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Output จากโครงการวิจัยที่ได้รับทุนจาก สกอ. และ สกว.

1. จากที่ได้ศึกษาเปรียบเทียบตัวอย่างหอยในกลุ่มที่ใกล้เคียงกับวงศ์ Camaenidae สกุล *Amphidromus* ซึ่งยังมีความสับสนอยู่มาก และจากการเก็บตัวอย่างทั่วประเทศไทยทำให้พบหอยชนิดใหม่ที่มีลักษณะของเปลือกใหล้เคียงกับหอยในสกุล *Amphidromus* แต่จากการศึกษาเพิ่มเติมและศึกษาตัวอย่างในพิพิธภัณฑสถานธรรมชาติวิทยาต่างๆ และร่วมหารือกับ Dr. Freed Naggs (London) ทำให้ค้นพบหอยชนิดใหม่ที่คล้ายคลึงกับ *Amphidromus glaucolarynx* และได้ตีพิมพ์บทความเกี่ยวกับหอยในสกุลนี้ 1 บทความ

Sutcharit, C., Naggs, F. and Panha, S. 2010. A first record of the family Cerastidae in Thailand, with a description of a new species (Pulmonata: Orthurethra: Cerastidae). The Raffles Bulletin of Zoology. 58: inpress.

ค่า Impact Factor = 0.800 (**ภาคผนวก 1**)

2. จากที่ได้ออกเก็บตัวอย่างทั่วประเทศๆ ไทยทำให้ได้พบหอยทากที่มีลักษณะพิเศษ และหลังจากได้ทำการวิเคาะห์ทางสัณฐานวิทยา และ ชีวโมเลกุลพบว่าเป็นกลุ่มหอยที่ มีความจำเพาะสูงมากและไม่เคยมีรายงานการศึกษามาก่อน จึงได้ร่วมกับ Dr. Freed Naggs, Dr. Chritopher Wade (London) เขียนบทความวิจัยเกี่ยวกับหอยวงศ์ใหม่นี้ 1 บทความ

Sutcharit, C., Naggs, F., Wade, C.M., Fontanilla, I., and Panha, S. 2010. The new family Diapheridae, a new species of *Diaphera* Albers from Thailand, and the position of the Diapheridae within a molecular phylogeny of the Streptaxoidea (Pulmonata: Stylommatophora). Zoological Journal of the Linnean Sociey. 160: 1-16.

ค่า Impact Factor = 2.031 (**ภาคผนวก 2**)

3. บทความที่คาดว่าจะตีพิมพ์ 2 บทความ

3.1 A new subgenus and new subspecies of *Amphidromus* Albers, 1850 from Thailand

ชื่อวารสารที่คาดว่าจะตีพิมพ์ Journal of Molluscan Studies

ค่า Impact Factor = 1.074 (**ภาคผนวก 3**)

3.2 Neotype Designation and Redescription of the Vanishing Tree Snail, *Amphidromus (Amphidromus) mundus* (Pfeiffer, 1853) (Pulmonata: Camaenidae)

ชื่อวารสารที่คาดว่าจะตีพิมพ์ The Raffles Bulletin of Zoology

ค่า Impact Factor = 0.800 (**ภาคผนวก 4)**

ภาคผนวก 1

THE RAFFLES BULLETIN OF ZOOLOGY 2010 **58**(2): 75–82
Date of Publication: 31 Aug.2010

A FIRST RECORD OF THE FAMILY CERASTIDAE IN THAILAND, WITH A DESCRIPTION OF A NEW SPECIES (PULMONATA: ORTHURETHRA: CERASTIDAE)

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ABSTRACT. – This first assessment of the status of the poorly known family Cerastidae in Thailand was made by comparing Thai material with types and additional specimens from natural history museums in Europe. *Rhachistia sulphurea* (Tomlin & Peile, 1930) and *Amimopina subangulatus* (Pfeiffer, 1862) were identified and a new species of *Rhachistia* from Thailand was recognised. We re-describe *A. subangulatus* and describe the new species *Rhachistia conformalis* Sutcharit & Panha, new species, which has a small, thin, elongately conic, dextral, yellowish-white to creamy ground coloured shell. Shell ornamentation consists of two rows of blackish spots and two spiral bands on the lower periphery. Radular teeth are typical of cerastids. The penial appendix is very long, being about twice that of the vaginal length, proximally thin, distally enlarged and of a cylindrical shape. The penis is short, small, proximally cylindrical and distally forming a swollen globular structure. The vagina is large, long and cylindrical in shape with blackish pigmentation along almost its entire length. The bud-like shaped gametolytic sac is very short.

KEY WORDS. – Cerastidae, systematics, taxonomy, anatomy, Orthurethra, Pulmonata, Southeast Asia, Thailand.

INTRODUCTION

The Cerastidae are a family of common orthurethran land snails and consists of approximately 15 genera which are principally represented in tropical Africa, East, South and Southeast Asia and Australia (Zilch, 1959; Mordan, 1984, 1998; Nordsieck, 1986; Solem, 1988; Vaught, 1989; Schileyko, 1998; Smith & Stanisic, 1998). Phylogenetic and biogeographic work on the Cerastidae has been focussed on their disjunct southern hemisphere distribution (Mordan, 1984, 1991, 1992, 1998) and current knowledge of the taxonomy and biogeography of this family is primarily based on African, Indian and Australian taxa (e.g. Gude, 1914; Pilsbry, 1919; Connolly, 1925; Solem, 1959b, 1964a, 1988; Verdcourt, 1961; Mordan, 1986; Smith & Stanisic, 1998; Naggs & Raheem, 2000). To date the only information on Southeast Asian endemic cerastids is the presence of two poorly known species (Pfeiffer, 1862; Tomlin & Peile, 1930). In this study, a new cerastid species from peninsular Thailand is described. *Amimopina subangulatus* (Pfeiffer, 1862), also from Thailand, is re-described following its rediscovery after many years. In providing a taxonomic revision of the Cerastidae in Thailand we fill an important distributional gap, which facilitates future phylogenetic and biogeographic work on this family.

MATERIALS AND METHODS

Snails were sampled throughout central, eastern and southern peninsular Thailand. Living snails were drowned in water and then fixed in 70% (v/v) ethanol for anatomical examination. The genitalia of 3-5 specimens of each species were examined. Radula morphology was examined under a scanning electron microscope. Dissections were carried out under a low power binocular microscope. In descriptions of the genitalia, we used 'proximal' to refer to the region closest to the genital orifice and 'distal' to refer to the region furthest away from the genital orifice.

Anatomical terms largely follow those of Solem (1964a), Mordan (1986, 1992) and Tillier & Mordan (1995), the exception being that we follow our use of gametolytic sac (Sutcharit & Panha, 2006, 2008; Sutcharit, Naggs & Panha, 2007) rather than the inappropriate term spermatheca adopted by these authors: a, anus; ag, albumin gland; ar, appendicular retractor muscle; at, atrium; au, auricle; e, epiphallus; fo, free oviduct; gs, gametolytic sac; hd, hermaphrodite duct; hg, hermaphroditic gland; i, intestine; k, kidney; mc, mantle collar; p, penis; pa, penial appendix; pf, penial flagellum; pn, pneumostome; pr, penial retractor muscle; pv, pulmonary vein; r, rectum; rnu, renal ureter; rtf, rectal fold; so, spermoviduct; v, vagina; vd, vas deferens; ve, ventricle.

The material examined in this study are deposited in the following institutions: The Natural History Museum, London (BMNH), Chulalongkorn University Museum of Zoology, Bangkok, Thailand (CUMZ), National Museum of Well, Cardiff (NMW), Forschungsinstitut und Naturmuseum Senckenberg, Frankfurt, a.m. (SMF), and the Zoological Reference Collection, Raffles Museum of Biodiversity Research, National University of Singapore, Singapore (ZRC).

All descriptions of new species are attributable only to first and third authors, Sutcharit and Panha, respectively.

SYSTEMATIC DESCRIPTIONS

Cerastidae Wenz, 1930

Rhachistia Connolly, 1925

Type species. – *Bulimulus rhodotaenia* Martens, 1869; by original designation Connolly, 1925; 163.

Remarks. – *Rhachistia* usually has comparatively small shells, thin to slightly solid and ovate to elongate conic. The surface is smooth, fairly glossy and cream with a series of dark spots and/or bands. The aperture is ovate, peristome simple; umbilicus narrow (Connolly, 1925; Solem, 1959b; Schileyko, 1998). Radula teeth are spatulate with monocuspid central teeth and bicuspid lateral teeth. The genitalia are typical of cerastids, with a very short gametolytic sac, a short to long penial appendix, short penis and a brownish spongy tissue lining the atrium and vagina (Solem, 1973; Smith & Stanisic, 1998).

Rhachistia sulphurea (Tomlin & Peile, 1930)
(Fig. 1A, B)

Errorachis sulphurea Tomlin & Peile, 1930: 153–154, pl. 17a. (Type locality: Pran, Siam).
Rhachistia sulphurea—Schileyko, 1998: 169. Hemmen & Hemmen, 2001: 41

Material examined. – The figured specimen in Tomlin & Peile (1930, pl. 17) is designated herein as the lectotype NMW 1955.158.01155 (Fig. 1A), and the paralectotype BMNH 1939.6.6.17 (Fig. 1B).

Remarks. – A bright creamy shell with a yellowish subsutural band clearly distinguishes this species from other known species in this region. Tomlin & Peile (1930) provided a full description of the shell and radula but the genital anatomy is unknown. Our land snail surveys in many locations throughout peninsular Thailand since 1994 have failed to find any specimens that resemble *R. sulphurea*. If the distribution was restricted to the type locality, Pran, Siam, then it is possible that this species is extinct. Pranburi (= Pran sensu Tomlin & Piele, 1930) lies in an area of western Thailand that has been subjected to extensive deforestation since 1930, with most trees having been felled.

