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A NEW *GEORISSA* (GASTROPODA: NERITOPSINA: HYDROCENIDAE) FROM A LIMESTONE CAVE IN MALAYSIAN BORNEO

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ABSTRACT

In a previous paper, we have reported on a new, troglobitic species of *Georissa* and its possible parapatric origin from *Georissa saulae* Benthem-Jutting, 1966, which occurs outside the cave system of Batu Sanaron, a limestone outcrop in Sabah, Malaysian Borneo. These analyses were based on genetic and morphometric data. Here, we formally describe the new species adding anatomical data derived from dissections and histological serial sections as well as fine structural data of shell, operculum and radula, and compare it with its stem species. The two species differ in shell and radular morphology as well as genital characters. Since we found anatomical differences between very closely related species, we assume that dissections would be of general use for the taxonomy of *Georissa* and the remaining nominal genus-group taxa of the poorly known Hydrocenidae.

INTRODUCTION

The fully terrestrial neritopsine family Hydrocenidae has a wide distribution from Europe and Africa through Asia to the Pacific region including the remote islands of Polynesia (Thompson & Huck, 1985; Solem, 1988; Preece, 1995; Auffenberg, 1998; Scott & Kenny, 1998) and probably had an early Mesozoic, Pangaean origin (Bandel, 2000; Kano, Chiba & Kase, 2002). In spite of the wide distribution and the apparently high diversity of these mostly minute snails, which rarely reach 5 mm in shell height, our knowledge of this group is still very limited. The taxonomy on both genus and species level is practically exclusively based on shell morphology. Only occasionally do descriptions include the operculum with its characteristic peg and we are aware of only three anatomical accounts on one species each (Thiele, 1910; Berry, 1965; Bernasconi, 1995). Therefore, definitions of taxa on both levels are often ambiguous and the family as a whole is in need of revision. Traditionally, species from the Australasian region including Southeast Asia are placed in the genus *Georissa* Blanford, 1864 (see e.g. Thompson & Dance, 1983; Solem, 1988). In Borneo, many species of *Georissa* have very limited ranges (Thompson & Dance, 1983). In a previous paper, we have reported on a new, troglobitic species of *Georissa* and its possible parapatric origin from *Georissa saulae* Benthem-Jutting, 1966, which occurs outside the cave system of Batu Sanaron, a limestone outcrop in Sabah, Malaysian Borneo. These analyses were based on sequences of mitochondrial 16S rDNA fragments and shell morphology. Both species are 'connected' by a morphologically intermediate population, which shares haplotypes with both and lives in the cave entrance (Schilthuizen, Cabanban & Haase, 2005). The aim of the present paper is the morphological and anatomical description of the new species including a comparison with its stem species. This is also an exploration of the taxonomic value of anatomical characters within the genus *Georissa*.

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MATERIAL AND METHODS

Specimens were collected in front of (*Georissa saulae*) and inside (*Georissa filiasaulae* new species) the cave system of the karstic limestone outcrop Batu Sanaron (Fig. 1). This outcrop measuring 600 by 300 m and dating from the Oligocene (Yin, 1985) is located in the Sepulut valley in the Interior Province of Sabah, Malaysian Borneo. The cave system including a small stream (Francis, 1987) is now partly explored (M. Schilthuizen, unpublished maps). The surrounding vegetation of Batu Sanaron consists of logged lowland dipterocarp rain forest on gently sloping ground. The limestone itself is covered with calciphilous vegetation (Vermeulen & Whitten, 1999).

Shells were measured under a dissecting microscope equipped with a measuring graticule. Shell height was taken along the spiral axis and shell width perpendicularly. Aperture height was measured at the inside of the aperture from the basal columellar corner to the parietal columellar corner. Aperture width was defined as the largest distance between columella and palatal side. Whorls were counted to the nearest eighth of a whorl. The anatomy was investigated by dissection as well as histologically. Two females and two males of *G. saulae* and two females and three males of *G. filiasaulae* sp. nov. were dissected. Histological serial sections were prepared from four females and two males of the former and four females and one male of the latter. The paraffin sections were 7 μm thin and were stained in Heidenhain's Azan. The genitalia and digestive system of *G. saulae* were reconstructed from one section series of each sex using the programme SurfDriver 3.5 (Moody & Lozanoff, 1999).

Shells, opercula and radulae were investigated by scanning electron microscopy using a Hitachi S-2460 N Natural Scanning Electron Microscope. These hard parts were cleaned with sodium hypochlorite prior to mounting and sputter-coated with gold.

