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A NEW GENUS AND NEW SPECIES OF DYAKIID SNAIL (PULMONATA: DYAKIIDAE) FROM THE PHU PHAN RANGE, NORTHEASTERN THAILAND

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***ABSTRACT.* –** *Phuphania globosa* new genus and new species is described from the Phu Phan range, northeastern Thailand. Morphological features are examined and compared with those of related genera. Most notable is the amatorial organ, which is hypothesized to exhibit the most derived state to be found in the Dyakiidae. The distribution of *Phuphania* correlates with a cladogram of related genera and we hypothesise that an ancestor from Borneo dispersed across a land bridge to Cambodia and that *Phuphania* subsequently separated from *Bertia* in Cambodia following uplift of the Khorat Plateau in the Early Tertiary.

***KEY WORDS.* –** Dyakiidae, Pulmonata, Phu Phan range, northeastern Thailand, anatomy.

INTRODUCTION

The Dyakiidae (Gude & Woodward, 1921) are a little-known family of the Limacoidea sensu lato (Baker, 1941*)* endemic to Sundaland (the landmass of the Sunda continental shelf). The Dyakiidae have received little attention; Laidlaw (1931) listed the genera and provided the first characterization of the family. Currently recognized genera (Table 1) include all those listed by Baker (1941), except *Staffordia* Godwin-Austen, 1907 (Zilch, 1959; Schileyko, 2003). The Dyakiidae are characterized by having the duct of the gametolytic sac connected to the base of the amatorial organ. A preliminary phylogenetic and biogeographic analysis was provided by Hausdorf (1995).

From May 2002 to October 2005 the first author collected land snails from the Mesozoic sandstone Phu Phan range (Fig. 1). One species with a dextral and semiglobose shell, exhibited a genital system with the gametolytic duct running from the base of the amatorial organ, a synapomorphy of the Dyakiidae within the Limacoidea sensu lato. Further examination showed that it is distinct from all known genera of Dyakiidae (Godwin-Austen, 1891, 1906, 1907; Laidlaw, 1931; Thiele, 1931; Baker, 1941; Zilch, 1959; Laidlaw, 1963; Solem, 1966; Hausdorf, 1995; Schileyko, 2003).

MATERIAL AND METHODS

Specimens were collected in dry dipterocarp and mixed deciduous forests of the Phu Phan range during the rainy seasons of May to October from 2002 to 2005. Samples were collected on the surface and under leaf litter prior to being drowned in water and fixed and preserved in 70% ethanol. Intact adult shells were measured for whorl number, shell height (h), and major diameter or shell width (d) using digital vernier calipers and the anatomy of the reproductive organs and radula were examined.

Type material is deposited in the following institutions: The Zoological Reference Collection (ZRC) of the Raffles Museum of Biodiversity Research, Department of Biological Science, National University of Singapore; The Natural History Museum, London (BMNH); Chulalongkorn University, Museum of Zoology, Bangkok, Thailand (CUMZ); Natural History Museum, Mahasarakham University, Mahasarakham, Thailand (NHMSU).

Table 1. List of genera and type species of the Dyakiidae.

Genera	Type species	Number of species
Quantula Baker, 1941	*Q. striata* (Gray, 1834)	1
Elaphroconcha Gude, 1911	*Ela. internota* (E. Smith, 1898)	10
Sasakina, Rensch 1930	*S. oxyconus* (Martens, 1896)	4
Pseudoplecta Laidlaw, 1932	*Pse. bijuga* (Stoliczka, 1873)	1
Aspertitus Gray, 1857	*A. rugosissima* (Moellendorff, 1903)	14
Dyakia Godwin-Austen, 1891	*D. hugonis* (L. Pfeiffer, 1863)	22
Rhinocochlis Thiele, 1931	*R. nasuta* (Metcalfe, 1852)	1
Kalamantania Laidlaw, 1931	*K. whiteheadi* (Godwin-Austen, 1891)	1
Everettia Godwin-Austen, 1891	*Eve. jucunda* (L. Pfeiffer, 1891)	15
Bertia Ancey, 1887	*B. cambojiensis* (Reeve, 1860)	1

***Abbreviations.* –** ag: albumen gland; am: amatorial organ; amg: amatorial organ gland; amr: amatorial organ retractor; at: atrium; bw: body wall; ep: epiphallus; fo: free oviduct; gd: gametolytic duct; gs: gametolytic sac; hd: hermaphroditic duct; p: penis; pam: papilla of amatorial organ; pg: prostate gland; pr: penial retractor; ut: uterus; vd: vas deferens.