Rhachistia conformalis Sutcharit & Panha, new species
(Figs. 1C, D, H; 2A, B; 3A–D)

Type material. – Holotype CUMZ 3796 (Fig. 1C). 1 Sep 2007. leg. S. Panha. Measurements: shell height 19.6 mm, shell width 10.7 mm and with 6½ whorls. Paratype BMNH 20090361 (2 shells); SMF 334685 (2 shells); ZRC MOL. 3008 (2 shells); CUMZ 3795 (7 shells), 3797 (1 shell; Fig. 1D), 4086 (5 shells), 4090 (14 shells), 4095 (4 shells), 4287 (7 shells).

Type locality. – Ban Karang, Kaeng Kracharn National Park, Phetchaburi, Peninsular Thailand (12°52'20.04"N 99° 18'20.73"E).

Other material examined. – Pa-La-Oo Waterfall, Kaeng Kracharn National Park, Phetchaburi: CUMZ 4080 (1 shell); Tam Khiriwong, Donsak, Suratthani: CUMZ 4093 (3 shells); Wat Tam Por-ngam, Donsak, Suratthani: CUMZ 4275 (3 shells); Km. 3 (road no. 4100) to Khiriratnikhom, Suratthani: CUMZ 4652 (14 shells); Wat Sathitkhirirom, Khiriratnikhom, Suratthani: CUMZ: 4653 (2 shells); Khao Phanomwang, Kanchanadit, Suratthani CUMZ 3794 (2 shells), 4300 (5 in ethanol), 4654 (6 shells), 4915 (1 in ethanol), 4916 (2 shells); Tam Lod, Khao Nan National Park, Nakhonsrithammarat: CUMZ 4288 (4 shells), 4655 (2 in ethanol).

Etymology. – The specific name is from the Latin '*conformalis*' meaning "like" or "similar". This name refers to the new species possessing a shell superficially similar to that of the sympatric species *Amphidromus glaucolarynx* (Dohrn, 1861) and *Amphidromus semitessellatus* (Morlet, 1884).

Diagnosis. – Comparison of this new species with the type species of *Rhachistia* demonstrates that it shares the generic characters cited above. This new species differs from *R. pulcher* (Gray, 1825) and *R. adumbratus* (Pfeiffer, 1855) from Sri Lanka (see Gude, 1914; Naggs & Raheem, 2000) by having a slightly thinner shell, a creamy ground colour ornamented with two rows of blackish spots on the upper periphery and two spiral bands on the lower periphery, whereas, *R. pulcher* has scattered blackish spots and pale spiral bands, and *R. adumbratus* has only blackish spiral bands on the whitish ground colour with a reddish subsutural band, pink columella area and a spiral band on the periphery.

Description. – Shell elongate conical, small, dextral, thin and fragile; apex acute with dark spot on tip. Whorls convex; suture depressed. Last whorl large, convex, yellowish-white to creamy ground colour with very fine growth lines. In the final whorl the upper periphery exhibits two rows of blackish spots, one just below the suture, the other runs approximately in middle of the last whorl; below the periphery are two brownish bands; one just below periphery, the other close to the umbilicus. Spire conical, having similar colour pattern to last whorl but slightly paler. Aperture ovate; lip simple and sharp. Parietal callus translucent. Umbilicus narrow; columella short, straight with triangular dilation.

Genitalia. – Atrium (at) rather large, long and without blackish pigments on male side (Fig. 2A). Penial appendix (pa) very long, about twice that of vaginal length, proximally thin, distally slightly enlarged and cylindrical. Penis (p) short, small, proximally cylindrical and distally forms swollen globular structure. Epiphallus (e) larger than vas deferens; penial flagellum (pf) very thin and short. Retractor muscle thin and split into two bundles: penial retractor muscle (pr) inserted on distal globular end of penis, and atrial retractor muscle (ar) inserted on proximal end of penial appendix. Vas deferens (vd) thin tube connected to head of epiphallus.

Vagina (v) large, long, cylindrical with blackish pigmentation along almost entire length (Fig. 2A). Gametolytic sac (gs) very short, bud-like. Free oviduct (fo) short; spermoviduct (so) enlarged and swollen. Albumin gland (ag) slightly enlarged, short and ligulate. Hermaphroditic duct (hd) slender and convoluted. Hermaphroditic gland (hg) forms multiple clumped alveoli embedded in digestive gland.

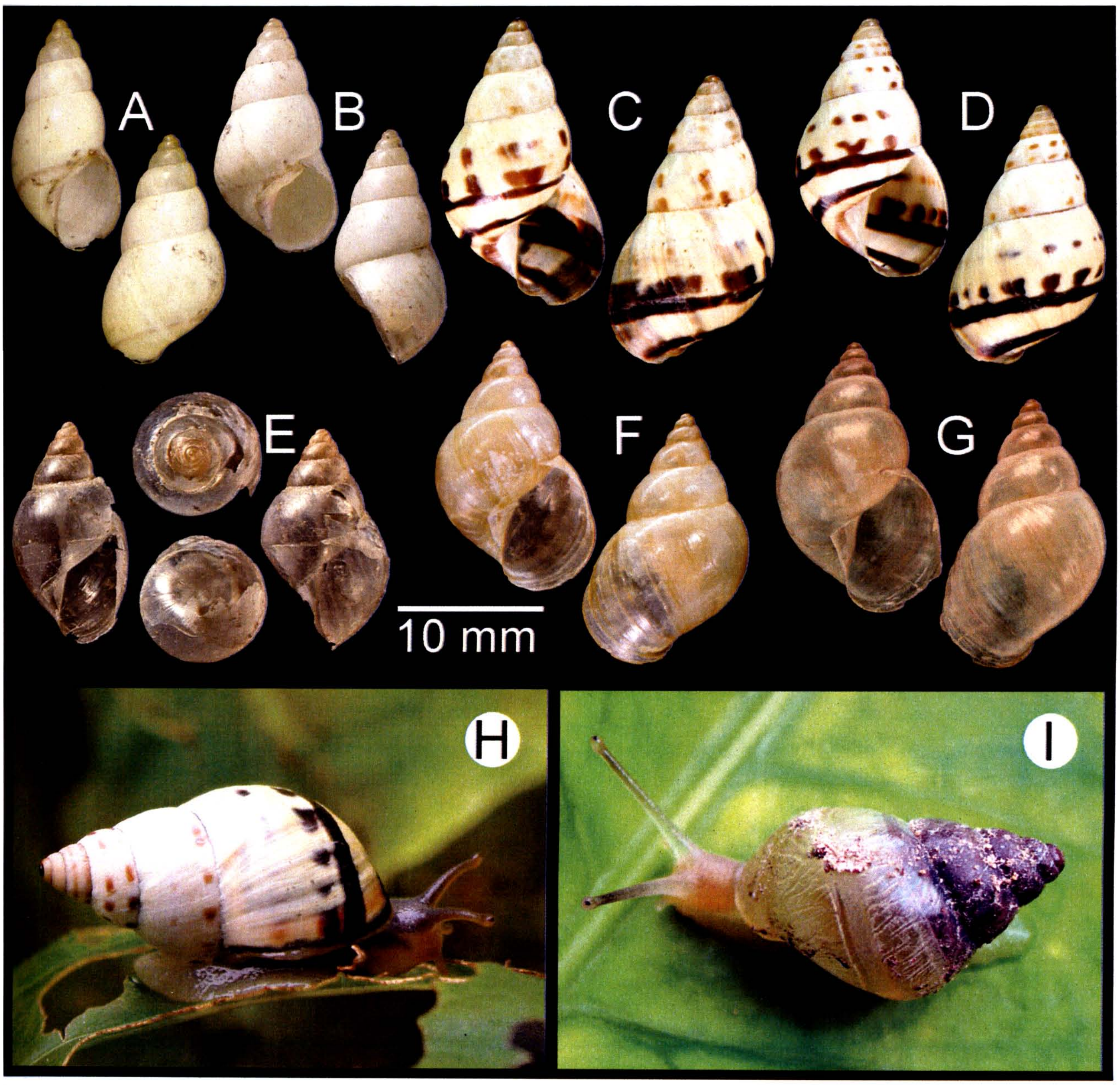

Fig. 1. A, B. Shell of *Rhachistia sulphurea*, (A) lectotype NMW 1955.158.01155, and (B) paralectotype BMNH 1939.6.6.17. C, D. Shell of *Rhachistia conformalis* Sutcharit & Panha, new species, (C) holotype CUMZ 3796, and (D) paratype CUMZ 3797. E–G. Shell of *Amimopina subangulatus*, (E) lectotype BMNH 1986166, (F, G) specimens from Jed Sao Noi Waterfall, Saraburi (CUMZ 3798, 3799). H. *Rhachistia conformalis* Sutcharit & Panha, new species, at type locality (shell height about 17 mm) CUMZ 3797. I. *Amimopina subangulatus* at Jed Sao Noi Waterfall, Saraburi (shell height about 15 mm) CUMZ 3650.

Pallial system. – Typical orthurethran form. Auricle (au) and ventricle (ve) located left of kidney (on right in figure). Pulmonary vein (pv) and blood vessel very distinct and well developed at anterior end near mantle collar (mc). Kidney (k) elongate, broadened at base and approximately half of lung cavity length.

Renal ureter (rnu) very thin and attached to kidney; renal fold (rtf) with very thin and transparent ridge located between kidney and rectum (r). Anus (a) adjacent to mantle collar (mc) (Fig. 2B).

