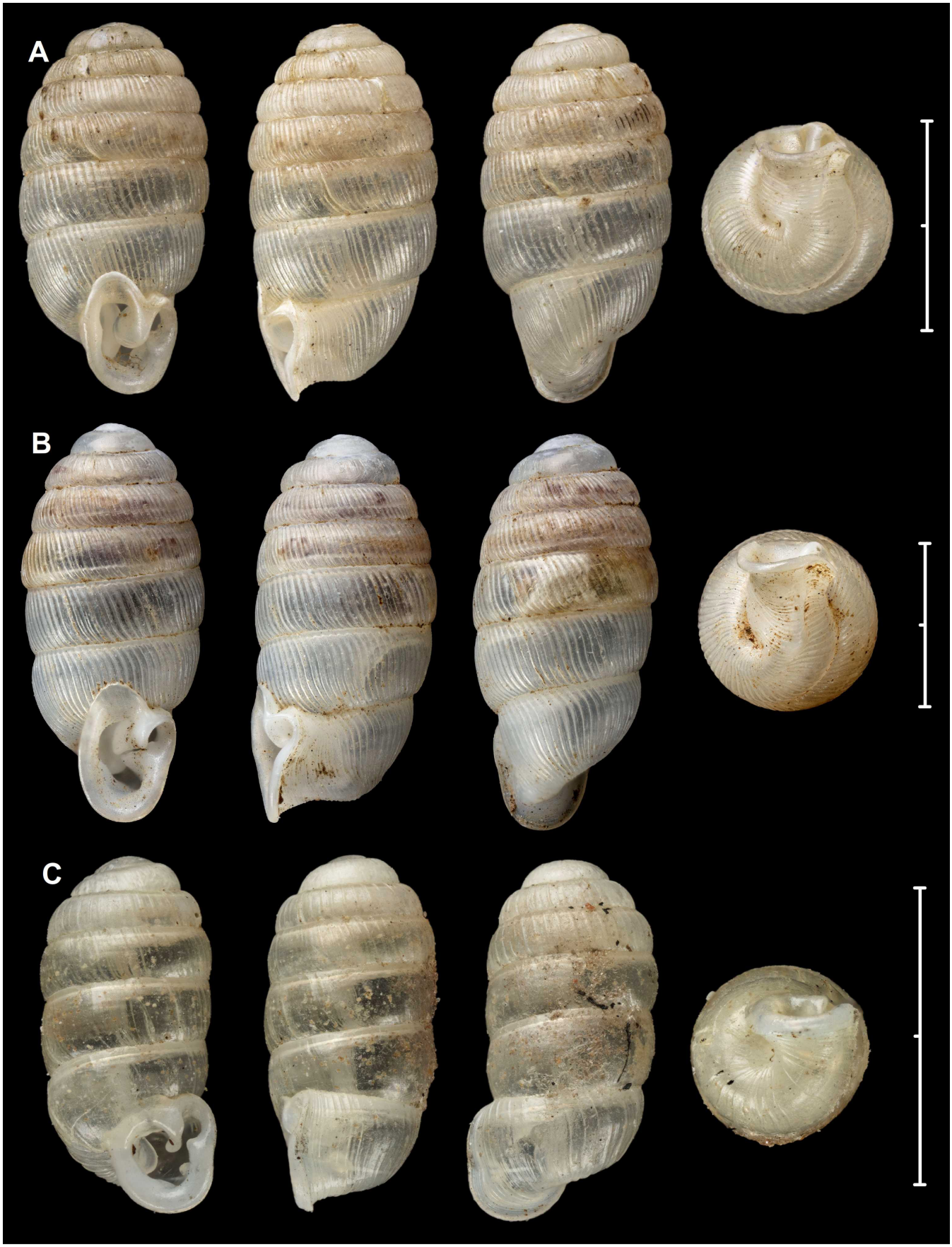

Fig. 16. A, *Sinoennea latens* Peile, 1935, NHMUK 1935.7.10.3–4 (holotype); B, *Sinoennea nagaensis* (W.T. Blanford, 1899), NHMUK 1906.1.1.950 (possible syntype); C, *Sinoennea milium* (Godwin-Austen, 1876), NHMUK 1903.7.1.2884 (probable holotype).

Fig. 17. Holotype (NZSI M.16940/2) of *Sinoennea moerchiana* (Nevill, 1881).

Lower palatal tooth longer, oblique, situated lower and deeper than the upper palatal tooth, the two palatal teeth are connected. Columellar lamella blade-like, sharp, oblique, its outer/lower end widened, triangular. The ovoid shell shape, the regularly ribbed shell surface, and the arrangement of the apertural barriers places this species unquestionably to *Sinoennea*.

The original description was based on a single shell (holotype).

Sinoennea montawana Páll-Gergely & Hunyadi, new species

(Figs. 18, 22M)

Type material. Holotype (H: 2.6 mm, D: 1.3 mm) (HNHM 104856) (Fig. 18B–K), Myanmar, Shan State, Taunggyi centre WSW, Montawa Cave, 20°45.282′N, 97°1.057′E, 1,260 m a.s.l. (locality codes: 2018/34 and 20181005C), coll. K. Okubo, J.U. Otani & A. Hunyadi, 05 October 2018. Paratypes. 1 shell (H: 2.5 mm, D: 1.3 mm) (Coll. HA), same data as holotype (Fig. 18A).