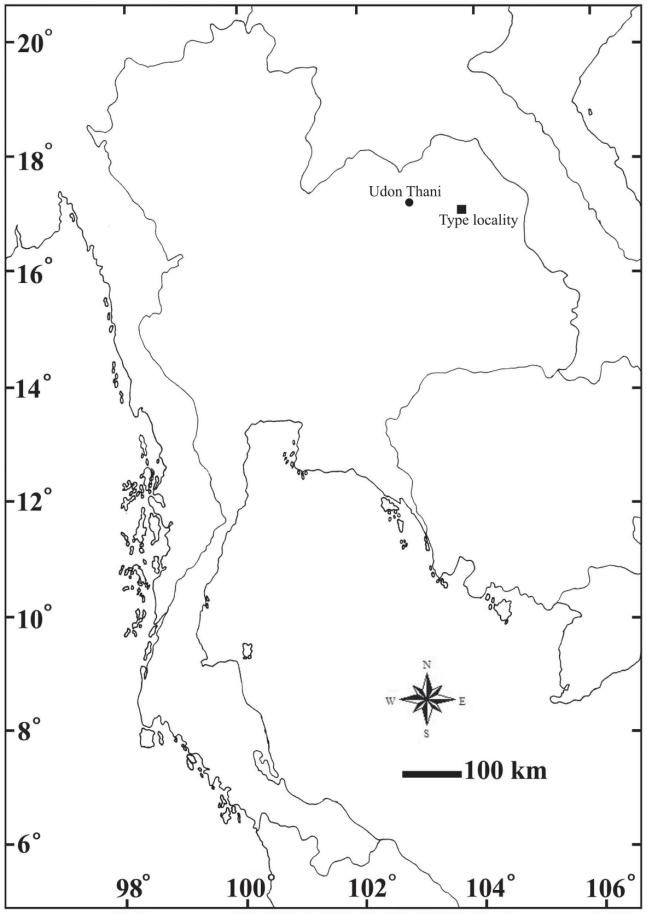


Fig. 1. Map of Thailand showing type locality of *Phuphania globosa*, new species, Ban Dong Kham Pho, Waritchaphum District, Sakon Nakhon Province. The location is on the east of Udon Thani Province.

SYSTEMATICS

DYAKIIDAE Gude & Woodward, 1921

DYAKIINAE Gude & Woodward, 1921

Phuphania, new genus

***Type species.* –** *Phuphania globosa*, new species.

***Diagnosis.* –** The key generic characters distinguishing *Phuphania* from other genera in the Dyakiidae are those of the amatorial organ: possession of small ducts clustered within the amatorial organ gland and fused lobes forming a cap over the amatorial organ. The amatorial organ of *Phuphania* most closely resembles those of *Kalamantania* and *Everettia* but in these genera the gland consists of few lobes, each entering the amatorial organ apically. In *Bertia* the amatorial organ is composed of many tightly packed lobes; each lobe with an individual duct apically entering the amatorial organ.

***Etymology.* –** '*Phuphania*' from the Phu (= Mountain) Phan range, the type locality.

Phuphania globosa, new species
(Figs. 2–5)

***Material examined.* –** Holotype: CUMZ 001760; type locality: Ban Dong Kham Pho (17º25'N 103°27'E), Waritchaphum District, Sakon Nakhon Province, northeastern Thailand.

Paratypes: nine paratypes: CUMZ 001761; one paratype: BMNH 20060750 and one paratype in the ZRC. Additional paratypes were collected from both the eastern and southern parts of the Phu Phan range through three provinces: Nakhon Phanom (east), Mukdaharn (south) and Kalasin (south). NHMSU: 0001 (3 specimens, 16º25'N 103°20'E); CUMZ: 001707 (3 specimens, 16º45'N 104°30'E).