Radula. – Teeth arranged in V-shaped rows. Each row contains about 88 (43-1-44) teeth. Central tooth monocuspid; broadly spatulate. Latero-marginal teeth (teeth no. 1-15) bicuspid, endocone similar to central tooth; ectocone located at base of tooth and with two pointed cusps. Outermost teeth (teeth no. 16 to 43 or 44) polycuspid; endocone spatulate with slightly outward oblique cusp; ectocones located laterally and progressively divided up into six pointed cusps.

Distribution. – Peninsular Thailand, ranging from Phetchaburi (the type locality) to Suratthani and Nakhonsrithammarat Provinces.

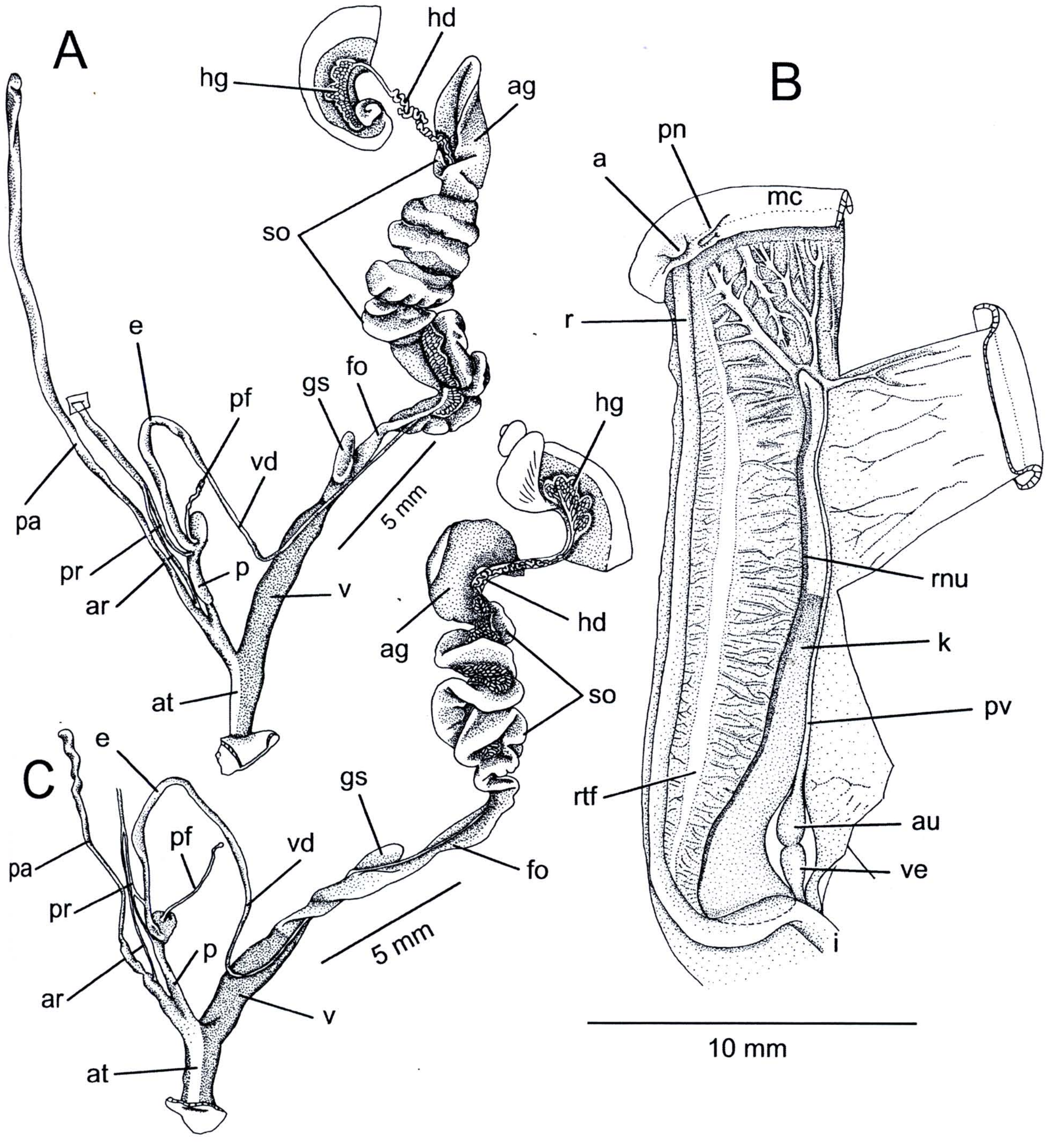

Fig. 2. A, B. Anatomy of *Rhachistia conformalis* Sutcharit & Panha, new species (Paratype CUMZ 3797), (A) reproductive system, and (B) pallial system. C. genitalia of *Amimopina subangulatus* from Jed Saw Noi Waterfall, Saraburi (CUMZ 3798).

Remarks. – Superficially similar but obviously distinct from the sympatric *Amphidromus semitessellatus* (Morlet, 1884) in having a smaller dextral shell, with simple lip. Although *A. glaucolarynx* (Dohrn, 1861) has dimorphic shell coiling, it differs by having a thinner and smaller shell, a simple lip and a creamy shell colour. The shapes of the radula teeth and genital morphology of *Amphidromus* and *Rhachistia* are also very distinct (Sutcharit, 2004).

Apart from our new species and *R. sulphurea* there are no unequivocal records of *Rhachistia* from the region. The shell of *R. sulphurea* can generally be distinguished from *R. conformalis* Sutcharit & Panha, new species, in that the former is thick-walled with a uniform sulphur to yellowish colour, as well as having a reddish subsutural band on the last whorl and a pink columella (Tomlin & Peile, 1930).

Rhachistia conformalis Sutcharit & Panha, new species, was found on tree trunks, branches, twigs and leaves of non-specific plants. The snails usually live higher than 2 m above ground, up to canopy height.

Amimopina Solem, 1964

Type species. – *Bulimus macleayi* Brazier, 1876; by original designation Solem, 1964a: 118.

Remarks. – *Amimopina* possesses an ovate conical, small, thin and translucent shell; uniformly corneous or light brownish with thin growth lines on the surface; aperture ovate with a simple peristome (Solem, 1964a; Schileyko, 1998). Radula teeth are monocuspid and spatulate. The genitalia are typical of cerastids with a short gametolytic sac (Solem, 1964a; 1973).

Negligible information is available on *Amimopina* systematics and distribution; the evidence for Schileyko's (1998) assertion that *Amimopina* includes two or three species is not clear. Solem (1964a, b; 1973) provided reliable reports of *Amimopina* from Australia and New Guinea but, primarily owing to the low abundance of these fragile shells and their exhibiting very few taxonomically informative characters, species limits have not been established. Our results and those of Solem (1959a) suggest a close relationship between *Rhachistia* and *Amimopina*. The genera are very similar in possessing a conical shell, a simple peristome and spatulate radula, as well as exhibiting a blackish pigment lining in the vagina and bud-shaped gametolytic sac. Only small differences in the thickness and translucence of the shell, in the very fine growth lines and the monochrome corneous to light brown colour separate them.

Amimopina subangulatus (Pfeiffer, 1862)
(Figs. 1E–G, I; 2C; 3E–H)

Bulimus subangulatus Pfeiffer, 1862: 274, 275. Type locality: Laos Mountains, Cambodia. Martens, 1867: 82. Pfeiffer, 1868: 148. Pfeiffer, 1877: 181.
Amimopina subangulatus—Mordan, 1992: 3, 4.

Material examined. – Lectotype BMNH 1986166 (Fig. 1E). Pu Kae Botanic Garden, Saraburi: CUMZ 4290 (3 shells). Jed Sao Noi Waterfall, Muaklek, Saraburi: CUMZ 3798 (2 shells; Fig. 1F), 3799 (2 shells; Fig. 1G), 4650 (8 shells). Muaklek Waterfall, Muaklek, Saraburi: CUMZ 4651 (2 in ethanol).

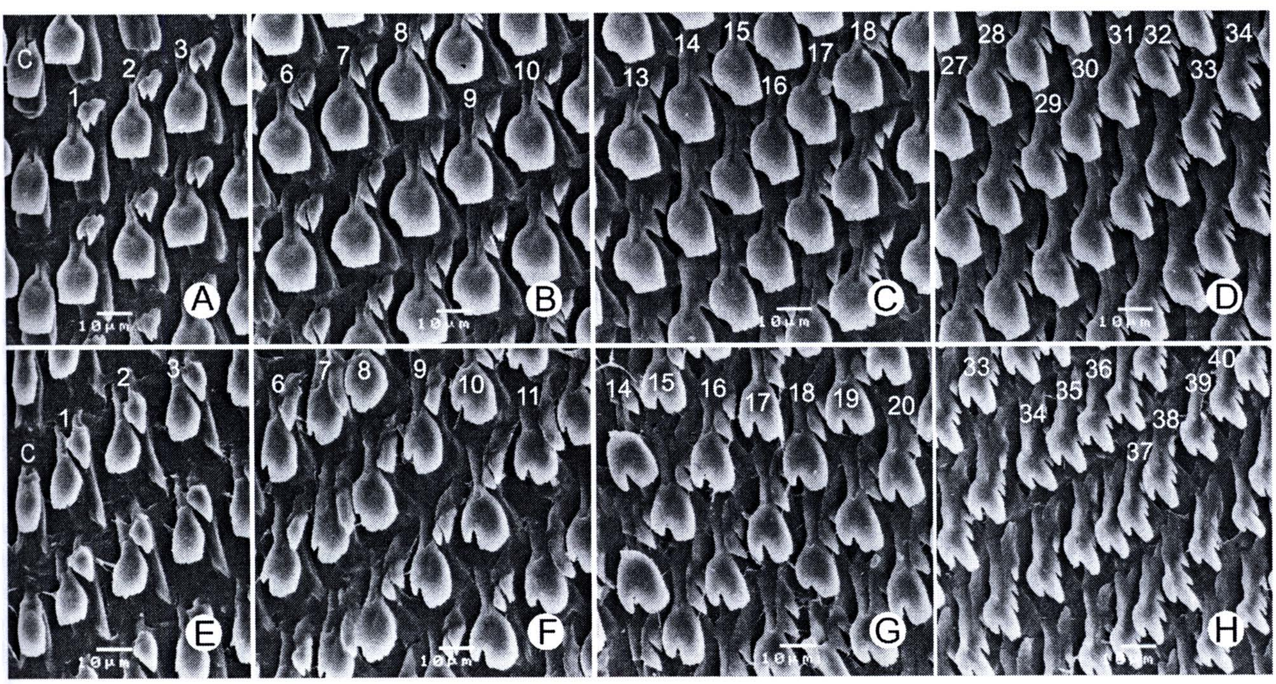

Fig. 3. Radula morphology. A–D. *Rhachistia conformalis* Sutcharit & Panha, new species (Paratype CUMZ 3797), (A) central tooth with first to third lateral teeth, (B, C) lateral teeth with bicuspid marginal teeth transition, and (C) outermost marginal teeth. E–H. *Amimopina subangulatus* (CUMZ 3798), (E) central tooth with first to third lateral teeth, (F, G) lateral teeth with bicuspid marginal teeth transition, and (H) outermost marginal teeth. The numbers indicate the order of the teeth and 'C' indicates the central tooth.