Additional material. 3 juvenile shells (Fig. 18L), same data as holotype, coll. HA.

Diagnosis. A small, ovoid *Sinoennea* species with elongate oval aperture, four normally developed apertural barriers, narrow, rounded umbilicus, and a moderate periumbilical keel.

Description. Shell shape ovoid to cylindrical, apex domed, the last three whorls the widest in standard apertural view. Shell colourless, semi-transparent, consisting of 5.5–5.75 whorls. Ribs low, fine, rather regularly arranged. Protoconch consisting of 1.5–1.75 whorls, glossy, almost smooth, very finely granular. Teleoconch sculpture glossier than that of protoconch, ribs rather regularly spaced, although the space between them increases on the last whorl towards aperture. Individual ribs look like low waves "pushed" backwards. Suture deep, whorls bulging, although side of body whorl straight with an outer angle of variable strength. Aperture elongate oval or almost rectangular, elongate. Parietal callus distinct, not "smeared" onto preceding whorl. Apertural dentition 4-fold. Parietal lamella moderately developed, nearly straight. Its outer part is slightly bent towards the parietal denticle, its inner part slightly bent towards the columella. Sinulus oval, opens slightly laterally, relatively small, and not conspicuously isolated due to the relatively weak parietal and palatal teeth. Palatal wall with two blunt, but well-developed denticles that are situated close to each other. Upper one situated on the peristome edge, lower one slightly lower in position and deeper. The inner one is slightly more elevated than the outer one. Columellar lamella situated relatively deep, but clearly visible from apertural view, rather low, elongated ridge-like, oblique to shell axis. Peristome strongly thickened and expanded, not reflected, relatively weak around the sinulus. Basal swelling very slightly indicated, nearly absent, situated relatively close to peristome. Depression anterior to basal swelling on the outer side very shallow (corresponding with the inner palatal tooth). Inner (umbilical) side with a slight depression corresponding with the columellar lamella. Umbilicus open, narrow, rounded. Periumbilical keel moderate, but relatively clearly visible from umbilical view, especially due to the slight furrow on the outer side.

Juveniles with a strong parietal and columellar lamella, and a lower palatal tooth (Fig. 18L).

Differential diagnosis. Only two *Sinoennea* species are known from Myanmar: *S. fartoidea* and *S. woodthorpei*. The former is more ovoid, has a closed umbilicus, lacks the columellar lamella, and has a very weak lower palatal tooth. *Sinoennea woodthorpei* is larger with stronger ribbing and its parietal callus is smeared onto the penultimate whorl.

Sinoennea nagaensis (W.T. Blanford, 1899), new combination

(Fig. 16B)

Ennea nagaensis W.T. Blanford, 1899: 769, pl. 50, fig. 22.
Ennea (*Indoennea*) *nagaensis* — Kobelt, 1904b: 277, pl. 33, fig. 1.
Ennea nagaensis — W.T. Blanford & Godwin-Austen, 1908: 17.
Ennea nagaensis — Richardson, 1988: 25.
Ennea nagaensis — Ramakrishna et al., 2010: 191.

Type locality. "in montibus Naga dictis".

Material examined. Syntype (NHMUK 1906.1.1.950), Naga Hills, coll. Blanford.

Remarks. Aperture suboval, parietal callus elongated, smeared onto the penultimate whorl and almost reaching halfway up it. Basal swelling behind peristome strongly indicated. Depression between basal swelling and peristome deep. Parietal lamella strong, end of outer part curved in the parietal direction, inner part curved slightly towards columella. Palatal wall with an elongated, sharp, elevated ridge (homologous with the lower palatal tooth) that nearly touches parietal lamella. Upper palatal tooth not conspicuous. Columellar lamella very deeply situated, its blade barely visible due to the parietal and palatal barriers. Based on the aperture shape, formation of apertural denticles, and the presence of a prominent basal swelling this species belongs to *Sinoennea*.

Sinoennea stenopylis (Benson, 1860)

Ennea stenopylis Benson, 1860: 460.
Ennea (*Huttonella*) *stenopylis* — Nevill, 1878: 7.
Ennea (*Indoennea*) *stenopylis* — Kobelt, 1904b: 158, pl. 20, fig. 23.
Ennea stenopylis — W.T. Blanford & Godwin-Austen, 1908: 17.
Indoennea stenopylis — Peile, 1929a: fig. 7 (drawings showing the dentate juvenile shell).
Sinoennea stenopylis — Richardson, 1988: 161.
Ennea stenopylis — Ramakrishna et al., 2010: 191.

Type locality. "in vallibus Rungnu et Rimmau (alt. 4000 ped.) prope Darjiling".

