

TAXONOMIC REVISION OF *DYAKIA JANUS* FROM PENINSULAR MALAYSIA (PULMONATA: DYAKIIDAE), WITH NOTES ON OTHER SINISTRALLY COILED HELICARIONOIDS

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ABSTRACT. — The taxonomic status of *Dyakia janus* (Beck, 1837), a poorly known Malayan land snail, is re-assessed and a neotype designated. *Dyakia janus* possesses a long epiphallus, but a flagellum and penial verge are both absent. The species is also characterised by having a long gametolytic duct, an amatorial organ comprising three major glands and a calcified, spiked papilla, a vagina surrounded by sponge-like tissue, a mantle collar that has a posterior right dorsal lobe, and a radula that exhibits unicuspid teeth. Two sinistral species previously misidentified as true *Dyakia*, namely *Helix retrorsa* Gould, 1844 and *Nanina salangana* Martens, 1883, were compared with *D. janus*. We show that the former two species differ from true *Dyakia* s.s. in the absence of an amatorial organ gland and presence of a penial sheath, epiphallal caecum, flagellum, and a gametolytic sac that is connected by a short duct to the vagina. The reproductive system is a significant source of taxonomic characters for generic classification, and these two species should rightly be assigned to the family Ariophantidae instead of Dyakiidae.

KEY WORDS. — Ariophantidae, *Hemiplecta*, land snail, systematics, Peninsular Malaysia

INTRODUCTION

The Dyakiidae are a diverse family of land snails containing more than 70 recognised species in Southeast Asia. They possess dextral or sinistral helicoid shells, and are characterised by having a unique amatorial organ structure in the genitalia (Gude & Woodward, 1921; Laidlaw, 1931; Hausdorf, 1995). The Dyakiidae include two sinistral genera *Dyakia* Godwin-Austen, 1891 and the monotypic *Rhinocochlis* Thiele, 1931. Thirteen dextral genera have been recognised (Hausdorf, 1995; Schileyko, 2003; Tumpeesuwan et al., 2007). Of these, 10 genera were included in a cladistic analysis based on morphological characters (Hausdorf, 1995). However, the relationships between genera were not fully resolved in that analysis.

Within the Dyakiidae, *Dyakia* is the most speciose genus (Hausdorf, 1995; Schileyko, 2003) with 22 recognised species of which six exhibit restricted distributions in Indochina

and peninsular Malaysia (Laidlaw, 1963; Maassen, 2001). It is widely recognised that shell characters are subject to homoplasy and shell morphology alone is often insufficient for establishing phylogenetic relationships. Characters of the reproductive system can provide more reliable characters than shells for establishing phylogenetic relationships in many stylommatophoran snail groups (e.g., Sutcharit & Panha, 2006, 2008; Wu & Guo, 2006; Wu et al., 2008; Winter, 2008; Liew et al., 2009), but unfortunately, the reproductive organs of only two *Dyakia* species, *D. hugonis* (Pfeiffer, 1863) and *D. rumphii* (von dem Busch, 1842) have been described (Semper, 1870; Godwin-Austen, 1891; Wiegmann, 1893, 1898).

Land snail surveys along the Malay Peninsula (southern Thailand and peninsular Malaysia) yielded three species that on the basis of their sinistral helicoid shells were provisionally placed in *Dyakia*. However, examination of the reproductive organs of these three species clearly

demonstrates that two species possess characters that place them in the Ariophantidae and only one of the species, *D. janus* (Beck, 1837), belongs in *Dyakia*.

MATERIAL AND METHODS

Examples of live *D. janus* collected from Pulau Besar, Johor, Malaysia were drowned in water prior to fixation and preservation in 70% ethanol. The genital organs of five specimens were examined. Radulae were extracted and examined under a scanning electron microscope (JEOL, JSM-5410 LV). The radula shape and teeth formula were observed and recorded.

Voucher specimens were deposited in Chulalongkorn University Museum of Zoology, Bangkok, Thailand (CUMZ). Specimens from general collections and type specimens were also examined at the Natural History Museum, London (BMNH); Muséum National d'Histoire Naturelle, Paris (MNHN); Museum für Naturkunde of the Humboldt University, Berlin (ZMB); and Zoological Museum, University of Copenhagen, Copenhagen (ZMUC).