Shell. – Shell rather small, dextral, pellucid, very thin and fragile, ovate conical, and narrowly perforate. Spire short conical; apex acute with dark spot on the tip; 5–6 whorls, slightly convex with depressed suture. Last whorl large, and round. Shell surface with very fine growth lines to nearly smooth. Last two whorls corneous to brownish; somewhat dark brown on first 2-3 whorls. Aperture ovate; lip simple; columella dilated and triangular. Parietal callus transparent.

Genitalia. – Atrium (at) rather large, long, with no black pigment on male side (Fig. 2C). Penial appendix (pa) relatively short, proximally with constriction and enlarging distally. Penis (p) small, distally forms round knotty shape; penial flagellum (pf) very thin and long. Epiphallus (e) slightly larger than vas deferens. Retractor muscle thin and split into three bundles: penial retractor muscle (pr) inserted on proximal end of penial appendix, and atrial retractor muscle (ar) inserted on globular end of penis and epiphallus. Vas deferens (vd) thin tube connected to head of epiphallus (Fig. 2C).

Female reproductive organ is similar to that described for *Rhachistia conformalis* Sutcharit & Panha, new species, except the spread and cover of prominent black pigments extends to approximately half the vaginal length.

Radula. – Teeth arranged in V-shaped rows, each row contains about 99 (48-1-50) teeth. Central tooth monocuspid with notable narrow extension (Fig. 3E). Lateral teeth bicuspid, endocone spatulate, ectocone triangular and located at tooth base (Fig. 3E, F). Marginal teeth tricuspid with small entocone; mesocone rather large with blunt cusp; ectocone with two to four cusps located laterally (Fig. 3G, H).

Distribution. – *Aminopina subangulatus* was described from the Laos Mountains, Cambodia (Pfeiffer, 1862), and so far no one has subsequently reported this species. Including data from the present study, the distribution of this species is confined to the type locality in Cambodia (Pfeiffer, 1862) and to Saraburi Province, central Thailand.

Remarks. – Originally, "*Bulimus subangulatus* Pfeiffer, 1862" was described from only two shells (Pfeiffer, 1862). In this study, we compared the recently collected specimens from Thailand to the lectotype (BMNH 1986166) and found no significant shell morphological differences. No other representatives of this species have been recorded since the types were described almost 150 years ago.

The shell shapes of *A. subangulatus* and *R. conformalis* Sutcharit & Panha, new species, are very similar; the principal differences between these two species are the translucent corneous shell, which is slightly darker in the earlier whorls of *A. subangulatus*, whilst *R. conformalis* has a creamy shell, decorated with two rows of black spots and spiral bands. *Aminopina subangulatus* has a short penial appendix, longer caecum and blackish pigments distributed approximately to half of the vaginal length, while it is spread over nearly the entire vaginal length in *R. conformalis* Sutcharit & Panha new species. The arrangements of excretory, respiratory and circulation systems are similar to the previously mentioned species and to *A. macleayi* (see Solem, 1964a; Smith & Stanisic, 1998).

DISCUSSION

Orthurethran land snails have long been considered to be a basal group within the Stylommatophora. Pilsbry (1900) was influential in establishing groups above family level within the Stylommatophora and introducing the group Orthurethra on the basis of what he considered to be a primitive renal system; the Orthurethra was subsequently described as a primitive and ancient group probably extant since the Palaeozoic (Hyatt & Pilsbry, 1910). Such views were supported by the determination of some Palaeozoic fossil snails as representing orthurethran taxa (Solem 1979; Solem & Yochelson, 1979). A Palaeozoic origin for orthurethrans allowed for the possibility of their having a Pangaean distribution in the early Mesozoic and a subsequent division into Laurasian and Gondwanan groups. Most orthurethran groups currently exhibit a northern distribution but the presence of cerastids in Africa, south-western Arabia, central and southern India, Sri Lanka, New Guinea and Australia provided a reasonable basis for Mordan (1984) to hypothesise that the cerastids have a Gondwanan origin. Tillier (1989) also recognised a basal division of the Orthurethra into Laurasian and Gondwanan clades that he hypothesised as having a vicariant origin. Further support for recognition of Palaeozoic orthurethrans was given by Nordsieck (1985, 1986) and most recently by Stworzewicz, Szulc & Pokryszko (2009). However, molecular phylogenetic trees (Wade, Mordan & Naggs, 2006) have robustly demonstrated that the Orthurethra is a derived group within the Stylommatophora and on that basis cannot be a basal Stylommatophoran Palaeozoic ancestor for the Stylommatophoran clade. Wade et al. (2006) expressed the view that the extent of homoplasy in pulmonate shell characters did not allow a clear basis for attributing Palaeozoic fossils to the Stylommatophora and suggested that the Palaeozoic snails reported on by Solem and Yochelson (1979) may represent an early colonisation of the land by gastropods that died out, possibly as victims of the Permian/Triassic extinction event (which, incidentally, is quite different to the interpretation attributed to Wade et al. (2006) by Storzewicz et al. (2009: 943) that 'most probably no land snails survived the end Permian mass extinction'). Having demonstrated that, on the evidence of their molecular phylogenetic tree, the Orthurethra is an advanced group, Wade et al. (2006) were nevertheless faced with the difficulty of attributing a time frame for their trees. Such a time frame for the origin and diversification of the Stylommatophora is still far from clear but, on available evidence, they concluded that the Orthurethra probably originated too late to owe its current distribution to Mesozoic plate tectonic events. Their conclusion was that the Orthurethra is probably of Laurasian origin and that the Cerastidae attained its current southern distribution by dispersal. Thus, our recording of cerastids in Thailand is of considerable interest in this debate. As part of the continental land mass of Asia, the presence of cerastids in Thailand could be attributed to their being representatives of the hypothesised original Laurasian cerastids. This interpretation would be supported if their inclusion in a molecular phylogenetic tree showed them to be basal to New Guinea and Australian cerastid taxa, whereas if they are shown to be a derived group it would support the hypothesis that cerastids are of Gondwanan origin.

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ภาคผนวก 2

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The new family Diapheridae, a new species of *Diaphera* Albers from Thailand, and the position of the Diapheridae within a molecular phylogeny of the Streptaxoidea (Pulmonata: Stylommatophora)

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The Streptaxoidea are an ancient and species diverse group that is poorly understood. Examination of the reproductive anatomy of *Diaphera* showed it to be notably distinct from that of most other streptaxid genera but to exhibit similarities with the reproductive anatomy of *Sinoennea* (Enneinae), *Careoradula* (Strepaxinae), *Discartemon* (Strepaxinae), *Augustula* (Strepaxinae), and a species of *Imperturbatia* (Gibbinae). Our molecular phylogenetic analysis placed the two genera with high-spired shells, *Sinoennea* and *Diaphera*, in an isolated position as a sister group to the Streptaxidae *sensu stricto*. This basal divergence within the Streptaxoidea provides support to the proposed recognition of a new family, the Diapheridae. None of the genera possessing low-spired shells, *Careoradula*, *Discartemon*, *Augustula*, and *Imperturbatia*, were available for inclusion in the molecular analysis and we therefore provisionally restrict the Diapheridae to *Diaphera* and *Sinoennea*. However, based on their reproductive anatomy *Careoradula*, *Discartemon*, *Augustula* and a species of *Imperturbatia* may cluster with the Diapheridae when included in a molecular analysis.

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ADDITIONAL KEYWORDS: Achatinoidea – carnivorous snail – land snails – molecular phylogeny – rRNA – taxonomy.

INTRODUCTION

The approximately 1000 described species in the Streptaxoidea have been placed in a single family and about 60 genera, largely on the basis of shell characters (Zilch, 1960; Bruggen, 1967; Richardson, 1988; Schileyko, 2000). The group is widely distributed in the tropics and some subtropical areas but is absent from the eastern and southern Pacific regions. Some 15 genera have been reported from South-East Asia. In reviewing the group, Schileyko (2000) recognized six subfamily categories and provided supporting information on the reproductive morphology. However, the internal anatomy of most species is unknown and the only evidence to support their inclusion in subfamily or generic categories is based on shell characters and, to some extent, this is influenced by geographical distribution. Shell shape is diverse ranging from helicoid to pupiform and turriform, often with axial distortion (Bruggen, 1967). In many stylommatophoran groups complex structures of the reproductive organs proximal to the genital orifice have proved to be valuable for recognizing species and genera. Apart from the possession of penial armature, generally in the form of hooks or claws, few accessory organs in the reproductive

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system of streptaxids have been recognized as providing useful characters for identifying generic groupings.