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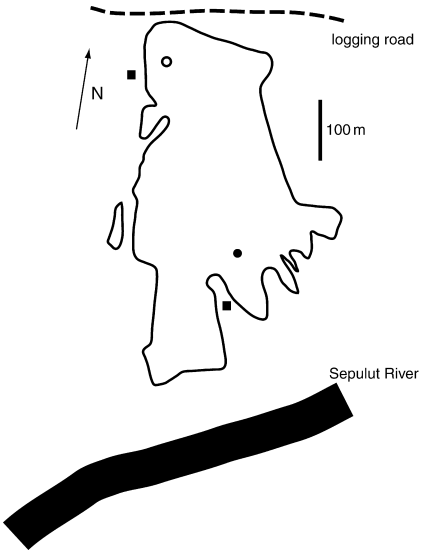

Figure 1. Map of limestone outcrop Batu Sanaron. Circles, *Georissa filiasaulae* new species; squares, *Georissa saulae*; filled symbols, sampling sites (see also Schilthuizen *et al*., 2005).

Type material of the new species is deposited in the Borneensis collection of the Universiti Malaysia Sabah (BOR/MOL) and the Zoological Museum of Berlin (ZMB). Types from the Zoological Museum of the University of Amsterdam (ZMA) were also examined.

SYSTEMATIC DESCRIPTIONS

Family Hydrocenidae Troschel, 1856

Georissa Blanford, 1864

Type species: Hydrocena pyxis Benson, 1856 by original designation.

Diagnosis: Thompson & Dance, 1983: 112, 113.

Georissa filiasaulae new species

(Figs 2A, B, E, 3A, 4A–C, 5, 6)

Types: Holotype: BOR/MOL/3795; six paratypes (shells): BOR/MOL/3491; seven paratypes (two shells, five histological series): ZMB 107143-107149, all from the type locality (Fig. 1): 120 m from south entrance into cave system of the karstic limestone outcrop Batu Sanaron, Sepulut valley, Interior Province of Sabah, Borneo, Malaysia; 450 m asl; 04°42.052'N, 116°36.016'E.

Etymology: *Filia* (Latin) means daughter. The name of the new species refers to its stem species *Georissa saulae* (see Schilthuizen *et al*., 2005).

Description: Shell (Fig. 2A, B, E): without colour, conical, about 1.2 times higher than wide (Table 1), whorls convex, stepped; columella only in body whorl, dissolved in upper