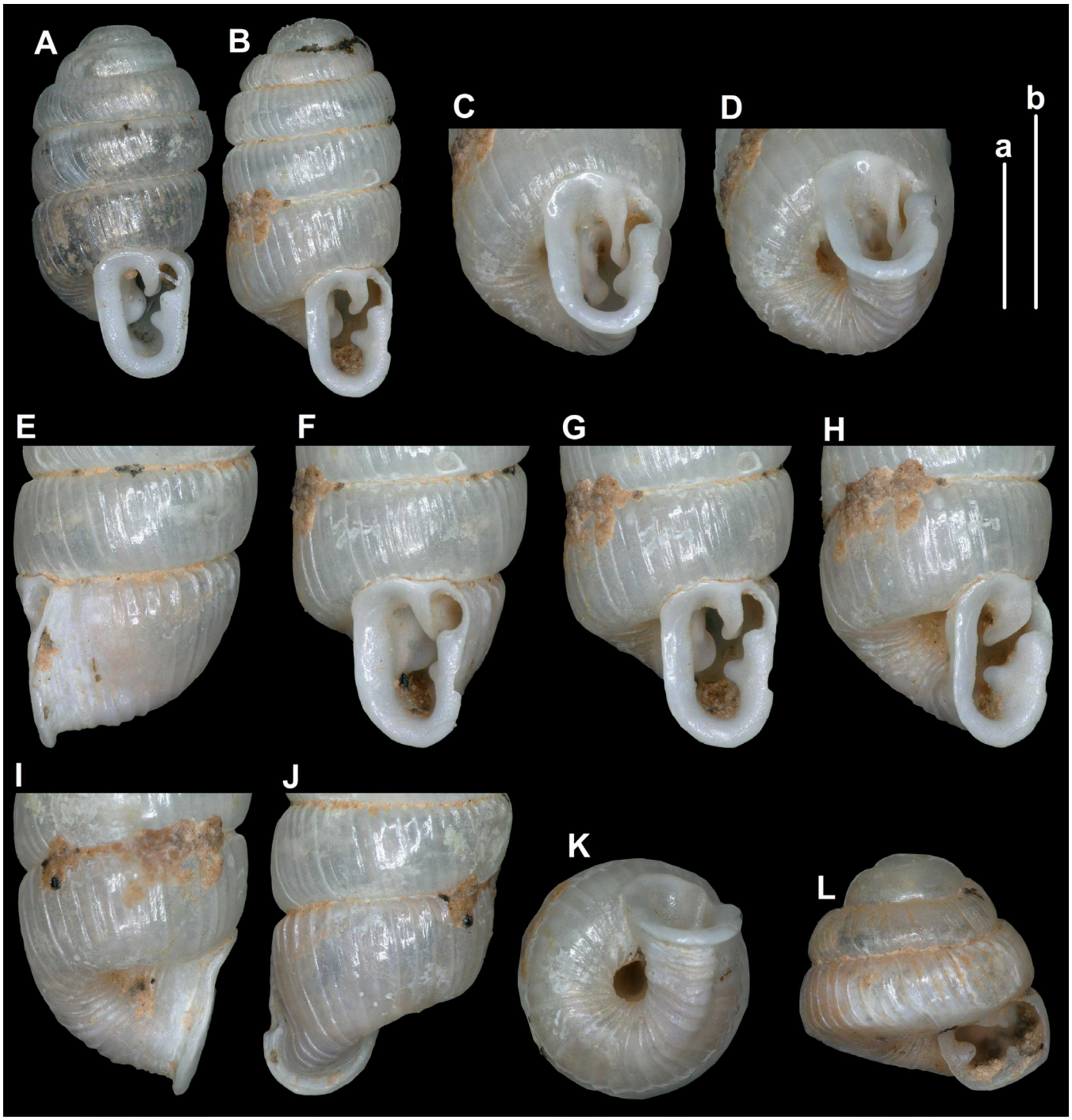

Fig. 18. Paratype (A), holotype (B–K), and juvenile shell (L) of *Sinoennea montawana* Páll-Gergely & Hunyadi, new species.

Material examined. 5 adult + 1 juvenile shells (NHMUK 1909.3.15.90a), Khasi Hills.

Remarks. Aperture suboval, parietal callus well-developed, rounded, reaching or extending beyond half the height of the penultimate whorl. Basal swelling strong, situated relatively close to peristome. Depression between basal swelling and peristome deep and slightly elongated. Parietal lamella strong, outer part slightly bent towards columella, whereas inner part bent towards the palatal wall. Palatal wall with a ridge-like tooth that runs together with the outer part of the parietal lamella. A small denticle might present on the upper part of the palatal lamella, sitting on the base of sinulus. The lower parietal tooth is not distinguishable, it is probably part of the elongated parietal ridge. A blunt basal denticle sits in some distance from the peristome. Columellar lamella very strongly elevated, curved, sharp, deeply situated, oblique to the shell axis. Based on the aperture shape, the presence of a basal swelling behind the peristome, and the arrangement of the apertural barriers, this species belongs to *Sinoennea*.