Diaphera Albers, 1850, is a poorly known genus endemic to the South-East Asian region. Bruggen (1967, 1972, 1974) and Dance (1970) suggested that *Diaphera* may have originated in the Philippines and subsequently dispersed to the Sunda shelf and to southern mainland South-East Asia. Of the 38 described species, most exhibit localized distributions in the Philippines, one species is recorded from Borneo, and six species are recorded from mainland southern South-East Asia (Stoliczka, 1871; Beddome, 1891; Quadras & Möllendorff, 1894: 1895, 1896; Blanford & Godwin-Austen, 1908; Zilch, 1961; Benthem Jutting, 1962; Bruggen, 1974; Richardson, 1988; Vermeulen, 1990). There have previously been no confirmed records of *Diaphera* from Thailand, only ambiguous statements by Blanford (1899) and Blanford & Godwin-Austen (1908) that *Diaphera seatoni* (Beddome, 1891) occurred near the Thai–Burmese border. *Diaphera* was discovered on several isolated limestone hills in eastern Thailand during malacological surveys carried out between 1999 and 2007. The striking turretted shell with a partly detached last whorl serves to distinguish *Diaphera* from other streptaxoid genera in the region.

MATERIAL AND METHODS

SAMPLES AND MORPHOLOGY

A total of 148 specimens collected from our eastern Thailand surveys were identified from the publications of Stoliczka (1871), Möllendorff (1887, 1890), Beddome (1891), Quadras & Möllendorff (1894, 1895, 1896), Kobelt (1904, 1910), Blanford & Godwin-Austen (1908), Zilch (1961), Benthem Jutting (1962), Dance (1970), Bruggen (1974, 1975), and Vermeulen (1990), and were subsequently compared with the relevant type specimens. Living examples of *Diaphera prima* sp. nov. were frozen at –20 °C and ten specimens were dissected and examined under a stereomicroscope as detailed below. With the aid of a camera lucida attachment, the genital morphology of one specimen was figured and shell sculpture and radula morphology (form and formula of radula teeth) were examined by scanning electron microscopy (SEM: JEOL, JSM-5410 LV). For details of other streptaxids, plus other stylommatophoran taxa used in the molecular analysis in this study, see Table 1.

MOLECULAR METHODS

DNA extraction, PCR amplification, and sequencing of a fragment of the rRNA gene spanning the 3′ end (~80 nucleotides) of the 5.8S gene, the complete internal transcribed spacer 2 (ITS-2) region, and the 5′ end (~840 nucleotides) of the large subunit (LSU; 28S) gene were undertaken on single samples of each species as described in Wade, Mordan & Naggs (2006). Sequences were assembled using the STADEN package (Staden, 1993) and aligned within the Genetic Data Environment (GDE) package (Smith *et al.*, 1994). Sequence analyses were performed using a representative subset of taxa (see Table 1 for details) selected from the phylogenies presented in Wade *et al.* (2006). In total, 823 nucleotide sites could be aligned unambiguously in comparisons of all taxa and analyses were therefore based on this 823 nucleotide dataset. As the ITS-2 region showed extremely high variability amongst taxa, all ITS-2 sites were excluded. Phylogenetic trees were constructed using neighbor-joining (NJ), maximum likelihood (ML), and Bayesian inference (BI). For all methods, the general time reversible model of sequence evolution incorporating a gamma correction to account for between-site rate variation ($GTR + \Gamma$) was used to account for multiple hits (this was determined to be the most appropriate model for the data based on likelihood ratio tests). NJ analysis was carried out using PAUP* (version 4.0b10) (Swofford, 2003), with ML analysis undertaken using PHYML (version 2.4.5) (Guindon & Gascuel, 2003). BI analysis was performed using MrBayes (version 3.1.2 (Huelsenbeck & Ronquist, 2001), with the tree space explored using four chains of a Markov chain Monte Carlo algorithm for 3 000 000 generations (heating parameter = 0.175), sampling every 100 generations. A consensus tree was built using the last 1000 trees with a burnin of 29001 samples. Bootstrap resampling (Felsenstein, 1985) with 1000 replicates was undertaken in order to assign support to particular branches within the NJ and ML trees. Nucleotide sequences new to this study have been deposited in GenBank under accession numbers GQ330503 to 330511.

ANATOMICAL ABBREVIATIONS

In the description of the genitalia the term 'proximal' refers to the region closest to the genital orifice and the term 'distal' refers to the region furthest away from the genital orifice. The following abbreviations were used following Stoliczka (1871), Berry (1963, 1965), Winter, Gomez & Prieto (1999), and Herbert (2002): ag, albumin gland; at, atrium; eg, egg; fo, free oviduct; g, gonad; hd, hermaphroditic duct; ov, oviduct; p, penis; pp, penial pilaster; pr, penial retractor muscle; sv, seminal vesicle; v, vagina; vd, vas deferens.

INSTITUTIONAL ABBREVIATIONS

BMNH, The Natural History Museum, London; CUMZ, Chulalongkorn University, Museum of

Table 1. Details of samples, collectors, localities, and GenBank accession numbers for the sequences used in the molecular phylogenetic analysis (Fig. 3)

Family	Species	Collection/location	Collector	GenBank accession nos
Stylommatophoran Pulmonates [Phylum Mollusca, Class Gastropoda, Subclass Pulmonata, Order Eupulomonata, Suborder Stylommatophora]				
Infraorder Orthurethra				
Pupillidae	*Pupoides albilabris* (Adams, 1841)	Wilson County, Tennessee, USA	J. Slapcinsky & B. Coles	AY841283 & AY841284
Orculidae	*Orcula austriaca* Zimmerman, 1932	Kuhberg, Austria	P. Miltner	AY014028
Chondrinidae	*Chondrina clienta* (Westerlund, 1883)	Villach, Austria	P. Miltner	AY014031
Enidae	*Buliminus labrosus* (Olivier, 1804)	Saladin's Castle, Syria	P. Mordan	AY014034
Partulidae	*Partula suturalis* Pfeiffer, 1855	Moorea	B. Clarke	AY014042
Infraorder Mesurethra				
Clausiliidae	*Albinaria xantostoma* (Boettger, 1883)	Crete	D. Thomaz	AY014048
	Mundiphaedusa decapitata (Pilsbry, 1902)	Osaka City, Japan	P. Callomon	AY014054 & AY014055
Infraorder Elasmognatha				
Succineidae	*Succinea putris* (Linnaeus, 1758)	Southampton, UK	C. MacDonald	AY014056 & AY014057
Athoracophoridae	*Athoracophorus bitentaculatus* (Quoy & Gaimard, 1832)	Mere Mere, New Zealand	G. Barker	AY014018
Infraorder Sigmurethra				
Orthalicidae	*Drymaeus discrepans* (Sowerby, 1833)	Guatemala	Unknown	AY841300
Amphibulimidae	*Gaeotis nigrolineata* Shuttleworth, 1854	El Yunque, Puerto Rico	A. Davison	AY841301
Cerionidae	*Cerion incanum* (Binney, 1851)	Florida Keys, USA	J. Taylor	AY014060
Ferussaciidae	*Ferussacia foilliculus* (Gmelin, 1791)	Los Alcornales, Prov Cadiz, Spain	M. Seddon	AY841302
Subulinidae	*Zootecus insularis* (Ehrenberg, 1831)	Dubai, United Arab Emirates	S. Green	AY014068
Glessulidae	*Glessula ceylanica* (Pfeiffer, 1845)	Colombo, Sri Lanka	P. Karunaratne	AY014063 & AY014064
Achatinidae	*Lissachatina fulica* (Bowdich, 1822) [=*Achatina fulica*]	Unknown (Zoological Society of London collection)	P. Pearce-Kelly	AY014069
Coeliaxidae	*Coeliaxis blandii* (Pfeiffer, 1852)	New Bradford, South Africa	N. Smith	AY841306 & AY841307
Thyrophorellidae	*Thyrophorella thomensis* Greeff, 1882	Zampala, São Thomé, West Africa	A. Gascoigne	AY841308
Spiraxidae	*Euglandina rosea* (Férussac, 1821)	Moorea (Zoological Society of London collection)	P. Pearce-Kelly	AY014074
Testacellidae	*Testacella scutulum* Sowerby, 1821	North London, UK	R. Hurst	AY014075
Streptaxidae				
Streptaxinae	* *Indoartemon* sp. A	Sri Lanka	D. Raheem	GQ330503
Enneinae	* *Streptostele* sp.	Kenya	M. Pickford	GQ330504
	* *Diaphera prima* n. sp.	Chonburi, Thailand	S. Panha	GQ330505
	* *Sinoennea ridleyi* (Piele, 1926)	Selangor, Malaysia	C. Sutcharit	GQ330506
Gibbinae	* *Gibbulinella dewinteri* Bank, Groh & Ripken, 2002	La Gomera Island, Canary Islands	M. Ibañez	GQ330507
	Gonaxis quadrilateralis Preston, 1910	Reunion	O. Griffiths	AY014076
	Gonospira sp.	Mauritius	O. Griffiths	AY014077
Marconiinae	* *Marconia* sp.	Kenya	M. Pickford	GQ330508
Odontartemoninae	* *Pseudogonaxis* sp.	Kenya	M. Pickford	GQ330509
Ptychotrematinae	* *Gulella caryatis diabensis* Connolly, 1939	Namibia	Unknown	GQ330510
	* *Huttonella bicolor* (Hutton, 1834)	Sri Lanka	D. Raheem	GQ330511