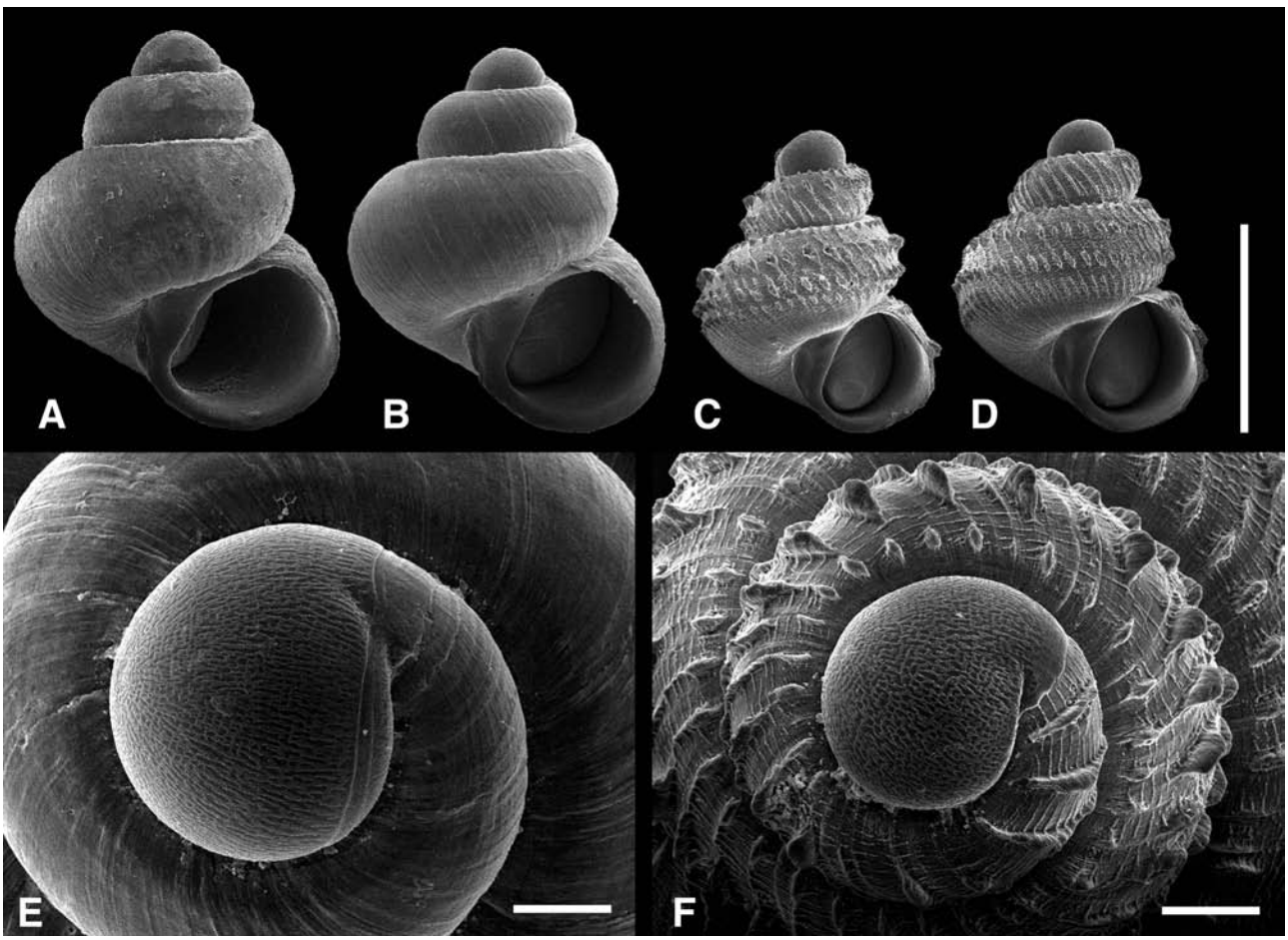

Figure 2. Shells. **A, B, E.** *Georissa filiasaulae* new species. **C, D, F.** *Georissa saulae*. **E, F.** Protoconchs. Scale bars **A–D** = 1 mm **E, F =** 500 μm.

Table 1. Shell morphometry of *Georissa* species.

Species		sh	sw	ah	aw	sh/sw	sh/ah	sw/aw
G. filiasaulae	holotype	1.78	1.60	0.69	0.69	1.12	2.58	2.32
n. sp. $N = 8$	median	1.83	1.59	0.70	0.69	1.19	2.61	2.30
	mean	1.84	1.57	0.72	0.69	1.18	2.55	2.28
	max	2.08	1.75	0.80	0.76	1.23	2.77	2.36
	min	1.63	1.44	0.64	0.63	1.12	2.32	2.15
	SD	0.15	0.10	0.05	0.04	0.04	0.15	0.06
	cv	7.25	5.74	6.60	5.32	2.98	5.17	2.44
G. saulae	median	1.59	1.21	0.60	0.53	1.31	2.65	2.27
$N = 30$	mean	1.63	1.23	0.60	0.54	1.32	2.70	2.28
	max	1.92	1.39	0.69	0.60	1.45	3.13	2.44
	min	1.47	1.15	0.53	0.47	1.23	2.47	2.17
	SD	0.13	0.07	0.04	0.04	0.06	0.15	0.06
	cv	7.78	5.57	6.37	6.38	4.33	5.35	2.74

Abbreviations: ah, aperture height; aw, aperture width; cv, coefficient of variation adjusted for sample size; *N*, number of specimens; max, maximum; min, minimum; SD, standard deviation; sh, shell height; sw, shell width; measurements in mm.

whorls; protoconch globular, comprising 0.5 whorls, with meshed sculpture, clearly delimited against teleoconch; teleoconch comprising up to 2.375 whorls, smooth; aperture ovate, only slightly higher than wide, lip thin; umbilicus closed by columellar shield.

Operculum (Fig. 3A): corneous, yellow, elongate-ellipsoidal, nucleus submarginal, concentric growth lines; long, slightly arched peg arising from white, noncalcareous base.

External features: cephalic tentacles very short lobes; epidermis without pigment; eyes black.

Mantle cavity: without ctenidium and osphradium.

Digestive system: radula (Fig. 4A–C) long reaching backwards over distal third of style sac, rhipidoglossate without central teeth, seven rows of teeth on each side becoming more slender, longer and delicate towards outside with outer teeth being about three times longer than inner teeth; all teeth with 15–18 denticles, denticles alternately long and short, this length difference most pronounced in inner-most teeth, where large denticles are almost claw-like, length difference decreasing towards outside, denticles of outer-most teeth no longer dimorphic; stomach with style sac but lacking appendages; intestine with two loops on opposing sides of style sac, then following straight along the pallial genitalia.

Excretory system: kidney a long tube forming an elongate loop of about 360°, distal end bent backwards, tapering before opening into mantle cavity.

Male genitalia (Fig. 5): testis a large sac of undefined shape; sperm storing vesicula seminalis coiling as a regular spiral with vas efferens forming nucleus and distal end continuing as delicate vas deferens towards male gland mass; male gland mass uniformly white, consisting of main body and diverticulum joining main body at about two-fifths of length; diverticulum very long, forming an 'extended' S shape, lying against stomach and embracing posterior loop of intestine; appendix resembling a female receptaculum seminis arising from distal end of diverticulum; posterior fifth of main body bent; vas deferens entering diverticulum ventrally in anterior third, still very delicate, easily destroyed and overlooked in dissections; genital opening at anterior end of male gland mass; no copulatory organ.