***Etymology.* –** From the Latin '*globosa*' meaning 'spherical' with reference to the shape of the shell.

***Diagnosis.* –** Diagnosis of species as described for genus above.

***Description of key features of species.* –** Shell: medium size for Dyakiidae, dextral, semiglobose, and thin with 5-6 slightly convex whorls. Aperture large ovate and distinctly oblique, lip neither expanded nor reflected. Reproductive anatomy: the amatorial organ is a thick-walled stoutly cylindrical sac, distally fused with a gland consisting of an internal cluster of numerous small ducts, closely connected apically to form a large cap covering the amatorial organ. Penis cylindrical almost the same size and length as free oviduct. Epiphallus short, equal to penis length, straight. Vas deferens small, one and half times penial length, entering from free oviduct and passing close to distal end of epiphallus. Gametolytic sac inflated, gametolytic duct enters near proximal part of amatorial organ (Fig. 4).

***Description of holotype.* –** Shell height from apex to aperture 34.08 mm, diameter 28.70 mm, with 5¾ convex whorls, dextral, semiglobose, thin, body whorl large consisting of almost ¾ of the shell width, rounded, not deflected or distinctly angulated at periphery, fulvous above, embryonic whorls smooth, subsequent whorls with fine radial growth lines. Aperture large ovate, distinctly oblique, lip neither expanded nor reflected. Umbilicus narrow (Fig. 2). Ground colour of body grey, marked with black spots. Foot fringe distinct, about 5 mm wide, foot sole undivided, caudal gland without overhanging lobe (Fig. 3).

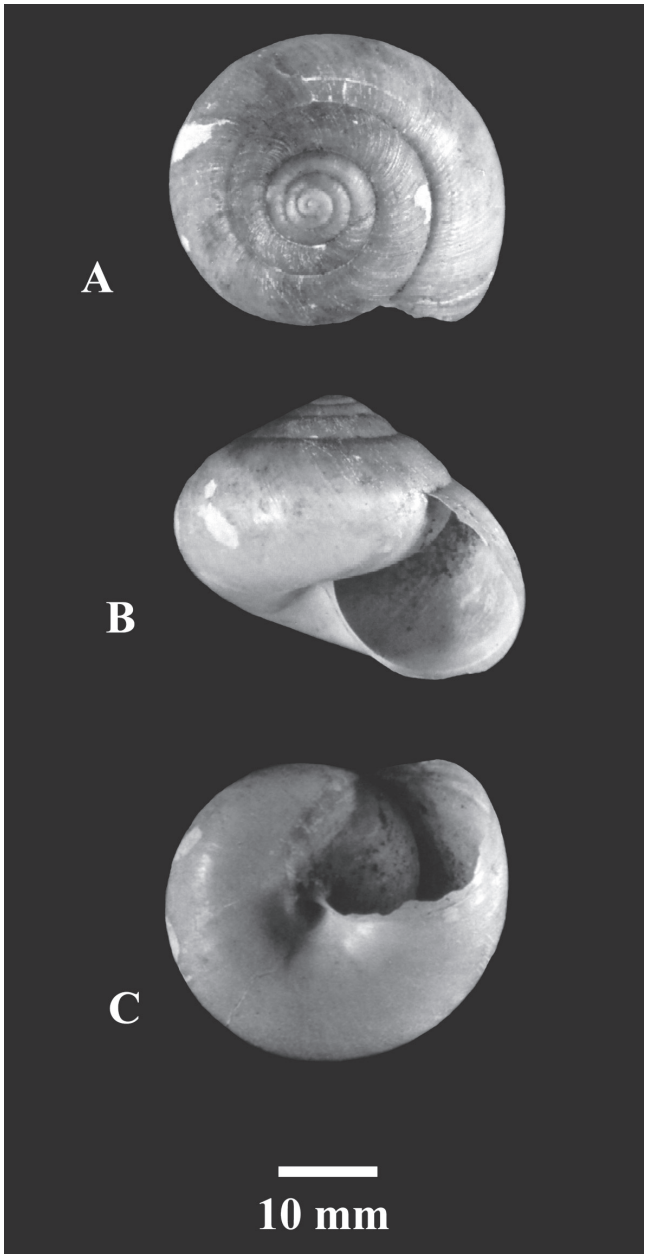


Fig. 2. External shell shape of *Phuphania globosa*, new species: A, dorsal view; B, apertural view; C, ventral view.