Sinoennea vara (Benson, 1859)

Pupa (*Ennea*) *vara* Benson, 1859: 188.
Ennea (*Huttonella*) *vara* — Nevill, 1878: 7.
Ennea (*Indoennea*) *vara* — Kobelt, 1904b: 160, pl. 20, fig. 24.
Ennea vara — W.T. Blanford & Godwin-Austen, 1908: 16, fig. 10.

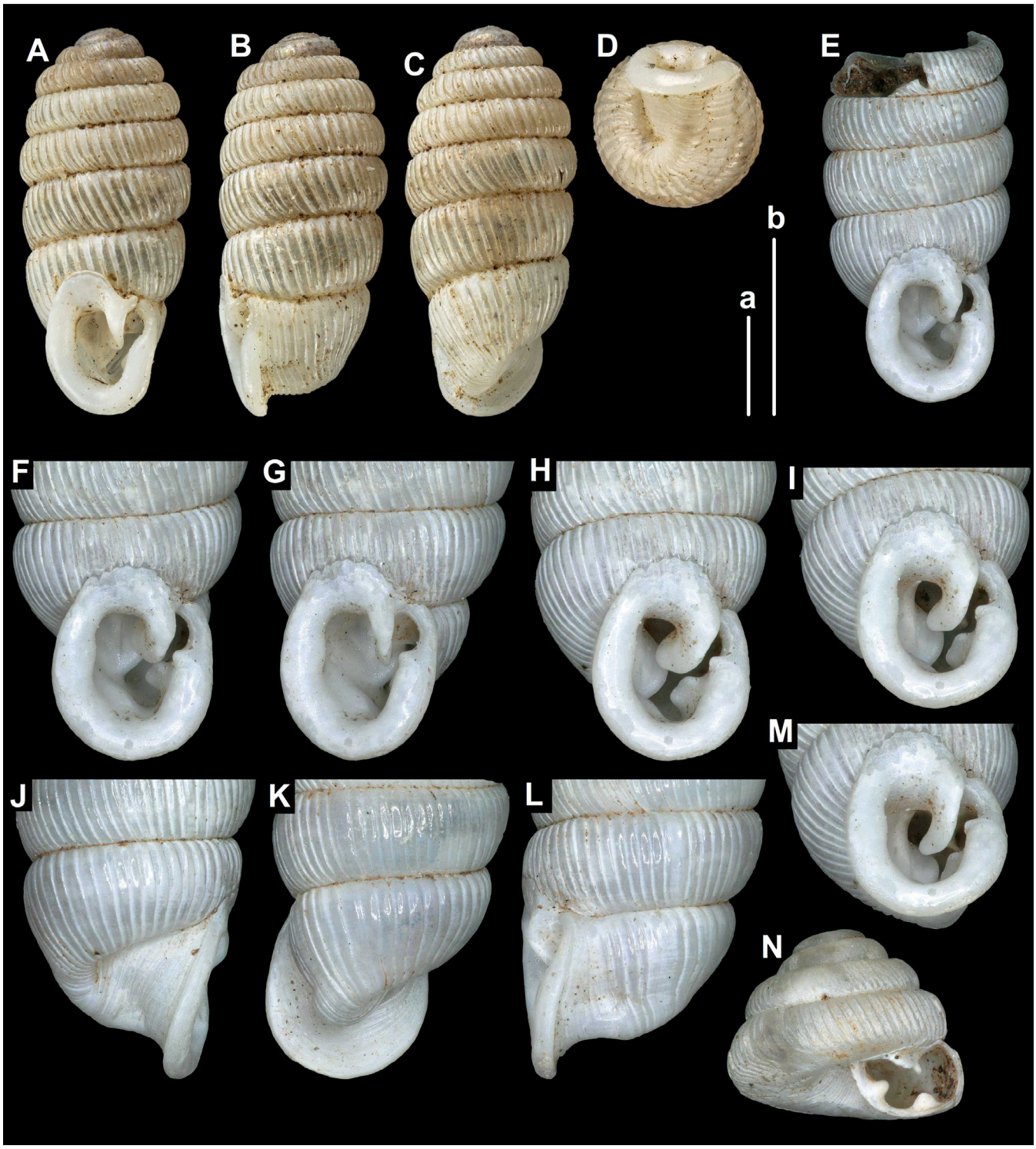

Fig. 19. *Sinoennea woodthorpei* (Peile, 1929). A–D, holotype (NHMUK 1903.7.1.3066); E–M, locality 2018/39, specimen 1; N, locality 2018/39, specimen 2. Both scales represent 1 mm; scale "a" refers to figs. A–E, scale "b" refers to figs. F–N.

Indoennea vara — Peile, 1929a: fig. 3 (drawings show the dentate juvenile shell).
Sinoennea vara — Richardson, 1988: 162.
Ennea vara — Ramakrishna et al., 2010: 191.

Type locality. "ad Nauclai (lat. 25°15′, long 92°30′)".

Material examined. Many shells (NHMUK), Cherrapunji, Assam, coll. Godwin-Austen.