Female genitalia (Fig. 6): ovary a large sac of undefined shape; oviduct proximally thinner than distally, at transition from thin to thick reddish-brown in one specimen, entering female gland mass in posterior fourth to fifth; receptaculum seminis pear-shaped with long duct, arising close to junction of oviduct and female gland mass; bursa copulatrix massive, pear-shaped with short, thick duct entering female gland mass distal to oviduct; female gland mass with two glandular portions, anterior third white, posterior portion yellow, occasionally, female gland mass and adjoining intestine entirely orange; genital opening at anterior end of female gland mass.

Habitat and distribution: wet limestone walls with black encrustations inside the cave system of Batu Sanaron.

***Georissa saulae* van Benthem-Jutting, 1966**

(Figs 2C, D, F, 3B, C, 4D–F, 7–10)

Hydrocena saulae van Benthem-Jutting, 1966: 40–41, Fig. 2 (Laying Cave, Crocker Range, Keningau, Sabah, Malaysia; holotype ZMA Moll. 3.66.003, cat. no 135731).

Georissa saulae—Thompson & Dance, 1983: 113, 118.

Material examined: Holotype ZMA Moll. 3.66.003, cat. no 135731, 142 paratypes ZMA Moll. 3.66.004, cat no 13559843, Laying Cave, Crocker Range, Keningau, Sabah, Malaysia. Other material: In front of southern entrance into cave system of the karstic limestone outcrop Batu Sanaron, Sepulut valley, Interior Province of Sabah, Borneo, Malaysia; 450 m asl; 4°42.052'N, 116°36.016'E.

Description: Shell (Fig. 2C, D, F): clear, reddish-brown, conical, about 1.3 times higher than wide (Table 1), whorls convex,

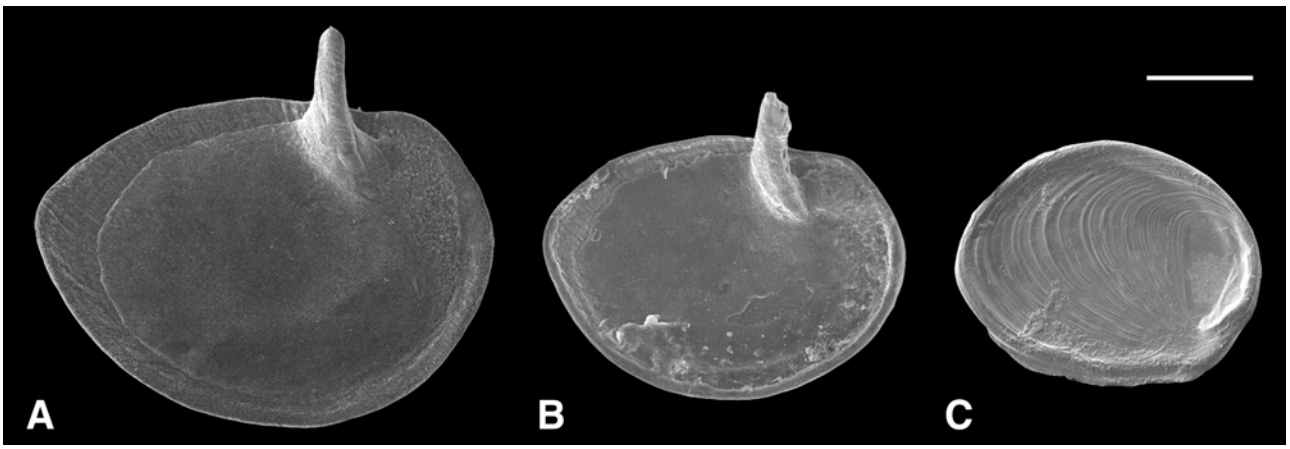

Figure 3. Opercula. **A.** *Georissa filiasaulae* new species. **B, C.** *Georissa saulae*. **A**, **B**. Inside with peg. **C.** Outside. Scale bar = 200 μm.