***Genital system.* –** Vas deferens marginally longer than penis and free oviduct, entering epiphallus subapically. Epiphallus almost equal in length to that of penis and to free oviduct, curved at junction with penis. Penis somewhat clavate, proximally wider than epiphallus, distal quarter narrows to width of epiphallus. Penial retractor muscle inserts near proximal end of epiphallus. Amatorial organ a stoutly cylindrical sac, inner surface of its prepuce with circular folds, muscular papilla of amatorial organ terminates in a minute pore, without thorn. The amatorial organ gland forms an ovate cap on the amatorial organ and consists of numerous ducts, leading from secretory cells lining the distal walls, the papilla forms a distal cap. Free oviduct rather long; a short wide duct proximal to the base of the amotorial organ prepuce expands into a large, elongate gametolytic sac, which possesses an apical ligament that attaches to the prostate gland (Fig. 4).

***Radula.* –** Central tooth indistinct tricuspid, narrow and elongate, the first and the second admedians tricuspid, narrow and elongate. Lateral teeth bicuspid with tiny ectocone, narrow and elongate. Marginal teeth narrow and elongate without lateral cusps (Fig. 5).

DISCUSSION

Phuphania globosa, new genus and new species, differs from other genera within Dyakiidae both in its genital system and shell shape. Conchologically, *Phuphania globosa* most closely resembles the larger shells of *Bertia*, but differs in being dextral and in lacking subperipheral dark bands. The genital system of *Phuphania* most closely resembles those of *Kalamantania, Everettia* and *Bertia* in the absence of a common amatorial organ duct and in containing more than four major amatorial gland lobes.

Fig. 3. Live adult of *Phuphania globosa*, new species.

Table 2. Comparison of shell and genital systems of new taxa and three related genera.

Character	*Kalamantania* (Schileyko, 2003)	*Everettia* (Schileyko, 2003)	*Bertia* (Schileyko, 2003)	*Phuphania*, new genus
Shell	dextral, depressed-subglobose	dextral, depressed-conic	sinistral, semiglobose	dextral, semiglobose-globose
Vas deferens	short, entering epiphallus subapically	short, entering epiphallus apically	long, entering epiphallus apically	rather short, entering epiphallus subapically
Epiphallus	rather long	rather long	moderately long	moderately long
Penis	clavate	clavate	cylindrical	clavate
Amatorial organ	rather bulky	rather bulky	very long, cylindrical	stoutly cylindrical sac
Gland of amatorial organ	consists of four lobes, each lobe with its own duct	consists of five lobes, each lobe with its own duct	many tightly packed lobes, each lobe with its own duct	the lobes fuse together as cap covers the tip of amatorial organ and consists of numerous ducts
Gametolytic duct entrance	between amatorial organ and free oviduct	upper prepuce of amatorial organ	lower prepuce of amatorial organ	lower prepuce of amatorial organ
Gametolytic duct and sac	without distinction	without distinction	very long duct and small sac	rather short duct and very large sac