In descriptions of the genitalia, we use 'proximal' to refer to the region closest to the genital opening and 'distal' to refer to the region furthest away from the genital opening. The genital terminology and abbreviations used here follows that of Godwin-Austen (1891), Tumpeesuan et al. (2007), and Sutcharit & Panha (2008): ad, amatorial organ duct; ag, albumin gland; am, amatorial organ; amg, amatorial organ gland; amp, amatorial organ pilaster; an, anus; ap, amatorial organ papilla; at, atrium; e, epiphallus; ec, epiphallic caecum; fl, flagellum; fo, free oviduct; gd, gametolytic duct; gs, gametolytic sac; h, heart; hd, hermaphroditic duct; hg, hermaphroditic gland; i, intestine; k, kidney; ldl, left dorsal lobe; ov, oviduct; p, penis; pp, penial pilaster; pr, penial retractor muscle; prdl, posterior right dorsal lobe; psh, penial sheath; pv, pulmonary vein; r, rectum; rdl, right dorsal lobe; rm, retractor muscle; ur, ureter; v, vagina; vd, vas deferens; vp, vaginal pilaster.

SYSTEMATIC ACCOUNT

Family Dyakiidae Gude & Woodward, 1921

Genus *Dyakia* Godwin-Austen, 1891

Types species. — *Helix hugonis* Pfeiffer, 1863, by original designation. Syntypes BMNH 1975118 (three shells; the specimen that most closely matches the description and measurements given in the original description is shown in Fig. 1A).

Remarks. — From previous records, six *Dyakia* s.l. species have been reported from Indochina and peninsular Malaysia (Laidlaw, 1963; Panha, 1996; Hemmen & Hemmen, 2001; Maassen, 2001). Three species, morphologically classified as "*Dyakia*" *retrorsa* (Gould, 1843), "*Dyakia*" *salangana* (Martens, 1883), and *D. janus*, were collected and examined (as interpreted by Laidlaw, 1963).

Helix retrorsa Gould, 1843 and *Nanina salangana* Martens, 1883 have large sinistral shells that are brown to yellowish with thin growth lines. The last whorl is large, with or without peripheral keels. These two species have similar genitalia, and *Nanina salangana* Martens, 1883 is figured as an example. The genitalia comprise a thin penial sheath (psh), straight epiphallic caecum (ec), short flagellum (fl), bulbous gametolytic sac (gs) and large cylindrical amatorial organ (am). The mantle collar has a large left dorsal lobe (ldl), undivided right dorsal lobe (rdl), and shell lappets are absent (Fig. 2A–C). The central tooth is unicuspid and triangular in shape; the lateral teeth are unicuspid whilst bicuspid marginal teeth are present towards the margins (Fig. 2D, E). The genitalia of these two species are clearly distinct from *Dyakia*, notably in the absence of an amatorial organ gland and presence of a penial sheath, epiphallic caecum, flagellum and a gametolytic sac connected by a short duct to the vagina. Clearly the sinistral shells, while showing marked similarity to true *Dyakia*, had misled previous workers and the assumption that such sinistral shells were uniquely derived in *Dyakia* (Hausdorff, 1995) is disproved. In fact the reproductive systems of *Helix retrorsa* Gould, 1843 and *Nanina salangana* Martens, 1883 demonstrate that they are better placed in the Ariophantidae sensu Schileyko (2002).

Dyakia janus (Beck, 1837)

Figs. 1B–F, 3; Table 1

Helix Ianus bifrons Chemnitz, 1795: 307, 308, pl. 213, Figs. 3016, 3017, type locality: Südsee [Rejected species-group name by the commission (ICZN, 1944: Opinion 184)]

Nanina (Ariophanta) janus Beck, 1837: 5, type locality: Südsee (=Islands of South Sea) and Java

Helix janus: Pfeiffer, 1847: 88, 89, pl. 11, Figs. 4–6; Pfeiffer, 1848: 77

Helix sannio Pfeiffer, 1854: 57, type locality: unknown; Pfeiffer, 1859: 253

Nanina albersi Martens, 1864: 265, type locality: Malakka; Martens, 1867: 224, 225, pl. 2, Fig. 3; Tryon, 1886: 20, pl. 3, Fig. 37

Nanina sannio: Tryon, 1886: 18, pl. 2, Fig. 26

Nanina janus: Tryon, 1886: 19, pl. 3, Figs. 34, 36

Dyakia albersi: Gude, 1903: 49

Dyakia sannio: Laidlaw, 1931: 191, 201; Laidlaw, 1933: 234; Laidlaw, 1963: 146; Maassen, 2001: 107

Dyakia janus: Laidlaw, 1931: 192, 200; Laidlaw, 1933: 226; Laidlaw, 1963: 141, 142; Maassen, 2001: 105

Type material. — Designated neotype BMNH 42.5.10.1463 (Fig. 1B, height 23.9 mm, width 37.5 mm, 6¾ whorls). Based on the neotype, the type locality is Mount Ophir, peninsulæ Malaccanæ [=Gunung Ledang, Johor, Malaysia (02°22'N, 102°36'E)]. Additional material from the same lot of neotype BMNH 42.5.10.1464–5 (2 shells, height 23.5, 24.2 mm, width 35.5, 36.1 mm, 6¾ whorls).