Table 1. *Continued*

Family	Species	Collection/location	Collector	GenBank accession nos
Dorcasiidae	*Dorcasia alexandri* Gray, 1938	Windhoek, Namibia	C. Boix-Hinzen	AY014079
Acavidae	*Acavus phoenix* (Pfeiffer, 1854)	Kitulgala, Sri Lanka	P. Karunaratne	AY014082 & AY014083
	Leucotaenius proctori (Sowerby, 1894)	Beheloa, Madagascar	O. Griffiths	AY014084 & AY014085
Chlamydephoridae	*Chlamydephorus burnupi* (Smith, 1892)	Pevensey, Natal	D. Herbert	AY014089
Corillidae	*Corilla adamsi* Gude, 1914	Sri Lanka	D. Raheem	AY014091 & AY014092
Discidae	*Anguispira alternata* (Say, 1816)	Wilson Co. Tennessee, USA	J. Slapzinsky & B. Coles	AY841309
Euconulidae	*Euconulus fulvus* (Müller, 1774)	New Forest, Hampshire, UK	P. Mordan	AY014098
Helicarionidae	*Rhysotina hepatizon* (Gould, 1848)	São Thomé	A. Gascoigne	AY014100
Ariophantidae	*Euplecta gardeneri* (Pfeiffer, 1846)	Sri Lanka	D. Raheem	AY841310 & AY841311
Vitrinidae	*Vitrina pellucida* (Müller, 1774)	Kirkdale, Derbyshire, UK	C. Wade	AY014111
Milacidae	*Tandonia budapestensis* (Hazay, 1881) [= *Milax budapestensis*]	Kirkdale, Derbyshire, UK	C. Wade	AY014117
Polygyridae	*Triodopsis alleni* (Wetherby, 1883)	Williams Creek, Iowa, USA	R. Cameron	AY841316
Camaenidae	*Amphidromus* sp.	Unknown	D. Reid	AY841317 & AY841318
Hygromiidae	*Cochlicella acuta* (Müller, 1774)	Porthcurnick, Cornwall, UK	E. Bailes	AY014126
Helicidae	*Helix lucorum* Linnaeus, 1758	Unknown	Unknown	AY841334
Helminthoglyptidae	*Cepolis streatori* (Pilsbry, 1889)	Grand Cayman	S. Chiba	AY841346
Arionidae	*Arion hortensis* Férussac, 1819	Kirkdale, Derbyshire, UK	C. Wade	AY014143
Philomycidae	*Philomycus carolinianus* (Bosc, 1802)	Wake Co., USA	A. Braswell	AY841349
Non-Stylommatophoran Pulmonates [Phylum Mollusca, Class Gastropoda, Subclass Pulmonata]				
Order Eupulmonata				
Ellobiidae	*Melampus luteus* (Quoy & Gaimard, 1832)	Souilla, Mauritius	O. Griffiths	AY014146
	Laemodonta sp.	Suralaya, West Java	B. Dharma	AY014147
Carychiidae	*Carychium tridentatum* (Risso, 1826)	Abelheira, São Miguel, Azores	P. Mordan	AY014148
Order Basommatophora				
Siphonariidae	*Siphonaria pectinata* (Linnaeus, 1758)	Zamara Los Atunes, Spain	S. Hawkins	AY014149 & AY014150
Order Systellomatophora				
Veronicellidae	*Laevicaulis alte* (Férussac, 1823)	Dubai, United Arab Emirates	A. Green	AY014151
Phylum Mollusca, Class Gastropoda, Subclass Opisthobranchia, Order Anaspidea				
Aplysiidae	*Aplysia punctata* Cuvier, 1803	Bessaker, Trondelag, Norway	J. Evertsen & T. Bakken	AY014153 & AY014154

*Denotes taxa which are new to this study.
The classification broadly follows Vaught (1989).

Zoology, Bangkok, Thailand; MNHN, Muséum National d'Histoire Naturelle, Paris; SMF, Forschungsinstitut und Naturmuseum Senckenberg, Frankfurt, a.m.; ZMA, Zoological Museum, Amsterdam, the Netherlands.

SYSTEMATIC DESCRIPTION

SUPERFAMILY STREPTAXOIDEA GRAY, 1860

FAMILY **DIAPHERIDAE** PANHA & NAGGS FAM. NOV.

Type genus: Diaphera Albers, 1850.

Diagnosis: Shell high spired and narrow or pupiform; whorls symmetrical about straight axis, apart from a portion of the last whorl, which is detached in *Diaphera*. Penis simple, long, and without a penial sheath or internal hooks.

Remarks: The Diapheridae is defined by the type genus *Diaphera*. On currently available evidence only *Diaphera* and *Sinoennea* Kobelt, 1904 are included in the Diapheridae. The shell form with a simple reproductive system, lacking a penial sheath and internal hooks, set *Diaphera* and *Sinoennea* apart from other streptaxoid taxa. Although no single morphological synapomorphy characterizing the Diapheridae has been identified, the robust, distinct, and basal position of the Diapheridae within the molecular streptaxoid clade presented below supports the distinct identity of this group.

GENUS *DIAPHERA* ALBERS, 1850

Type species: Cylindrella cumingiana Pfeiffer, 1845, by original designation; lectotype BMNH 20080230 (Fig. 1A); type locality: the Philippines ('in grass, Guimaras, the Philippines', given on original label).

Diagnosis: Shell ovate to cylindrical, thin, transparent, and glossy, surface smooth or sculptured; apex obtuse, surface smooth, subsequent whorls smooth or with radial ribs; part of last whorl always detached; aperture circular to ovate; lip expanded and slightly reflexed; apertural dentition usually comprised of parietal, palatal, basal, and columellar lamellae. Radula plate narrow; teeth lanceolate, central tooth minute, lateral and marginal teeth similar with long cusp. Genitalia with well-developed penis; penial sheath, verge, and spines are absent.

Remarks: Diaphera currently includes 39 nominal species that range from Burma, Thailand, Cambodia, and the Philippines to Kalimantan (Blanford, 1899; Bruggen, 1975; Richardson, 1988; Vermeulen, 1990; Schileyko, 2000). In Thailand *Diaphera* can be distinguished conchologically from similar genera such as *Sinoennea* (with six to seven whorls) by possessing a greater number (eight to 20) of more elongate, cylindrical whorls; partially detached last whorl and ovate aperture (Tryon, 1885; Zilch, 1960; Richardson, 1988; Schileyko, 2000).

Diaphera was treated as a subgenus of *Gibbus* Montfort, 1810 by Tryon (1885) and of *Gulella* Pfeiffer, 1856 by Thiele (1931). Zilch (1960) subsequently treated *Diaphera* as a distinct genus. Richardson (1988) placed 46 species from the Philippines and Indochina in *Diaphera*. However, Richardson's inclusion of the two pupiform Madagascan species, *Gulella miaryi* (Fischer-Piette & Bedoucha, 1964) and *Gulella gallora* (Fischer-Piette, Blanc & Salvat, 1975), both of which lack a detached last whorl, seems unjustified (see Fischer-Piette & Bedoucha, 1964; Fischer-Piette *et al.*, 1975). The Madagascan taxa are likely to be part of or allied to the *Gulella* group. Eight cylindrically shelled species from the Philippines *Ennea sericina* Möllendorff (1887), *Ennea hidalgoi* Möllendorff, 1888, *Ennea cardiostoma* Quadras & Möllendorff, 1894, *Ennea nitidula* Quadras & Möllendorff, 1894, *Ennea otostoma* Quadras & Möllendorff, 1894, *Ennea cylindrica* Quadras & Möllendorff, 1895, *Ennea cristatella* Möllendorff, 1896, and *Ennea samarica* Möllendorff, 1896 were placed in *Diaphera* by Zilch (1961) and Richardson (1988). However, these taxa lack a partially detached last whorl and are thus more likely to be related to *Ennea* H. & A. Adams, 1855. Richardson (1988) followed Kobelt (1904) and Blanford & Godwin-Austen (1908) in placing *Ennea brevicollis* Blanford, 1899 in *Sinoennea*, but this species possesses a multi-whorled turriform shell with detached body whorl and belongs in *Diaphera* (Table 2).

DIAPHERA PRIMA PANHA SP. NOV. (FIGS 1B–G, 2)

Type material: Holotype CUMZ 3544 (height 6.2 mm, width 2 mm, whorls eight) (Fig. 1B, C); paratypes CUMZ 3543 (2a shells), 3545 (3a ethanol; Fig. 1G), 3627 (8a + 8j shells), 3629 (13a ethanol; Fig. 1E, F), 3630 (1j shell; Fig. 1D), 3649 (10a + 13j shells), 4299 (10a + 3j ethanol), 4656 (5a shells); BMNH 20070007 (2a shells); MNHN 21991 (2a shells); SMF 333515 (2a shells); ZMA 409052 (2a shells). Type locality: Khao Cha Ang-Oan, Bor Thong, Chonburi, Thailand (13°11′5″N, 101°34′59″E). *Other material examined*: Khao Chakan, Srakeo, Thailand (13°39′80.2″N, 102°05′71.1″E): CUMZ 3541, 3542, 3546, 3628, 3650, 4296, 4297, 4298. Tam Khao Loy, Khao Chamao, Rayong, Thailand (13°03′28.9″N, 101°36′27.6″E): CUMZ 3800.