Remarks. Parietal callus reaches ca. half of penultimate whorl, smeared onto it. Basal swelling situated relatively close to peristome, slight, but clearly visible. Parietal lamella strong, outer portion rather straight or slightly curved in palatal direction, inner part curved towards columella. Palatal wall with a strong, sharp, elevated ridge that runs together with the parietal lamella. A small denticle is attached to the palatal ridge and situated on the basal part of the sinulus. Columellar lamella almost horizontal, deeply situated, sharp, its blade is visibly in oblique view to the aperture.

An additional, blunt denticle is situated on the columellar peristome, near the columellar-parietal junction. Based on the aperture shape, the presence of a basal swelling, and the arrangement of the apertural barriers, this species is a member of the genus *Sinoennea*.

Sinoennea woodthorpei (Peile, 1929)
(Figs. 19, 22O)

Indoennea woodthorpei Peile, 1929b: 271, fig. 2.
Sinoennea woodthorpei — Richardson, 1988: 163.

Type locality. "Fort Stedman, Burma".

Material examined. 1 holotype (Fig. 19A–D) + 5 paratypes (NHMUK 1903.7.1.3066 [inventory number for both the holotype and the paratypes]), Fort Stedman, Burma (S. Shan Country), leg. Woodthorpe, coll. Godwin-Austen. 1 shell (Coll. HA), Myanmar, Shan State, Hsihseng centre E ca. 4.5 km, left side of rd. + 1.7 km on unpaved rd., limestone rocks, 20°9.359′N, 97°17.883′E, 1,140 m a.s.l. (locality codes: 2018/39 and 20181007A), coll. K. Okubo, J.U. Otani & A. Hunyadi, 07 October 2018.

Remarks. Aperture subovoid-quadrangular, parietal callus reaches ca. half of penultimate whorl, rounded. Basal swelling situated in normal distance from peristome, the depression of the palatal wall between the swelling and the peristome clearly visible, corresponding with the lower palatal tooth. Parietal lamella well-developed, its outer end rather straight in the type specimens but curved in the newly collected shell. The outer part of the parietal lamella slightly bent towards columella, inner portion bent in the other direction. Upper palatal tooth low, inconspicuous. Lower palatal tooth situated lower and deeper, elongated, clearly visible from straight view to the aperture. Columellar lamella sharp and relatively low, visible from oblique view to the aperture. Based on the aperture shape, the presence of a basal swelling, and the arrangement of the apertural barriers, this species is classified in *Sinoennea*.

According to the original description "the best preserved shell has been selected as the type". Thus, the photographed shell is the holotype.

Tonkinia J. Mabille, 1887

Tonkinia J. Mabille, 1887: 9.
Tonkinia — Zilch, 1960: 560.
Tonkinia — Richardson, 1988: 263.
Tonkinia — Schileyko, 2000: 785.

Type species. *Tonkinia mirabilis* Mabille, 1887, by monotypy.

Diagnosis. "Shell depressed, lenticular, thin, transparent, glass-like, of 3–4 slightly convex, somewhat shouldered whorls. Last whorl turned upward, with peripheral keel or angle. Colourless. Embryonic whorls smooth, subsequent whorls without regular sculpture. Aperture solute, irregularly quadrangular, nearly horizontal, with a little thickened, expanded margins and small parietal lamella. Palatal margin with thickening. Umbilicus wide, perspective" (Schileyko, 2000).

Distribution. Northern Vietnam.

Family Streptaxidae Gray, 1860

Streptaxidae Gray, 1860: 268.

Remarks. The genera *Ennea* and *Gulella* (*Huttonella*) are presented here for comparative purposes, no taxonomic action is done in relation to them.

Ennea H. Adams & A. Adams, 1855

Ennea H. Adams & A. Adams, 1855: 171.
Ennea — Zilch, 1960: 577.
Ennea — Richardson, 1988: 19.
Ennea — Schileyko, 2000: 798.

Type species. *Pupa elegantula* L. Pfeiffer, 1847 (Fig. 20), by subsequent designation (Martens, 1860: 302).

Remarks. *Ennea* is characterised by deeply situated long parietal plicae, which are absent in the genus *Sinoennea*. Although the southern Indian *Rowsonia*, new genus, has similar plicae, the close relationship between African *Ennea* and *Rowsonia* is unlikely due to biogeographical reasons (see also under *Rowsonia*, new genus).

Gulella L. Pfeiffer, 1856

Subgenus *Huttonella* L. Pfeiffer, 1856

Ennea (*Huttonella*) L. Pfeiffer, 1856: 174.
Gulella (*Huttonella*) — Zilch, 1960: 570.
Huttonella — Schileyko, 2000: 821.

Type species. *Pupa bicolor* Hutton, 1834, by subsequent designation (Nevill, 1878: 6).

Remarks. The type species of *Huttonella* has a pantropical distribution (Berry, 1965; Simone, 2013), and it probably originated from Asia (Naggs, 1989; Rowson & Herbert, 2016).

Molecular phylogeny showed that it is closely related to "true" *Gulella* L. Pfeiffer, 1856 (Rowson et al., 2010), and it was treated as a subgenus of *Gulella* in the most recent revision (Rowson & Herbert, 2016).