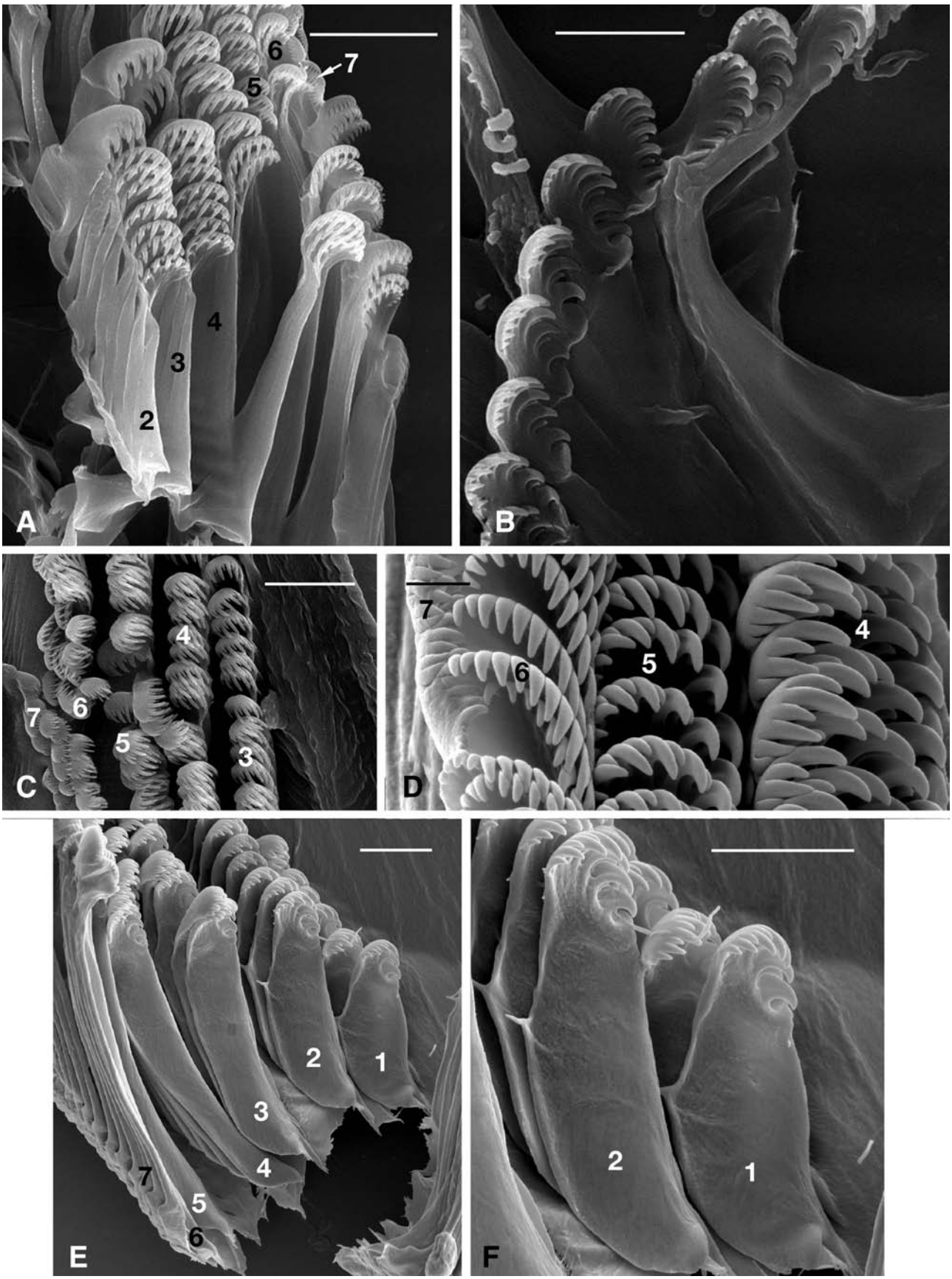

Figure 4. Radulae. **A–C.** *Georissa filiasaulae* new species. **D–F.** *Georissa saulae*. **A.** Teeth 2–7 from right half-row. **B.** Third line of teeth from left side. **C.** Teeth 3–7 from left half-row. **D.** Teeth 4–7 from left half row. **E.** Left half-row. **F.** Detail from **E.** Scale bars **A, C** = 10 μm, **B, E, F** = 5 μm; **D** = 1 μm.

stepped; columella only in body whorl, dissolved in upper whorls; protoconch globular, comprising 0.5 whorls, with meshed sculpture, clearly delimited against teleoconch; teleoconch comprising up to 2.75 whorls, with 3–6 spiral bands of nodes, which are most prominent at the periphery; aperture ovate, only slightly higher than wide, lip thin; umbilicus closed by columellar shield.

Operculum (Fig. 3B, C) and external features: as in *G. filiasaulae* new species.

Digestive system (Figs 4D–F, 7, 8): radula long reaching backwards over proximal third of style sac, rhipidoglossate without

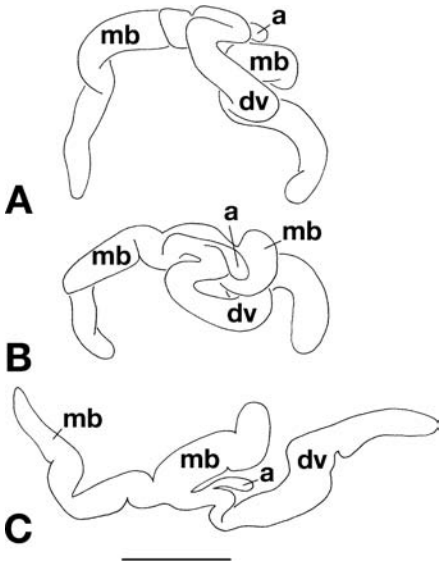

Figure 5. Male genitalia of *Georissa filiasaulae* new species. **A.** Lateral. **B.** Dorsal. **C.** Dorsal, organs separated. Abbreviations: a, appendix; dv, diverticulum; mb, main body. Scale bar = 500 μm.