Other material. — The specimen that most closely matches the description and measurements given in the original description is designated here as the lectotype of *Helix sannio* Pfeiffer, 1854, BMNH 20100242.1 (Fig. 1E), and paralectotype BMNH 20100242.2 (1 shell). Syntypes of *Nanina albersi* Martens, 1864, ZMB 57526 (Fig. 1F) and 57525 are from Malacca. Other specimens from Malacca, Malaysia: BMNH 1904.5.26.36 (1 shell), 58.5.12.267 (3 shells), A. S. Kennard coll. (1 shell). Perak, Malay Peninsular: BMNH 97.3.13.5–6 (2 shells), 92.8.24.24 (1 shell). Batang Padang,

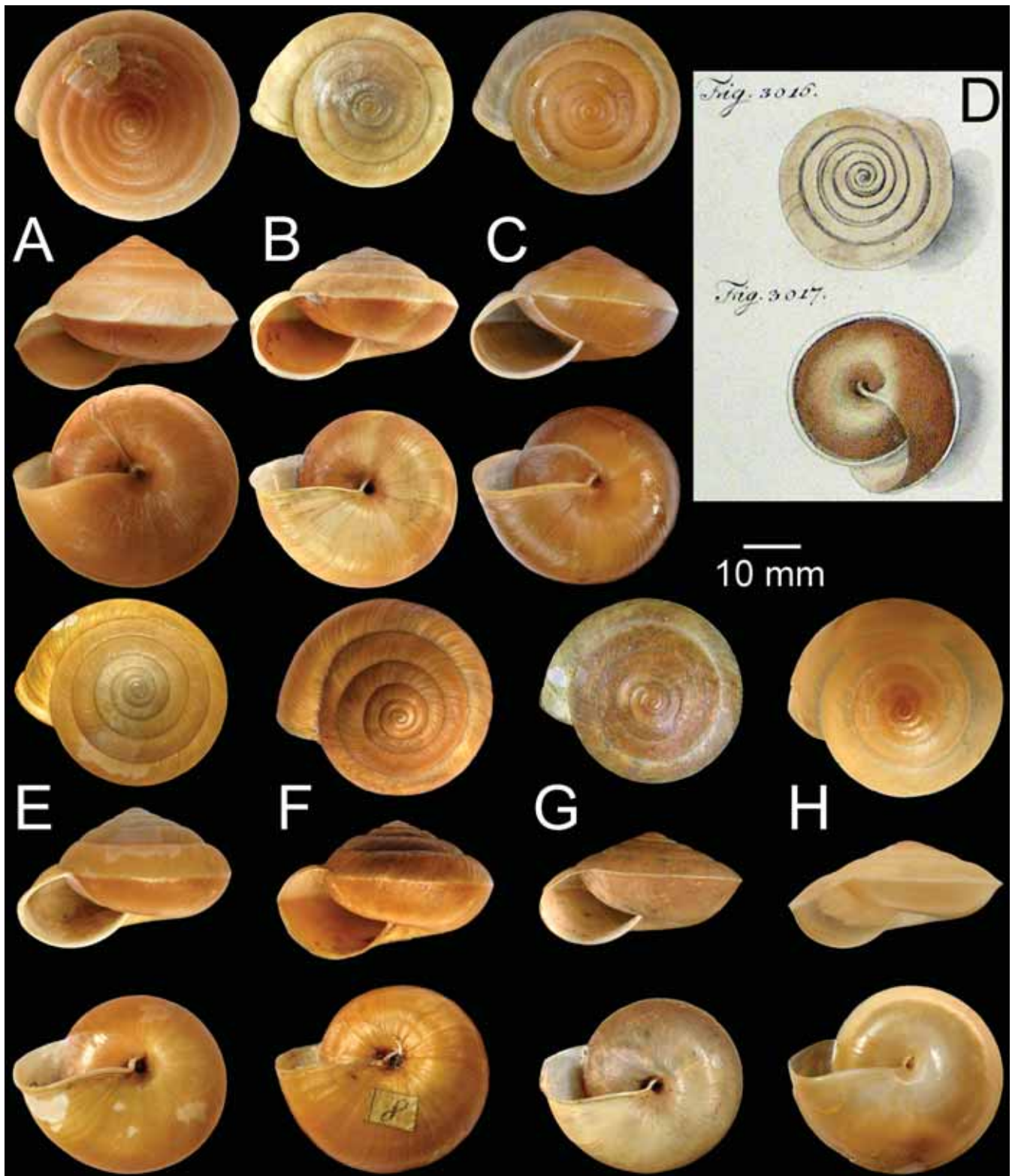


Fig. 1. Shells of *Dyakia* species. **A.** Syntype of *Dyakia hugonis* (BMNH 1975118). **B–F.** *Dyakia janus*; **B.** neotype (BMNH 42.5.10.1463) from Malacca, Malaysia; **C.** examined specimen from Johor, Malaysia (CUMZ 4919); **D.** figures of “*Helix janus bifron*” after Chemnitz (1795, pl. 213, Figs. 3016, 3017); **E.** lectotype of *Helix sannio* Pfeiffer, 1854 (BMNH 20100242); and **F.** syntype of *Nanina albersi* Albers, 1864 (ZMB 57526). **G.** Syntype of *Dyakia kintana* (MNHN, 8 shells). **H.** Holotype of *Dyakia lindstedti* (BMNH).

Table 1. Comparisons of shell, genital system, mantle collar, and radula morphology among the three species of *Dyakia* s.s. Data concerning *D. rumphii* and *D. hugonis* were based on Semper (1870), Wiegmann (1893, 1898), Godwin-Austen (1891), Hausdorf (1995), and Schileyko (2003). *Data from Godwin-Austen (1891: 30). **Data from Wiegmann (1898: pl. 26, Fig. 18). ?Data not found in the literature. ¹Abbreviations used are explained in the Material and Methods section.

Characters	<i>Dyakia janus</i> (Beck, 1837)	<i>Dyakia rumphii</i> (von dem Busch, 1842)	<i>Dyakia hugonis</i> (Pfeiffer, 1863)