Gulella (*Huttonella*) *bicolor* (Hutton, 1834)
(Figs. 21, 22A)

Pupa bicolor Hutton, 1834: 86, 93.
Ennea (*Huttonella*) *bicolor* — Nevill, 1878: 6.
Ennea (*Huttonella*) *bicolor* — Kobelt, 1904b: 128, pl. 19, figs. 1–3.
Ennea (*Huttonella*) *bicolor* — W.T. Blanford & Godwin-Austen, 1908: 19.
Gulella bicolor — Richardson, 1988: 56.
Gulella (*Huttonella*) *bicolor* — Ramakrishna et al., 2010: 192.

Fig. 20. Possible syntypes of *Ennea elegantula* (L. Pfeiffer, 1847), NHMUK 20110185a. Scales represent 5 mm.

Type locality. "Mirzapoor beneath garden pots and at the base of the walls of my bungallow".

Material examined. 9 shells (NHMUK), Rajmahal, India, coll. Dr. T.V. Oldham.

Remarks. Peristome discontinuous, the parietal callus is only very slightly indicated by transparent calcareous layer. Parietal lamella relatively low and short, no inner and outer parts distinguishable. Palatal wall with a single, pointed, inward-pointing hook-like denticle, which is probably homologous with the lower palatal tooth of *Sinoennea* species. In some *G. bicolor* shells there is an additional tooth closer to the peristome edge, which may be homologous with the upper palatal tooth. Basal tooth pointed. Columellar lamella slightly oblique to shell axis, rather sharp. Basal swelling prominent, situated close to peristome.

The overall aperture shape and the arrangement of the barriers is similar to that of *Sinoennea*. The differences are the following: the parietal lamella of *Sinoennea* is long and consists of an inner and outer portion, which usually differ in orientation; peristome is continuous in most *Sinoennea*, and the parietal callus is clearly developed; the basal tooth, if present, only weakly developed in *Sinoennea*; *Sinoennea* shells are almost always ribbed; juveniles are edentate, whereas in many (all?) *Sinoennea* species juveniles are dentate.

DISCUSSION

Originally two genera, namely *Diaphera* and *Sinoennea*, were included in the Diapheridae, and their positions were supported by molecular phylogenetic analysis (Sutcharit et