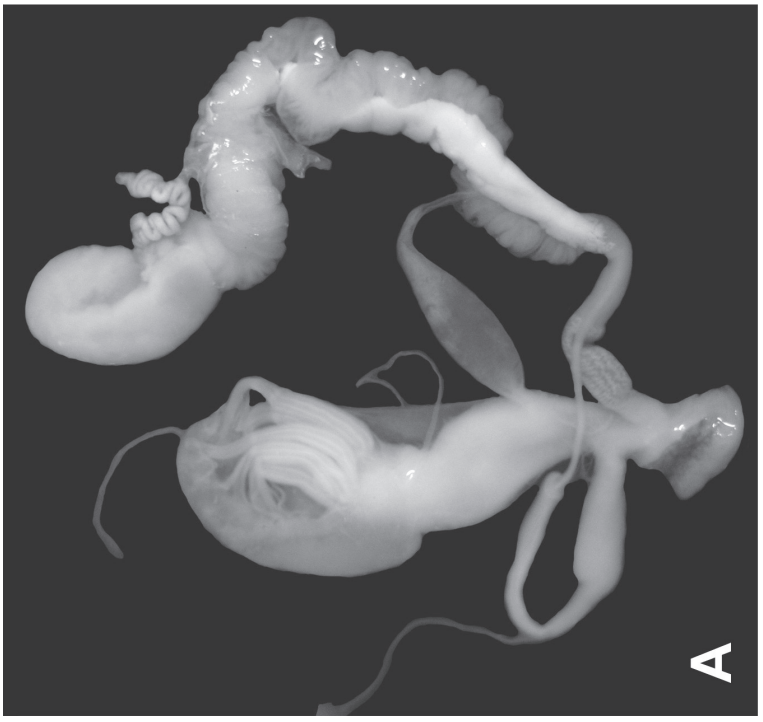
Hausdorf (1995) constructed a provisional morphological phylogeny of the Dyakiidae, indicating a close relationship between *Kalamantania* and *Everettia* based on the absence of a common duct in the amatorial organ gland leading to the papilla. However, morphological information on *Bertia* cited by Schileyko (2003) was not available to Hausdorf. In *Phuphania*, the rather short vas deferens inserting subapically on the epiphallus is similar to that found in *Kalamantania* (Godwin-Austen, 1891; Schileyko, 2003). However, the penis is larger and shorter than in *Kalamantania, Everettia* and *Bertia* (Schileyko, 2003). The amatorial organ most closely resembles that in *Kalamantania*, which is shorter than that of *Bertia* (Schileyko, 2003)**.** The inner surface of the *Phuphania* prepuce most closely resembles that in *Kalamantania.* The amatorial organ gland is distinct from that in other dyakiid genera, its fused lobes form a cap covering the tip of the organ, this cap consists of numerous ducts entering the amatorial organ apically. The gametolytic duct inserting on lower prepuce of the amatorial organ is similar to that found in *Bertia* but it is shorter and the gametolytic sac is larger than in *Bertia* (Schileyko, 2003)**,** with a terminal ligament attached to the prostate gland. All of these comparisons are shown in Table 2.

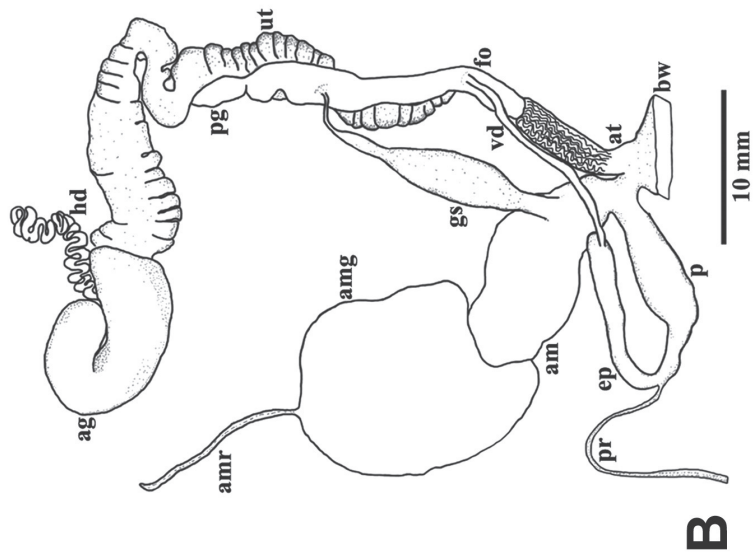
Hausdorf (1995) considered that the Dyakiidae represent an early divergence of the Limacoidea and that current distribution of the group offers potential for tracing Mesozoic vicariant events. He proposed two alternative hypotheses offering scenarios dominated by either dispersal or vicariant events for the geographical origin of the Dyakiidae. These were colonisation of Sundaland from Eurasia or origins via Mesozoic tectonic plate fragments from Gondwana. Hausdorf's (1995) phylogeny of the Dyakiidae was largely based on a transformation series of increasing complexity and number of glands and ducts supplying the amatorial organ. Polarity was hypothesized to be based on a plesiomorphic condition in which one or two glands are connected by a single duct, such as in Q*uantula,* with increased complexity in gland and duct numbers as the condition of derived states. *Everettia* exhibited the most derived character state in Hausdorf's cladogram. However, using an extension of Hausdorf's transformation series, the *Bertia* amatorial organ system is more derived than that of *Everettia* and *Phuphania* possesses the most derived state in the Dyakiidae, with numerous ducts supplying glandular secretions to the amatorial organ.