Shell	helicoid sinistral	helicoid sinistral	helicoid sinistral
Penis	cylindrical	long cylindrical	cylindrical
Epiphallus	present, approximately same length with penis	present, shorter than penis	present, approximately same length with penis
Penial retractor muscle	attached at penis and epiphallus junction	attached at penis and epiphallus junction	attached at penis and epiphallus junction
Vas deferens	enters epiphallus apically	enters epiphallus apically	enters epiphallus apically
Penial verge	absent	?	?
Amatorial organ	bound with oviduct	?	?
Number of lobes on amatorial organ gland	three	four	four
Duct of amatorial organ gland	each lobe has its own duct, and fused before entering amatorial organ	fused before entering amatorial organ	fused before entering amatorial organ
Gametolytic duct / sac	same length with amatorial organ / large sac	shorter than amatorial organ / large sac	longer than amatorial organ / indistinct sac
Free oviduct	thin and distinct wall	?	?
Radula: Central tooth	unicuspid	tricuspid (very small lateral cusp)	unicuspid* / tricuspid**
Radula: Lateral teeth	unicuspid	tricuspid (very small lateral cusp)	unicuspid* / tricuspid**
Radula: Marginal teeth	unicuspid	unicuspid	unicuspid* / bicuspid**
Mantle edge structure ¹	ldl, rdl, prdl	?	ldl, rdl, prdl
Geographical distribution	Perak, peninsular Malaysia	west Java, southern Sumatra	north Borneo, Natuna Islands

Malay Peninsula: BMNH 97.3.15.17–18 (2 shells). Gunung Benom, Malaya: BMNH ex. University of Malaya coll. (1 shell). Bukit Besar, Malaysia: BMNH 1904.5.26.36 (1 shell). Pulau Besar, Mersing, Johor, Malaysia (2°26'17.24"N, 103°58'51.75"E): CUMZ 4918, 4919 (Fig. 1C). Südsee [=Islands of South Sea] ex. Spengler collection ZMUC GAS-411 ex. Spengler's coll. dated before 1795 (2 shells, fragile juveniles).