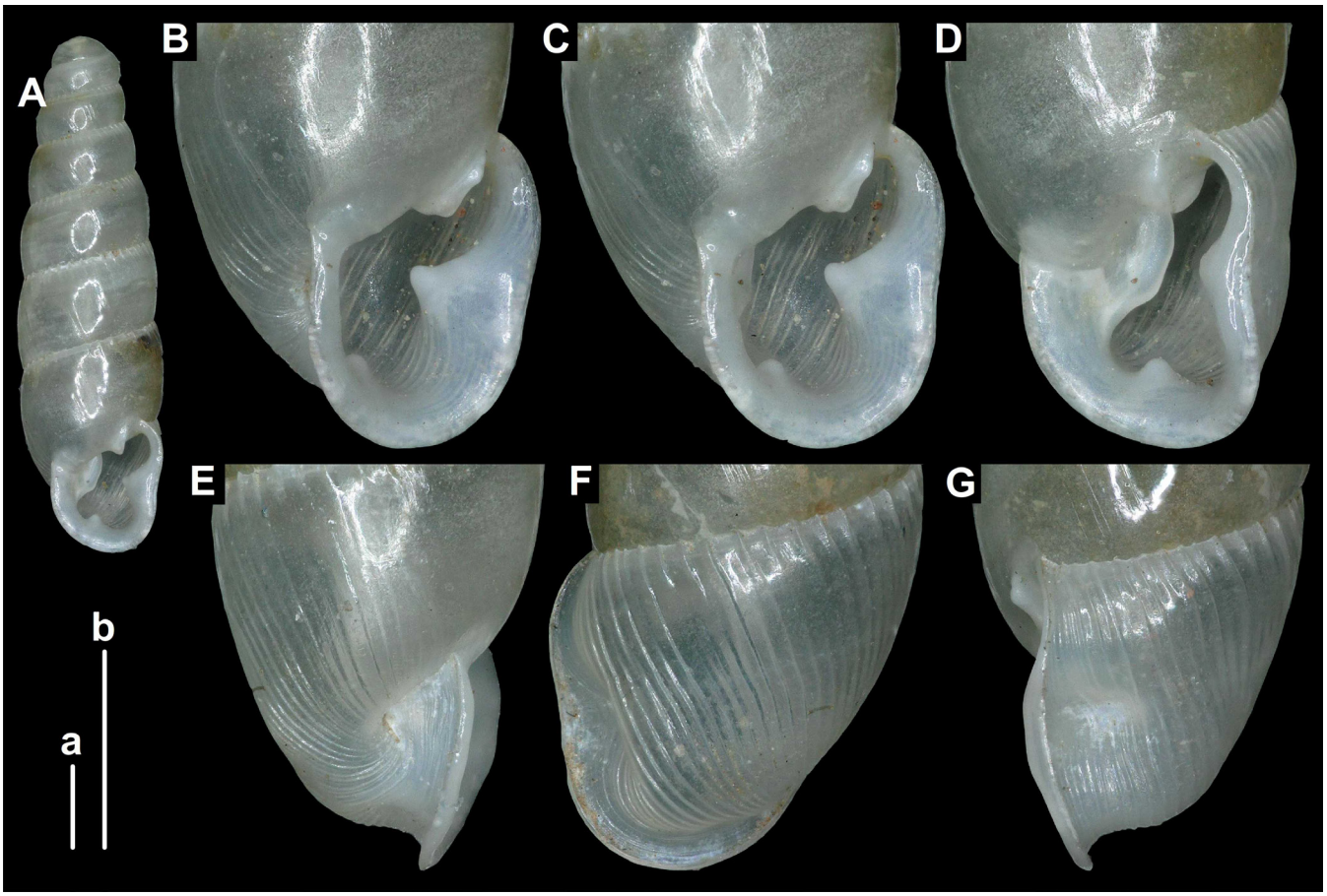

Fig. 21. *Gulella* (*Huttonella*) *bicolor* (Hutton, 1834), NHMUK. Both scales represent 1 mm; scale "a" refers to fig. A, scale "b" refers to figs. B–G.

al., 2010). The genera *Bruggennea*, *Laoennea*, *Platycochlium*, and *Tonkinia* are included in Diapheridae due to their conchological similarity with *Sinoennea*. The apertural dentition of *Bruggennea* agrees with that of *Sinoennea* and differs from it based on the presence of varices (Vermeulen, 2007). The latter trait is present in *Discartemon* L. Pfeiffer, 1856 (see Siriboon et al., 2014), which is a member of the Streptaxidae. *Platycochlium* and *Tonkinia* differ from the other diapherid genera by the low spire but are similar in the formation of the apertural barriers, and they show similarity to *Bruggennea* in the presence of the varices in the adult shell.

Indoennea was moved to the synonymy of *Sinoennea* already by Peile (1935), and we agree with that decision based on the close similarity of the type species of *Sinoennea* and *Indoennea* in terms of shell and aperture shape, and the arrangement of the apertural barriers.

Examination of all *Sinoennea* species (illustrations in the literature or type specimens in museums) revealed that the species from the southwestern Himalaya area until Japan and Borneo share the same type of apertural dentition (parietal lamella + columellar lamella, upper palatal tooth situated on peristome, lower palatal tooth situated deeper, and they are more or less in contact, Fig. 22I–P). A few species of *Sinoennea* from southern China and northern Vietnam are moved to *Parasinoennea*, new genus, mostly based on the oval shell and adnate aperture (Fig. 22H).

Four species from India and Myanmar are here moved from the (sub)genera *Ennea*, *Gulella*, and *Huttonella* to *Sinoennea* (*Sinoennea fartoidea*, *S. milium*, *S. moerchiana*, *S. nagaensis*). Thus, with the exception of the pantropical *Gulella* (*Huttonella*) *bicolor*, there are no high-spired streptaxoid species in the Oriental Region belonging to those genera having mostly African distributions (Schileyko, 2000).

We also recognised that the apertural dentition of southern and central Indian species differs from other *Sinoennea* considerably, and their aperture is adnate to the penultimate whorl. To separate them from *Sinoennea* in a meaningful way, three new genera (*Rowsonia*, *Platylennea*, and *Pupennea*), defined on the basis of conchological characters, had to be erected. The former genus possesses deeply-set plicae (Figs. 12J–Q, 22B), which are probably homologous with the basal denticles of *Platylennea*, new genus (Figs. 12A–I, 22C). These traits are absent in other genera of the Diapheridae and are similar to the longitudinal palatal folds of the African *Ennea* (Fig. 20). However, an African evolutionary connection would be surprising, because the land snail fauna of the Western Ghats is almost exclusively of Southeast Asian origin (Raheem et al., 2014; Fred Naggs, pers. comm., October 2019).