Based on the geographic pattern of endemism, the range of dyakiid snails can be divided into four areas after modification from Fig. 3 of Hausdorf (1995): Area 1, Sumatra, Java to Lesser Sunda Islands; Area 2, Borneo and part of Sulawesi; Area 3, Malay Peninsula, south and east of Thailand; Area 4, northeast Thailand and Cambodia. Areas 1 and 2 are considered to have been parts of a peninsula projecting southward from the Asian continent during the glacial periods of the Pleistocene (Heaney, 1991). Many mammalian species in this region are widely distributed, demonstrating dispersals across the Sunda Shelf during those periods (Heaney, 1984). Areas 1 and 3 have been assigned to different provinces in zoogeographic classifications of Southeast Asia on the basis of other taxonomic groups (e.g., Lepidoptera in Holloway, 1987); entomologists and ornithologists have linked Area 4 and Area 3 (Holdhaus, 1934; Mayr, 1940). Northeastern Thailand and Cambodia have been considered to form a distinct biogeographical area, the Indo-Chinese or Siamese area (Solem, 1959). We discuss the zoogeography of dyakiid snails on the basis of these four areas.

Phuphania is restricted to Area 4. *Elaphroconcha* to Area 1, *Everettia* and *Kalamantania* to Area 2, *Quantula* to area 3, *Pseudoplecta* to Areas 1 and 2. *Asperitas* ranges east from Sulawesi into the Auatralasian Region and *Dyakia* has the widest distribution in Areas 1, 2 and 3.

The distribution of *Phuphania* in the Phu Phan range is the northernmost distribution of the Dyakiidae and this is





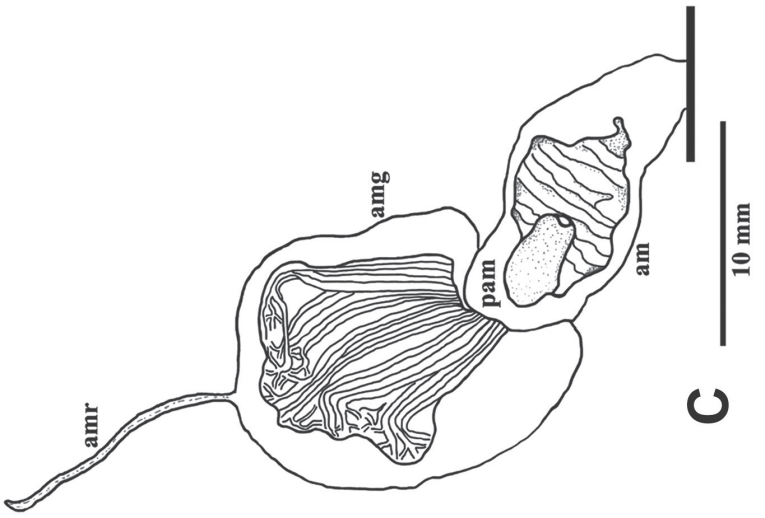


Fig. 4. Genital system of *Phuphania globosa*, new species: A, genital system; B, schematic drawing of genital system; C, interior structures of amatorial organ gland (amg) and amatorial organ (am).

consistent with Hausdrof's area cladogram. The ancestor of the *Asperitas* + *Dyakia* + *Kalamantania* + *Everettia* clade probably originated in Borneo (Hausdorf, 1995). Housdorf suggested two hypotheses for dispersal of the ancestor of this group. An extention north to Cambodia and the Khorat Plateau, might have occurred during the Pleistocene Ice age when sea levels were much lower than those of today and Sundaland was a continuous land area. This would give a time scale of only two million years. The alternative hypothesis is that the generic level differences may have originated very much earlier and the separation of these populations might be correlated with the fragmentation of Sundaland as a result of the rise in sea levels during the late Cretaceous or early Tertiary (Audley-Charles, 1987). The separation of *Phuphania* from *Bertia* might have arisen following uplift of the Khorat Plateau from the Thailand and Cambodian lowlands in the early Tertiary. This would have allowed time for *Phuphania* to become adapted to the unique dry climatic pattern that became established on the Phu Phan range. Placement of the Australian snail *Craterodiscus* in the Dyakiidae (Wade et al., 2001; Wade et al., 2006) provides support for Hausdorf's hypothesis that the Dyakiidae may have a Gondwana origin.