Taxonomic remarks. — Chemnitz (1795) species level names, including *Helix Ianus bifrons*, were rejected by the ICZN (1944) on the basis that binomial nomenclature was not consistently maintained in this work. The combination *Nanina (Ariophanta) janus* was made available by Beck (1837) and specimens in “Museo Spengleriano” as indicated by Chemnitz (1795: 309), and known to H. Beck (1837), are acknowledged as the original type series (ICZN, 1999: Art. 72.4). Unfortunately, both syntype lots cannot be located and are assumed to be lost. The nominal species-name is considered as doubtful application and confusing status. In addition, Chemnitz's figures are poor and inadequate for recognising the identity of this species (Fig. 1D). We therefore consider *Nanina (Ariophanta) janus* Beck, 1837 to be a nomen dubium. However, the species has been consistently known and understood sensu Pfeiffer (1847; Fig. 1B). Pfeiffer provided an accurate figure and description for the specimen, on which he based his descriptions (Pfeiffer, 1842: 87; 1847:

88, 89). Therefore, this specimen is designated herein as the neotype (BMNH 42.5.10.1463, Fig. 1B).

Shell. — Shell large, depressed conic, thickened and sinistral. Whorls 6–7, increasing regularly, slightly convex, with very wide and shallow suture. Spire convex; apex acute; embryonic shell smooth; following whorls with thin growth lines and spirally undulated surfaces. Last whorl rounded to shouldered, with slight peripheral keel that disappears proximal to the aperture; a narrow dark brown peripheral band usually present; periostracum thin corneous. Upper shell surface shades of pale to somewhat darker brown; lower shell surface usually darker brown. Aperture ovate; lip slightly thickened in adult snails. Columella slightly dilated; parietal callus thin and translucent. Umbilicus narrow and deep.

Genitalia. — Atrium (at) very short. Penis (p) proximally enlarged, cylindrical, and tapering to small tube. Penial retractor muscle (rm) thin and long. Epiphallus (e) long and slender tube, similar in length to penis and with similar diameter to distal part of penis; flagellum absent. Vas deferens (vd) relatively small and thin tube extending from free oviduct (fo) and entering the epiphallus distally. Internal wall of penis: proximally with large and irregular penial pilasters (pp) for around one-third length of chamber; distally with

very thin, smooth longitudinal pilasters; penial verge absent (Fig. 3A, B).

Gametolytic duct (gd) a long and large cylinder, distally with elongated and bulbous gametolytic sac (gs). Amatorial organ (am) well developed, large elongated cylinder; proximally attached to gametolytic duct. Amatorial organ gland (amg) composed distally of three major lobes bounded to amatorial organ by thin connective tissue. Each of the three major lobes of the amatorial organ gland extends proximally into thin ducts (ad) that are twisted together and bound with thin connective tissue before fusing prior to entering the distal tip of the amatorial organ. The internal wall sculpture of the amatorial organ consists of small longitudinal amatorial organ pilasters (amp); proximally these are interrupted to produce irregular papillary knobs arranged in lines that occupy one-third of the chamber; distally they are connected to form

uninterrupted longitudinal pilasters. The conical amatorial organ papilla (ap) is tipped by a small calcified spike (Fig. 3A, B).

Vagina (v) long, cylindrical, and surrounded by sponge-like tissue. Internal wall of introverted chamber consists of strong irregular shaped but smooth pilasters (vp). Oviduct (ov) long, with lobules; prostate gland bound to oviduct. Albumen gland (ag) large and lingulate. A small convoluted hermaphrodite duct (hd) connects lobules of the hermaphroditic glands (hg) with the talon (Fig. 3A, B).

External features. — Living snail with long and greyish-brown tentacles. Skin reticulated brown with black reticulations around head. Foot sole relatively elongated, broad and unipartite. Sole of foot brownish and unspotted; side of body brownish; upper part of tail appears dark greyish.