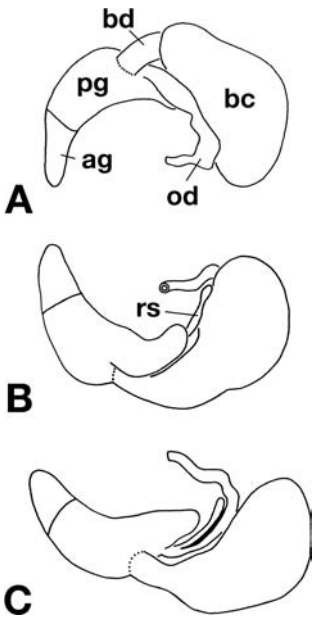

Figure 6. Female genitalia of *Georissa filiasaulae* new species. **A.** Lateral. **B.** Dorsal. **C.** Dorsal, organs separated. Abbreviations: ag, anterior gland; bc, bursa copulatrix; bd, bursal duct; od, oviduct; pg, posterior gland; rs, receptaculum seminis. Scale bar = 500 μm.

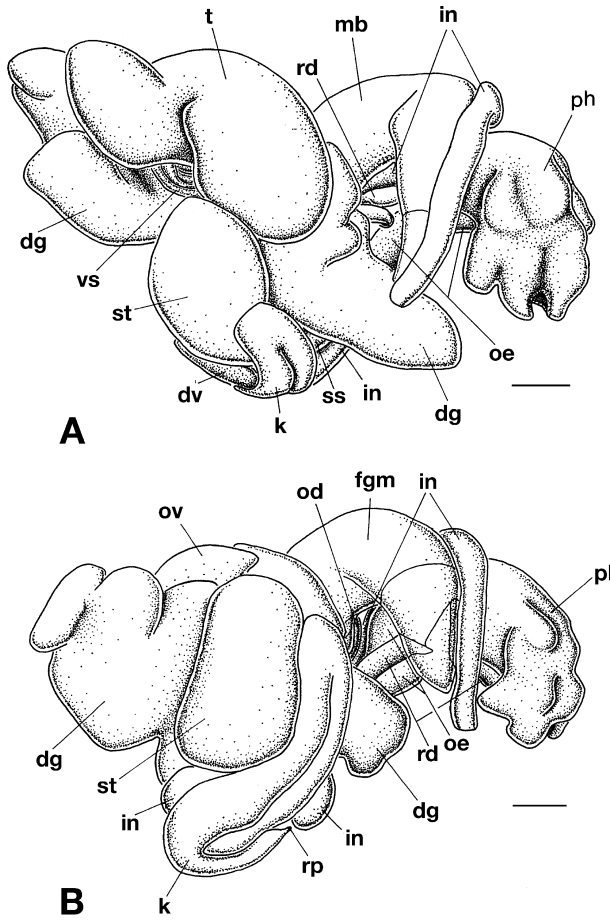

Figure 7. Reconstructions of digestive system and genitalia of *Georissa saulae*. **A.** Male. **B.** Female. Abbreviations: dg, digestive gland; dv, diverticulum of male gland mass; fgm, female gland mass; in, intestine; k, kidney; mb, main body of male gland mass; od, oviduct; oe, oesophagus; ov, ovary; ph, pharynx; rd, radular sheath; rp, renal pore; ss, style sac; st, stomach; t, testis; vs, vesicula seminalis. Scale bar = 100 μm.

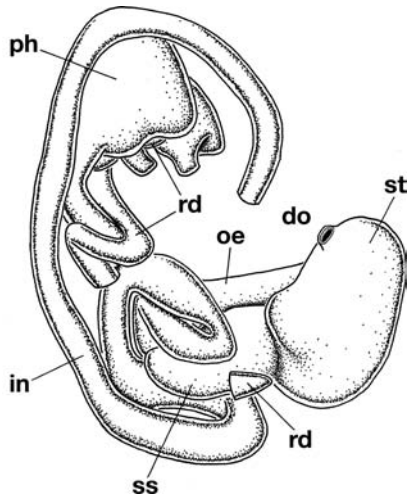

Figure 8. Reconstruction of digestive system of *Georissa saulae*, section of radular sheath removed. Abbreviations: do, opening of digestive gland; in, intestine; oe, oesophagus; ph, pharynx; rd, radular sheath; ss, style sac; st, stomach. Scale bar = 100 μm.