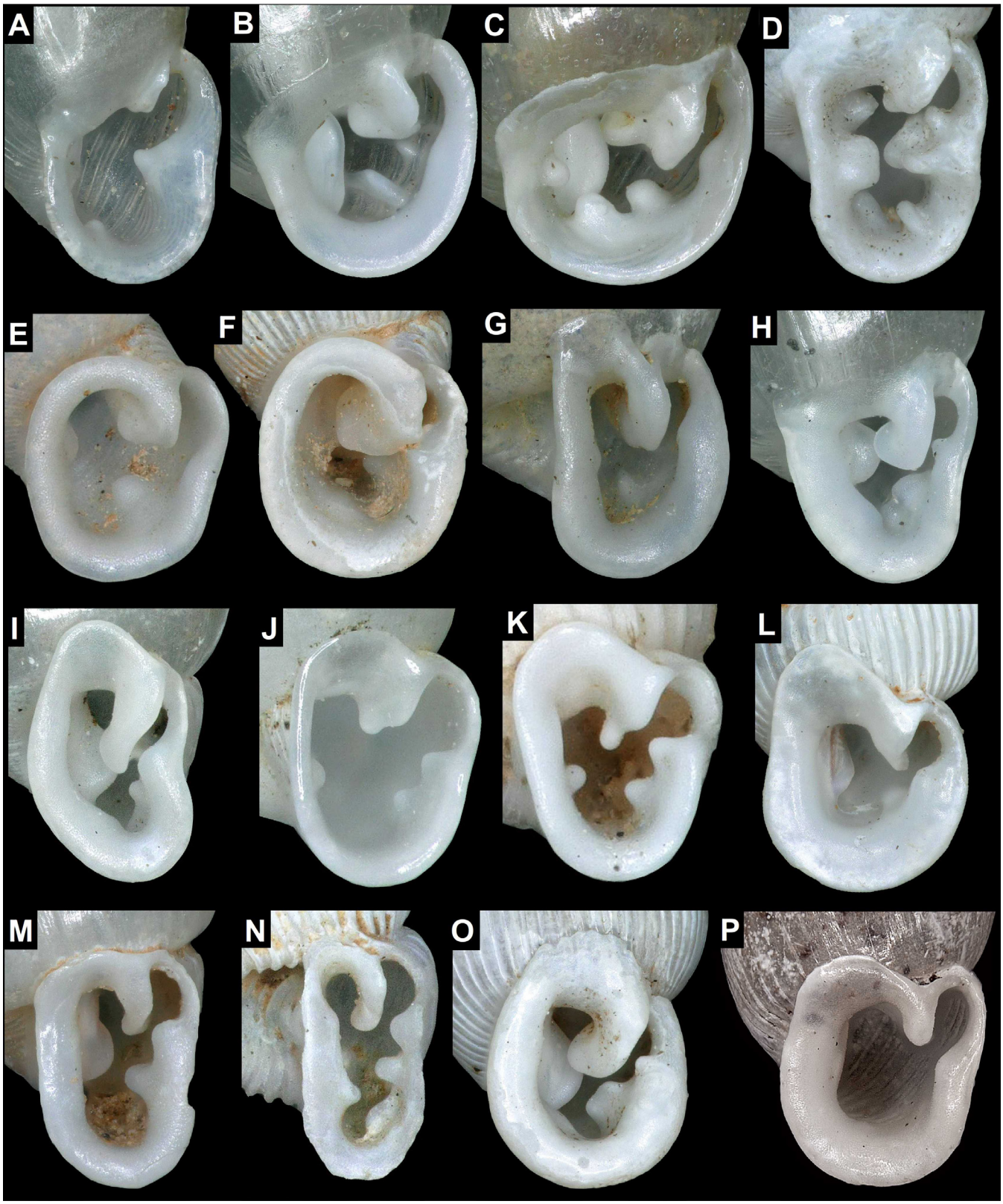

Fig. 22. Apertures of Streptaxidae (A) and Diapheridae (B–P). A, *Gulella* (*Huttonella*) *bicolor* (Hutton, 1834); B, *Rowsonia beddomei* (W.T. Blanford, 1881); C, *Platylennea subcostulata* (W.T. Blanford, 1881); D, *Pupennea planguncula* (Benson, 1863); E, *Diaphera polita*, Páll-Gergely new species; F, *Diaphera cylindrelloidea* (Stoliczka, 1871); G, *Bruggennea* cf. *bongi* (Dance, 1970), H, *Parasinoennea ovulum* (Bavay & Dautzenberg, 1912); I, *Sinoennea otostoma* Páll-Gergely, A. Reischütz & Maassen in Páll-Gergely, Reischütz, Maassen, Grego & Hunyadi, 2020; J, *Sinoennea infantilis* Páll-Gergely & Grego in Páll-Gergely et al., 2020; K, *Sinoennea variabilis* Páll-Gergely & Grego in Páll-Gergely et al., 2020; L, *Sinoennea sutchariti* Páll-Gergely & Hunyadi in Páll-Gergely et al., 2020; M, *Sinoennea montawana* Páll-Gergely & Hunyadi, new species; N, *Sinoennea angustistoma* Páll-Gergely, A. Reischütz & Maassen in Páll-Gergely et al., 2020, O, *Sinoennea woodthorpei* (Peile, 1929); P, *Sinoennea fartoidea* (Theobald, 1870). Not to scale.

Another problematic issue in the systematics of Diapheridae is the monophyly of the genus *Diaphera*. This genus is defined on the basis of the free last whorl (see the type species in Bruggen, 1975 and Sutcharit et al., 2010). *Diaphera* is mostly radiated in the Philippines, where at least 40 species are known exhibiting incredible variability in terms of shell shape, seven of them even without having a free last whorl (Zilch, 1961). The *Diaphera* species reported from Borneo are similar to those of the Philippines and are probably related (Vermeulen, 1990). Some of the continental species, such as *D. prima*, *D. densecostulata*, and *D. saurini*, fall within the morphological variability of Philippine *Diaphera* by having a "distorted" last half whorl. On the other hand, the species from Myanmar possess a "protruding" terminal part of the body whorl, suggesting that might have an independent origin from the rest of *Diaphera* species. Future anatomical and molecular information should target these questions.

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