Description: Shell small, turreted, tapering slightly away from apex, thin, transparent, and glossy when fresh; part of last whorl detached (Fig. 1B). Apex

Table 2. Comparison of shell characters amongst five species of *Diaphera* Albers, 1850 from Indochina

Characters	***D. prima* sp. nov.**	*D. saurini**	*D. brevicollis*†	*D. seatoni*†	*D. cylindrelloidea*†
Shell height of holotype in mm	6.2	8.8	8	9.5	4.5
Shell width of holotype in mm	2	3	2	2.25	1.3
Number of whorls	7–8	10	11	11	8
Apex	Obtuse and smooth	Obtuse and smooth	Obtuse and smooth	Obtuse and smooth	Obtuse and smooth
Shell sculpture	Almost smooth, only short ribbed below suture	Distinct rib	Distinct rib	Not closely ribbed	Closely ribbed
Shape of aperture	Rounded	Rounded	Rounded	Ovate	Rounded
Apertural lamellae	Parietal, 2 palatals, basal, columellar	Parietal, palatal, columellar	Parietal, thin palatal	Parietal, palatal, columellar	Parietal, thin palatal
Distribution	Eastern Thailand	Battambang, Cambodia	Moulmein, Tenasserim, Burma	Tenasserim, Burma	Moulmein, Tenasserim, Burma
Total number of specimens examined	46	2	1	1	1

*Holotype ZMA 3.62.016.
†Indicates data derived from Stoliczka (1871); Beddome (1891); Blanford (1899); Blanford & Godwin-Austen (1908).

smooth, obtusely conical. Whorls seven to eight (excluding detached section) slightly convex; suture depressed. Shell surface with very fine growth lines in appearance; short transverse ridges immediately below suture extend around circumference of detached section of body whorl. Detached part of last whorl long, being approximately one third the length of last whorl, descending, with sutural line extending as vallicular depression and corresponding with parietal lamella (P). Umbilicus wide, deep with strong transverse ribs. Aperture circular (Fig. 1C); inner surface with thin wrinkles. Lip slightly thickened and expanded. Dentition of peristome comprises one large and curved parietal lamella fold and two small palatal lamellae (Pl) (one on the margin of the peristome and one inside the peristome), one convex basal lamella (Bl), and one large internal columellar lamella (Cl) (Fig. 1C). Juvenile shell composed of about four whorls and shows distinct parietal, palatal, basal, and columellar lamellae in peristome (Fig. 1D).

Animal body colour externally pale greenish yellow; digestive gland pale brownish yellow, extended body entirely lacking bright skin pigmentation and bright red, orange, or yellow eye retractor muscles often associated with streptaxids (Fig. 1E, F). Foot narrow and undivided (holopoda), anterior long, posterior rather short as typical of streptaxids. Upper tentacle long with black eye spot on tip, lower tentacles very short.

Radula: Radula teeth arranged in anteriorly pointed V-shaped rows on the dorsal odontophore, each row contains 31–33 teeth with formula (15–16)–1–(15–16). Central tooth triangular, minute with pointed cusp. Lateral and marginal teeth weakly differentiated, unicuspid, lanceolate, basal plate well developed; lateral teeth gradually reduced in length and size towards radular margin; inner lateral teeth straight and slightly curved cusp (Fig. 1G).

Genitalia: Genital atrium (at) short. Penis (p) very long, slender with thick muscular wall. Epiphallus, penial verge and penial sheath absent. Vas deferens (vd) small tube, inserting on penial apex and almost coincident with attachment of penial retractor muscle. Penial retractor muscle (pr) thin, very long, originating from columellar muscle (Fig. 2A). Internal wall of penis smooth with two longitudinal pilasters (pp); major pilaster extends almost the entire penis length; minor pilaster about half as long. Penial armature in form of hooks characteristic of streptaxids entirely absent (Fig. 2B). Vagina (v) short, about one fifth of the length of the penis. Duct of gametolytic organ (gd) slender and short, ending without distinct gametolytic sac, and attached to free

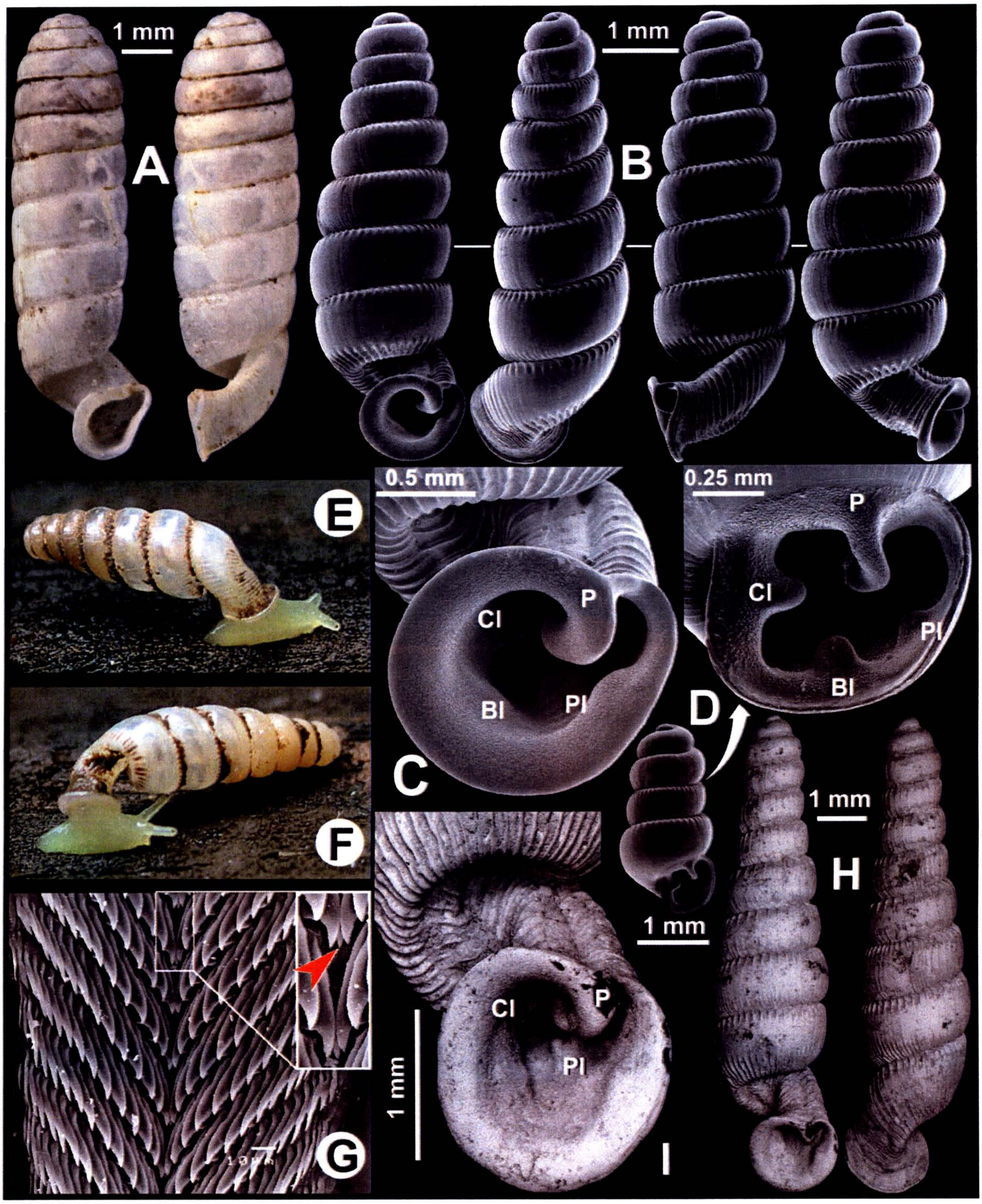

Figure 1. A, shell morphology of *Diaphera cumingiana* (Pfeiffer, 1845) (lectotype BMNH 20080230). B–G, morphology of shell and radular and living animals of ***Diaphera prima* sp. nov.** B, the shell and C, the aperture of holotype (CUMZ 3544) showing lamellae. D, juvenile specimen showing apertural lamellae (paratype CUMZ 3630). E, F, living animals (paratype CUMZ 3629): E, shell height 6.5 mm; and F, shell height 6.8 mm. G, radula morphology (paratype CUMZ 3545); arrow on top-right inset indicates the central tooth. H, I, morphology of shell of *Diaphera saurini* Benthem Jutting, 1962. H, the shell and I, aperture of holotype (ZMA 3.62.016) showing lamellae. Abbreviations: P, parietal lamella; Pl, palatal lamella; Bl, basal lamella; Cl, columellar lamella.

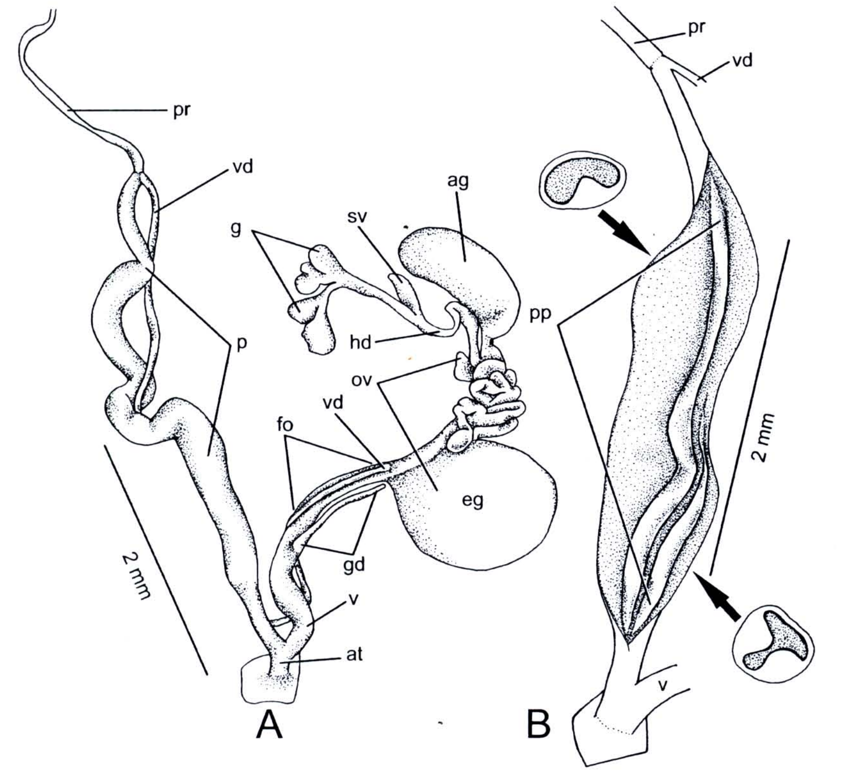

Figure 2. Genitalia of ***Diaphera prima* sp. nov.** (paratype CUMZ 3545). A, whole genital system. B, details of internal wall of penis. Abbreviations: ag, albumin gland; at, atrium; eg, egg; fo, free oviduct; g, gonad; hd, hermaphroditic duct; ov, oviduct; p, penis; pp, penial pilasters; pr, penial retractor muscle; sv, seminal vesicle; v, vagina; vd, vas deferens.

oviduct by thin connective tissue. Free oviduct (fo) long; oviduct (ov) enlarged with lobular shape (figured specimen contained one large spherical egg proximally). Inconspicuous prostate gland bound to external section of oviduct. Albumen gland (ag) thick, bean-shaped. Gonad (g) lobular; hermaphroditic duct (hd) slender and straight, bearing globular seminal vesicle (sv) in middle (Fig. 2A).