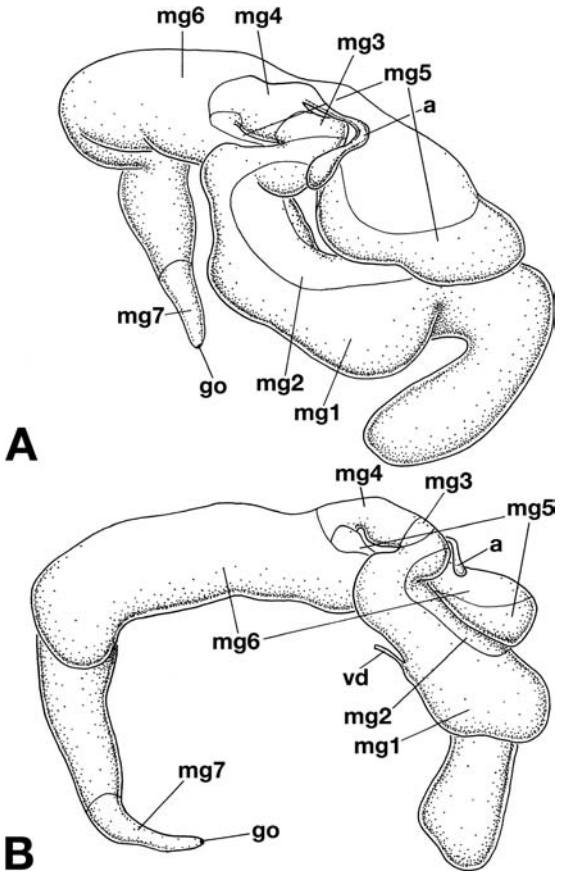

Figure 9. Reconstruction of male genitalia of *Georissa saulae*. **A.** Posterodorsal. **B.** Lateral aspect. Abbreviations: a, appendix; go, genital opening; mg1–7, male glands 1–7; vd, vas deferens. Scale bar = 100 μm.

central teeth, seven rows of teeth on each side becoming more slender, longer and delicate towards outside with outer teeth being about 4–5 times longer than inner teeth; all teeth with 12–15 denticles, denticles alternately long and short, this length difference most pronounced in inner-most teeth, where large denticles are almost claw-like, length difference decreasing towards outside, denticles of outer-most teeth no longer dimorphic; otherwise digestive system as in *G. filiasaulae* new species.

Excretory system (Fig. 7): as in *G. filiasaulae* new species.

Male genitalia (Figs 7A, 9): testis a large sac of undefined shape; sperm storing vesicula seminalis coiling irregularly; vas deferens delicate; male gland mass consisting of main body and diverticulum joining main body at about two fifths of length; diverticulum very long, forming an 'extended' S, lying against stomach and embracing posterior loop of intestine; appendix resembling a female receptaculum seminis arising from distal end of diverticulum; main body straight; in histological sections diverticulum consisting of four differently staining glandular portions, main body of three; vas deferens entering diverticulum ventrally in anterior third, still very delicate; genital opening at anterior end of male gland mass; no copulatory organ.

Female genitalia (Figs 7B, 10): ovary a large sac of undefined shape; oviduct proximally thinner than distally, with three differently staining portions, entering female gland mass in posterior fourth to fifth; receptaculum seminis pear-shaped with long duct, arising close to junction of oviduct and female gland mass; bursa copulatrix a massive, elongate sac with short, thick duct entering female gland mass distal to oviduct; female gland mass macroscopically with two glandular portions, anterior third white, posterior portion yellow, histologically each portion consisting of three differently staining glandular sections; genital opening at anterior end of female gland mass.

Habitat and distribution: On limestone and other rocks, in soil of coastal and lowland forests throughout central and western Sabah.

DISCUSSION

The morphological differences between *Georissa filiasaulae* new species and its stem species *Georissa saulae* have already been discussed by Schilthuizen *et al.* (2005). In brief, the shell of *G. filiasaulae* is larger, proportionately wider, and lacks pigment as well as any spiral sculpture. Apart from these, we also found differences in radular morphology and in anatomy. Radular teeth of *G. filiasaulae* have more denticles and the length difference between inner- and outermost teeth is smaller. In males of the new species the vesicula seminalis is a regular spiral whereas in *G. saulae* it coils irregularly, and the posterior end of the main body of the male gland mass is bent in the former whereas it is straight in the latter. Females of *G. filiasaulae* have a smaller bursa copulatrix and the female gland mass as well as the adjoining intestine may be orange. In contrast, the female gland mass of *G. saulae* always has white and pale yellow portions.

Superficially, *G. filiasaulae* may resemble *G. borneensis* Smith, 1895 and *G. xesta* Thompson & Dance, 1983. However, both these have a more or less distinct shell sculpture, whereas *G. filiasaulae* is absolutely smooth, and both are much narrower than the new species (see Thompson & Dance, 1983).