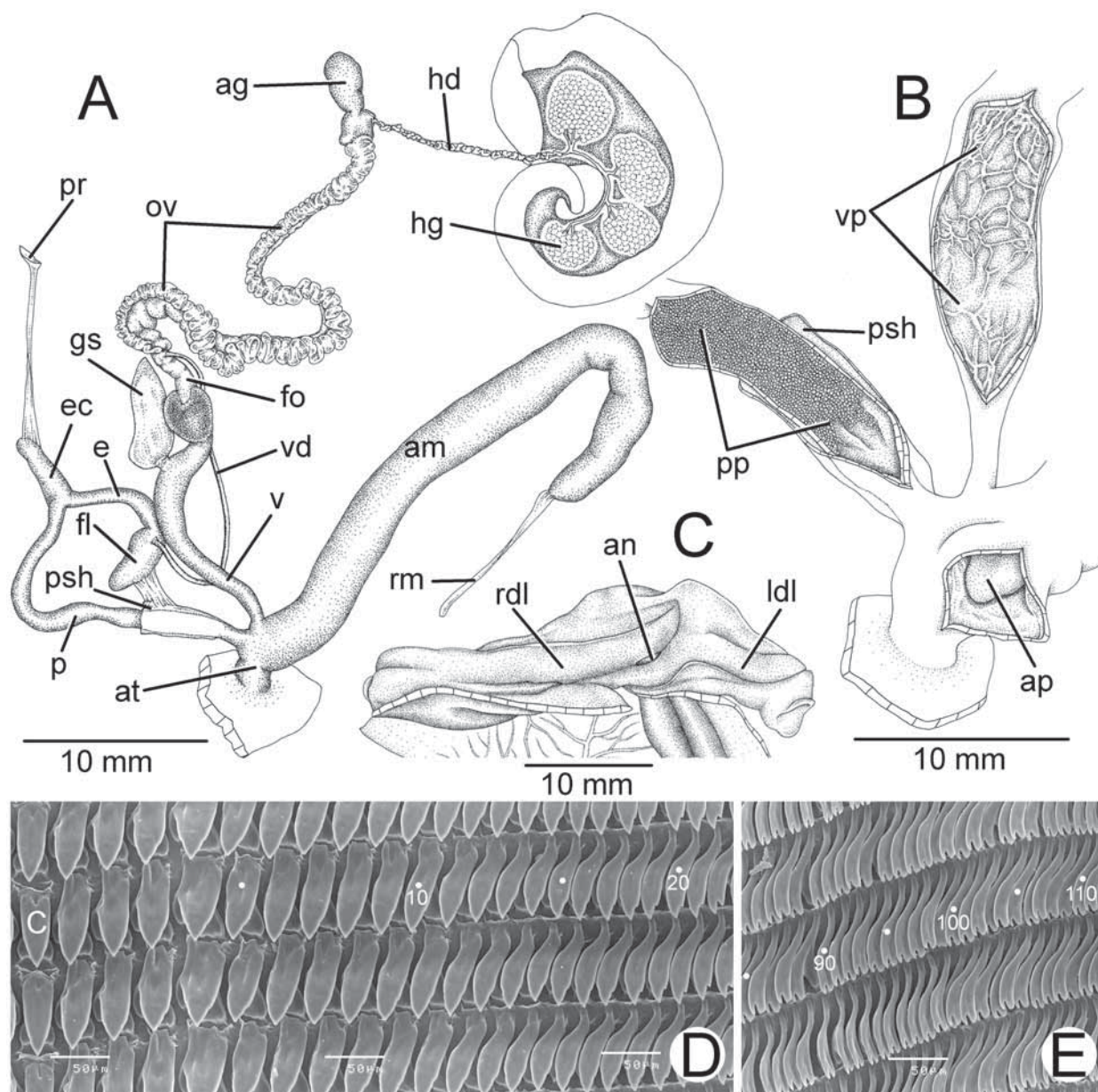


Fig. 2. Genitalia, mantle collar, and radula morphology of *Nanina salangana* Martens, 1883 from Songkhla, Thailand (CUMZ 4920). **A.** Whole genital organ. **B.** Internal wall sculpture of penis, vagina and amatorial organ. **C.** Ventral view of mantle collar region. **D, E.** SEM image of radula; central tooth indicated by 'C'. Numbers indicate tooth order from lateral to marginal end.

Tail long, curved mid-dorsally, tall dome-shaped in cross section. Caudal horn not overhanging; caudal foss, short vertical slit in tail above sole margin. Pedal groove typical aulacopodoid and well defined (Fig. 3C).

Viewed internally (thus with reversed left/right orientation in Fig. 3D), mantle collar with large shell lobes. Left dorsal lobe (ldl) large and thickened. Right dorsal lobe (rdl) undivided. Small ear-shaped posterior right dorsal lobe (prdl) present. Right and left shell laps absent (Fig. 3D).

Pulmonary cavity with typical sigmurethan heart (h, auricle and ventricle) located near the kidney (k). Pulmonary cavity approximately four times longer than broad. Pulmonary vein (pv) and venation on lung cavity well developed and distinct. Kidney (k) elongated and slender, approximately one-third of pulmonary cavity length. Ureter (ur) sigmoid, closed tube arising from tip of kidney, extending along the kidney, and curved adjacent to rectum (r). Anus (an) adjacent to mantle collar (Fig. 3D).