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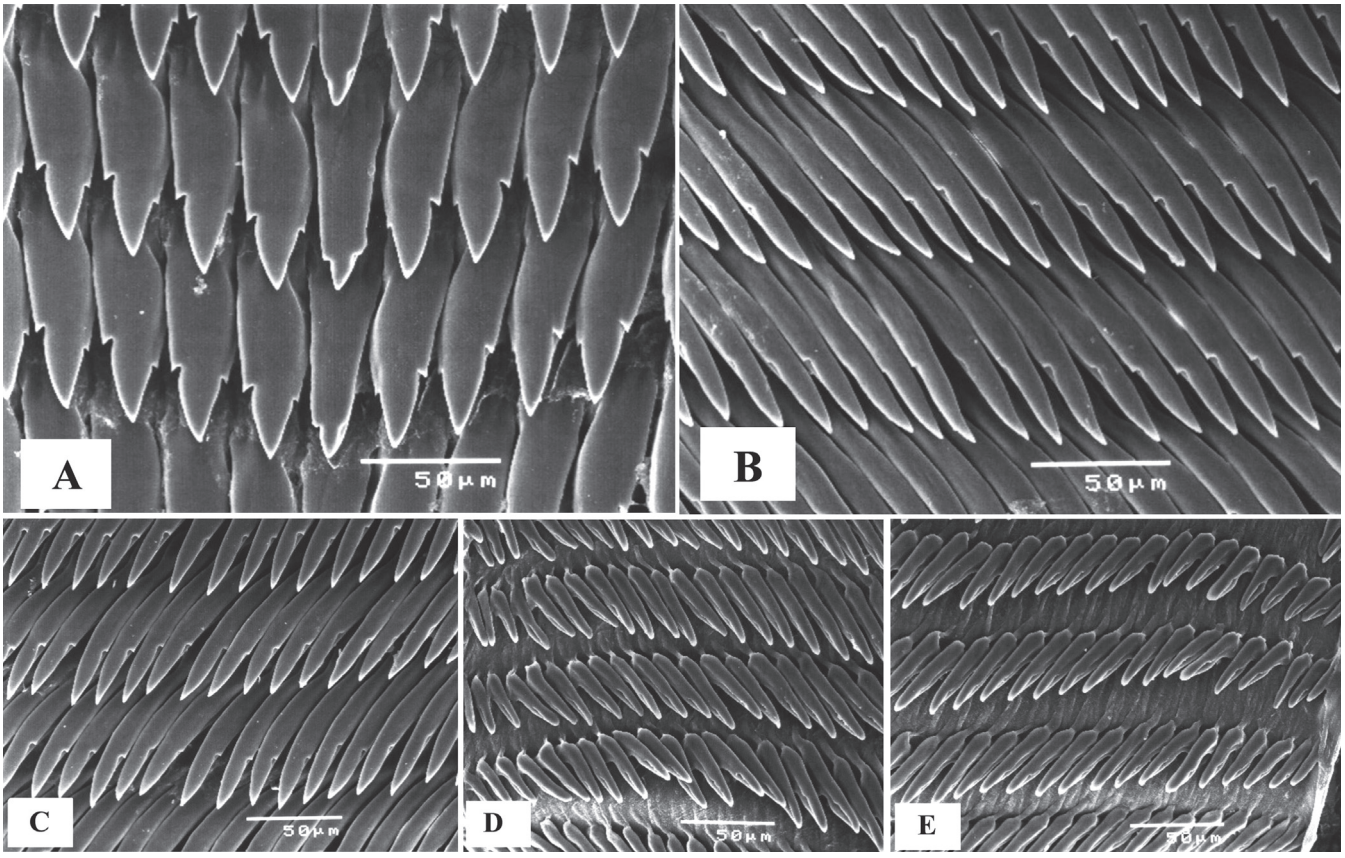

Fig. 5. Radula of *Phuphania globosa*, new species: A, central tooth and lateral teeth; B, left lateral teeth; C, right lateral teeth; D, left marginal teeth; E, right marginal teeth.

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