We have no explanation as to why the female gland mass and intestine of *G. filiasaulae* are occasionally orange. The function of the different glandular portions of the distal genitalia of both sexes is not known. In addition, our findings are quite different from the few published accounts on hydrocenids (Thiele, 1910; Berry, 1965; Bernasconi, 1995; see below). Therefore, we chose very general terms to identify these parts in order to avoid the suggestion of certain functions or homologies.

The distal genitalia of males and females are surprisingly similar and obviously develop from identical *anlagen*. The posterior part of the main body of the male gland mass appears to correspond to the large bursa copulatrix, the diverticulum to the oviduct, and the appendix is identical in shape and position with the receptaculum seminis.

There are only few accounts on the anatomy of hydrocenids. Most recently, Bernasconi (1995) described radula, stomach and intestine, and the genitalia of *Georissa papuana* Bernasconi, 1995 from the Western Province of Papua New Guinea. While the traits of the digestive system are in accordance with our findings, the organization of the genitalia appears to be considerably different. In females, the oviduct is distally thickened before entering the female gland mass. The seminal receptacle is connected to the female gland mass and the bursa copulatrix is globular and has a relatively narrower and longer duct than our species. The male genitalia of *G. papuana* lack the blind extension of the main body of the gland mass as well as the small appendix. What we call the diverticulum in the species from Borneo is much shorter in *G. papuana*.

Berry's (1965) description of the genitalia of *Hydrocena monterosatiana* Godwin-Austen & Nevill, 1879 from peninsular Malaysia is more similar to Bernasconi's than to our findings. Berry did not find a seminal recaptacle in females, assuming that what he identified as receptacle was in fact the bursa copulatrix. The male genitalia have two diverticula, one distal, close to the genital pore, the other one in a more

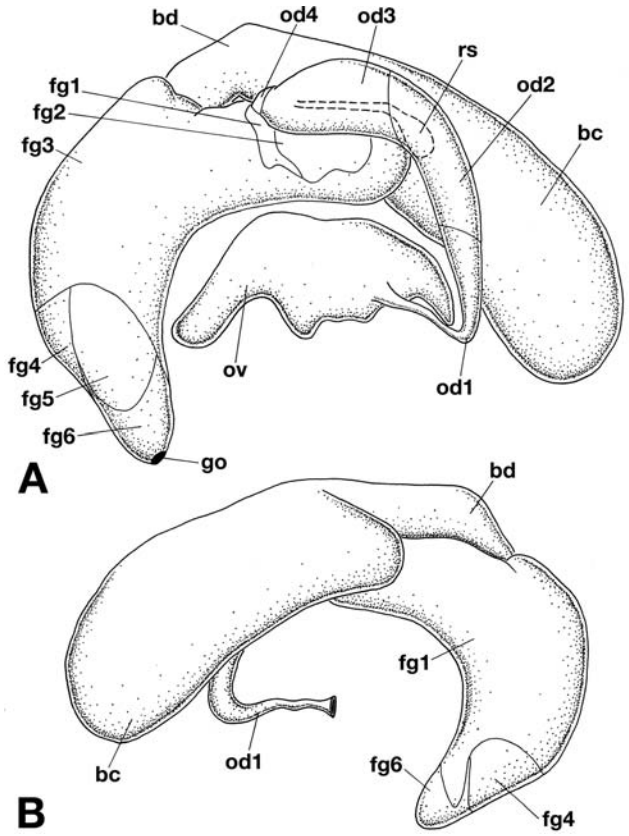

Figure 10. Reconstruction of female genitalia of *Georissa saulae*. **A.** Left. **B.** Right aspect. Abbreviations: bc, bursa copulatrix; bd, bursal duct; fg1–6, female glands 1–6; od1–4, oviduct 1–4; ov, ovary; rs, receptaculum seminis. Scale bar = 100 μm.

central position. The small appendix of the Bornean species seems lacking as well.

In contrast, Thiele's (1910) description of the female genitalia of *Hydrocena cattaroensis* (L. Pfeiffer, 1841) from Montenegro, based on the manual reconstruction of histological serial sections, is very similar to our results. The only difference is the receptaculum seminis arising directly from the female gland mass and not from the distal oviduct as in our *Georissa* species. Thiele also investigated the remaining organ systems, but gave only verbal descriptions, or at best figures of sections. Therefore, further comparisons were too difficult.

The distinct differences in genital anatomy discussed above suggest that more than two genera are involved. Since we also found anatomical differences between very closely related species, we assume that dissections will be of general use for species-level taxonomy of hydrocenids (see Thompson & Dance, 1983; Scott & Kenny, 1998). A revision of the family should be based on a phylogenetic analysis of sequence data in combination with anatomy and morphology. Such a comprehensive analysis would also provide insight into the evolution and biogeographic history of this enigmatic family of neritopsine land snails.

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