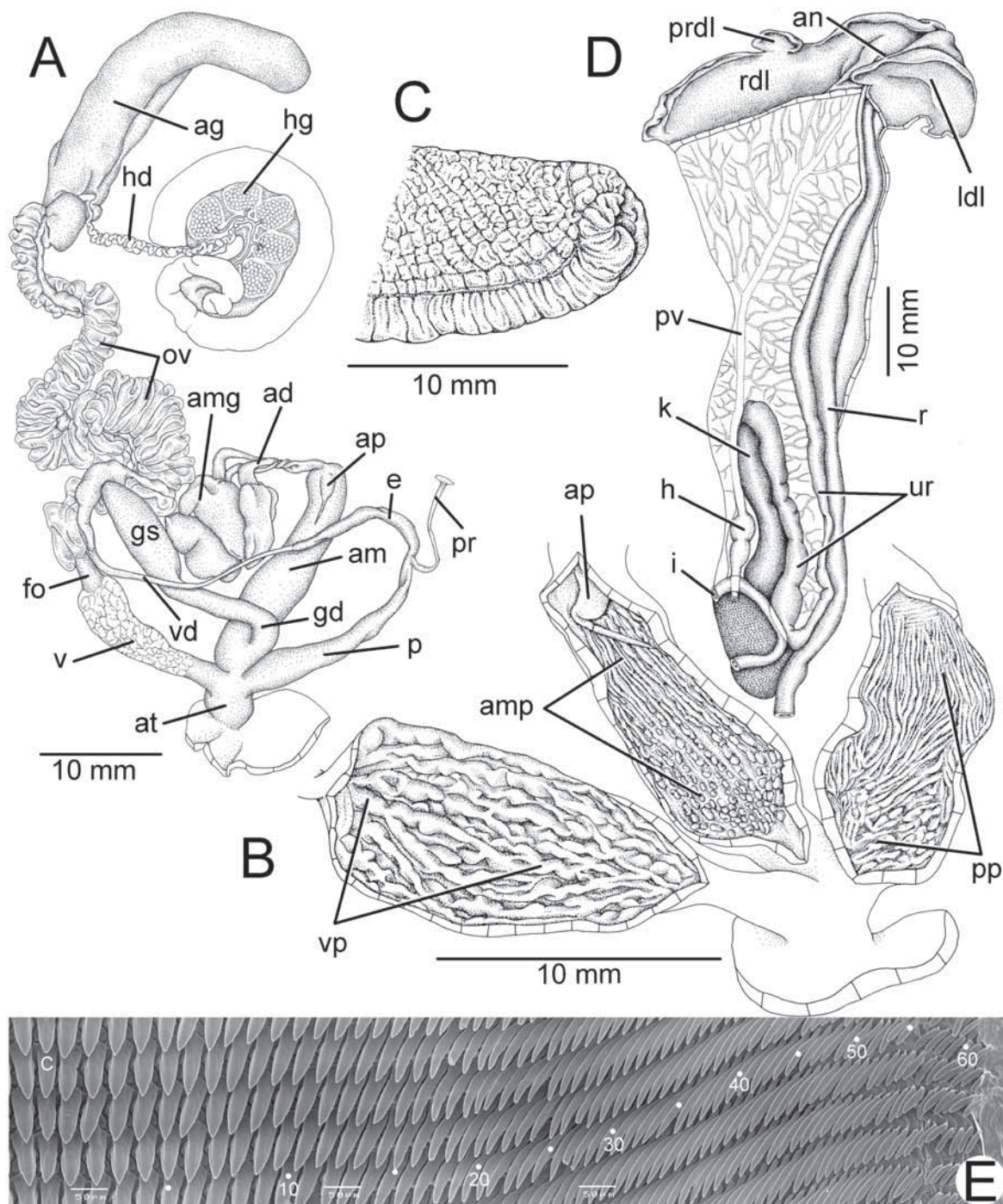


Fig. 3. Genitalia, pallial system, caudal region, and radula morphology of *Dyakia janus* from Johor, Malaysia (CUMZ 4919). **A.** Whole genital organ. **B.** Internal wall sculpture of penis, amatorial organ and vagina. **C.** Left view of caudal region. **D.** Pallial system, lung cavity and ventral view of mantle edge. **E.** SEM image of radula; central tooth indicated by 'C'. Numbers indicate tooth order from lateral to marginal end.

Table 2. Comparisons of shell and genital system of *Dyakia* and *Rhinocochlis*, two closely related genera. The nominal species name in the parentheses is the type species. The data are taken from Wiegmann (1893, 1898), Godwin-Austen (1891), Hausdorf (1995), and Schileyko (2003).

Characters	<i>Dyakia</i> Godwin-Austen, 1891 (<i>Helix hugonis</i> Pfeiffer, 1863)	<i>Rhinocochlis</i> Thiele, 1931 (<i>Helix nasuta</i> Metcalfe, 1852)
Shell	sinistral, turbate	sinistral, lens-shaped
Penis	cylindrical	short bulky
Penial verge	absent	present
Amatorial organ gland	3–4 lobes, bound with amatorial organ	2 lobes, bound with amatorial organ
Duct of amatorial organ gland	twisted, and fused before entering amatorial organ	twisted, and entering amatorial organ directly
Gametolytic duct / sac	long / with large, distinct sac	long / indistinct subdivision
Free oviduct	distinct wall	indistinct wall
Geographical distribution	Indochina, Greater Sunda islands	restricted on Borneo

Radula. — Teeth arranged in V-shaped rows with approximately 134 (68–(15–20)–1–(15–20)–65) teeth. Central tooth symmetric unicuspid and sword-shaped. Lateral teeth asymmetric unicuspid, sword-shaped, and inclined towards central tooth. Marginal teeth start from tooth 15–20, elongate sword-shaped, apically pointed; outermost teeth shorter and apically more rounded than inner teeth (Fig. 3E). Jaw smooth (without vertical ribs), crescentic, with anteriorly convex cutting margin.

Distribution. — Chemnitz (1795) gave the locality of this species as “Islands of the South Sea” (Laidlaw, 1931: 193), and “Java” was subsequently (and inaccurately) added by Beck (1837). The type locality is Mount Ophir, peninsular Malaccanae. Further distribution records demonstrated its geographic range to be restricted to the southern region of peninsular Malaysia: Mount Ophir, Malacca (Pfeiffer, 1847); Malaya, Billiton, Bangka, Selangor, Malacca, Pulau Aor in Johor, Sungei Rumpon in Pahang, and Singapore (Laidlaw, 1931, 1933, 1963; Benthem Jutting, 1949). Fresh material examined in the current study is from Pulau Besar, a small granitic island about 10 km from Mersing, Johor, off the east coast of peninsular Malaysia.

CONCLUSIONS

Six nominal species have previously been placed in synonymy with *D. janus*: *Helix balesteriana* Lea, 1841, *Helix mackensiana* Souleyet, 1841, *Helix sannio* Pfeiffer, 1854, *Helix lindstedti* Pfeiffer, 1856, *Nanina albersi* Martens, 1864, and *Ariophanta kintana* Morgan, 1885 (Pfeiffer, 1847; Godwin-Austen, 1891; Laidlaw, 1933, 1963). Following examination of type material of *Helix sannio* and *Nanina albersi*, we confirm their status as junior synonyms of *D. janus*. Type material of *Helix balesterianus* and *Helix mackensiana* has not been located and we have provisionally treated them here as distinct species.

On the basis of current evidence available for shell morphology, we recognise *D. lindstedti* and *D. kintana* as distinct, valid species. *Dyakia lindstedti* differs from *D. janus* by having a smooth shell surface, with low and depressed

spire (or lenticular shell shape). The last whorl has a sharp, continuous peripheral keel to aperture, and its peristome is narrow and sickle shaped, with a simple apertural lip (Fig. 1H). *Dyakia kintana* is distinguished by its larger shell size (width 30–35 mm), thickened apertural lip and in having its last whorl angulated with a strong peripheral keel (Fig. 1G). In contrast, the smaller shell (width 25–30 mm) of *D. janus* has a surface with thin radial ridge and an elevated spire (dome shaped), with its last whorl rounded to slightly angulated and having an ovate aperture.

Relationships of *Dyakia* species. — Hausdorf (1995; Table 1) carried out a morphological phylogenetic analysis of *Dyakia* s.l. Amongst current recognised genera of the Dyakiidae, *Dyakia* s.l. and *Rhinocochlis* possess sinistral shells, and the analysis suggested their uncertain relationships due to the incomplete anatomical information available for *Rhinocochlis* (Hausdorf, 1995). A comparison of taxonomic characters of these two genera is provided in Table 2. A close relationship between *Dyakia* s.s and *Rhinocochlis* is suggested, and sinistral shell coiling is regarded as a synapomorphic character. However, the amatorial organ gland comprising two attached lobes, and the direct insertion of a duct into the amatorial organ gland, are unique characters that distinguish members of the two genera (Table 2; Hausdorf, 1995; Schileyko, 2003). Nevertheless the relationships between *Dyakia*, *Rhinocochlis*, and other genera such as *Asperitas*, *Kalamantania* and *Everettia*, are still uncertain.

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