Distribution: The species is presently known from three localities, namely the isolated limestone hills at the type locality, at Khao Chakan, Srakeo, Thailand, and at Tam Khao Loy, Khao Chamao, Rayong, Thailand. The shells of specimens from Khao Chakan are slightly smaller than those from the type locality, but shell shape, sculpture, and apertural dentition are essentially identical to that of the type specimens. The slight difference in size is probably indicative of local population variation.

Etymology: From the Latin *'prima'* meaning 'first, original'. It refers to the fact that this new species is the first *Diaphera* definitely recorded from Thailand.

Remark: Several of the Philippines *Diaphera* such as *Diaphera canaliculata* (Quadras & Möllendorff, 1896) are pupiform with few whorls, and are quite distinct from the more common high, narrow shelled species (Zilch, 1961). These two groups may represent distinct genera. We limit our discussion of *Diaphera* species to *D. prima* sp. nov. and the four high-spired geographically proximal (from Indochina) species, *Diaphera cylindrelloidea* (Stoliczka, 1871), *D. seatoni* (Beddome, 1891), *Diaphera brevicollis* (Blanford, 1899), and *Diaphera saurini* Benthem Jutting, 1962.

Diaphera prima sp. nov. can be distinguished from these four regional species on the basis of several conchological characters (Table 2). *Diaphera cylindrelloidea* and *D. brevicollis* from Burma resemble each other in shell form with smooth embryonic whorls, distinct transverse ribs on the later whorls, and only parietal and thin palatal lamellae in the aperture (Stoliczka, 1871; Beddome, 1891; Blanford, 1899; Blanford & Godwin-Austen, 1908). Compared to other species within the genus, *D. seatoni* from Mooleyit Mountain, Tenasserim, Burma, possesses a higher shell with distinct transverse ribs and the detached part of the last whorl is slightly shorter than *D. prima* sp. nov. (Blanford, 1899; Blanford & Godwin-Austen, 1908). *Diaphera seatoni* can be distinguished from *D. cylindrelloidea* and *D. brevicollis* by its higher shell, ovate aperture with a sinus on upper corner, the presence of a basal lamella and shorter detached part to the last whorl (Stoliczka, 1871; Beddome, 1891; Blanford & Godwin-Austen, 1908). In the morphologically similar species *D. saurini* from Cambodia (Fig. 1H, I), the fourth and later whorls have strong transverse ribs, the penultimate and last whorls are enlarged, and the basal lamella is absent (Benthem Jutting, 1962).

The soft internal anatomy of a limited number of streptaxid genera has been previously described (Table 3) and this is the first account of the reproductive anatomy of *Diaphera*. The anatomical descriptions of *Sinoennea kanchingensis* Tomlin, 1948 and *Huttonella bicolor* (Hutton, 1834) were the most comprehensive available for comparing the morphology of *Diaphera* (Stoliczka, 1871; Berry, 1963, 1965; Schileyko, 2000). *Diaphera* possesses a very long penis, the penial retractor muscle inserts on the distal penis, being almost coincident with entry of the vas deferens; the gametolytic organ is slender, a short duct, and lacks a distinct gametolytic sac; the seminal vesicle is cylindrical. In *Sinoennea* and *Huttonella* Pfeiffer, 1856 the penis is shorter, the vas deferens inserts centrally on the penis, remote from the distally inserting penial retractor muscle; and the gametolytic organ has a long duct and terminates in a globular gametolytic sac.

MOLECULAR RESULTS

rRNA sequences of nine new streptaxoid genera were obtained in this study. Together, with the two streptaxid rRNA sequences obtained by Wade, Mordan & Clarke (2001), molecular data for the rRNA gene are now available for 11 streptaxoid genera (Table 1), with at least one representative species from each of the six currently recognized subfamilies in the Streptaxidae. A phylogenetic tree showing the evolutionary relationships amongst the Streptaxoidea and its position within the Stylommatophora is presented in Figure 3. The tree is rooted on the aplysiid opisthobranch *Aplysia punctata*. The phylogeny is based on the analysis of 823 unambiguously aligned nucleotide sites, of which 287 were variable and 206 were parsimony informative. DNA base frequencies were highly consistent across all taxa in the tree, ranging from 60.0 to 63.5% GC.

The Streptaxoidea are a monophyletic group within the rRNA molecular phylogeny supported in 100% of NJ and ML bootstraps and with a Bayesian posterior probability of 1.00. Representatives from all six currently recognized streptaxoid subfamilies are included in the tree (Fig. 3; Schileyko, 2000; Bouchet & Rocroi, 2005). *Diaphera prima* and *Sinoennea* cluster together within the tree with 100% NJ and 98% ML bootstrap support and with a Bayesian posterior probability of 1.00. This 'diapherid' group is a sister group of the Streptaxidae *sensu stricto*, following a basal divergence within the Streptaxoidea and is highly divergent from the other streptaxoids with the branch falling at a similar depth to that between the Ferussaciidae and the Achatinidae/Subulinidae clade.

DISCUSSION

In many Stylommatophoran groups complexities in morphology of the reproductive system have proved to be of considerable value for recognizing species, genera, and higher level taxa. Despite the relative simplicity of reproductive morphology in the achatinoid/streptaxoid clade (discussed below) genitalic characters have nevertheless been of value in recognizing achatinoid species and genera (Naggs, 1994). However, the same does not hold for the streptaxoids as few characters have proved to be of value for recognizing systematic groups. For example, judged by current concepts of subfamily units, the presence or absence of a penial sheath appears to be of little value in recognizing groups above generic level in streptaxids. A penial sheath is present in 23 streptaxid genera and is recorded as being absent not only in *Diaphera* but also in *Augustula* Thiele, 1931 and *Careoradula* Gerlach & Bruggen, 1999 (Streptaxinae), *Sinoennea* (Enneinae), *Gulella* and *Huttonella* (Ptychtrematinae), and *Odontartemon* Pfeiffer, 1856 (Odontartemoninae) (Table 3).

Penial armature in the Mollusca is confined to the Euthyneura and occurs in some carnivorous opisthobranchs and such diverse stylommatophoran taxa as the Himalayan arionid slug Anadenus Heynemann, 1863 (lanceolate penial armature), the African urocyclid Polytoxon (calcareous needles located in penial pits), and the Streptaxidae (Godwin-Austen, 1882; Schileyko, 2002) (generally cat-like claws). Penial armature is clearly an important feature within the Streptaxidae; it has been considered to be an apomorphy for the group and its absence in streptaxids is assumed to be secondary. For example, Schileyko (2000: 771) asserts that 'rarely hooks secondarily disappear'. However, in the case of *Diaphera* and *Sinoennea*, which on molecular phylogenetic evidence diverged at a basal stage in the streptaxoid clade (Fig. 3), it seems reasonable to hypothesize that the absence of penial armature is a plesiomorphic condition. Of the 60 currently recognized streptaxoid genera, some internal anatomy has been described for 37 genera and, of these, 28 possess penial armature.

Table 3. List of streptaxoid subfamilies and genera compiled primarily from Schileyko (2000)

Taxa	Known anatomically	Penial hooks or spines	Penial sheath	Distribution
Streptaxinae				
Scolodonta	No			Argentina
Martinella	No			Ecuador, south Brazil
Rectartemon	Yes	+	+	Brazil, Venezuela, Caribbean Islands
Streptaxis	No			Brazil, Colombia, Venezuela
Hypselartemon	No			Brazil, Colombia
Sairostoma	No			North-east Brazil
Streptartemon	Yes	+	+	South America (Brazil, Bolivia, Colombia, Venezuela, Guyana)
Seychellaxis	Yes	+	+	Seychelles
Indoartemon	No			Sri Lanka, South-East Asia, Hainan
Stemmatopsis	No			North Vietnam
Perrottetia	Yes	+	+	South India, South-East Asia, Mascarenes
Acanthennea	Yes	+	+	Silhouette and Mahé Islands, Seychelles
Glabrennea	Yes	+	+	Seychelles
Stereostele	Yes	+	+	Seychelles
Silhouettia	Yes	+	+	Silhouette Island, Seychelles
Augustula	Yes	–	?	Seychelles
Careoradula	Yes	–	–	Seychelles
Discartemon	Yes	–	+	South-East Asia
Glyptoconus	No			Busuangga Island, Philippines
Micrartemon	No			Philippines
Platycochlium	No			Kalimantan, Borneo
Tonkinia	No			North Vietnam
Gibbinae				
Edentulina	Yes	+	+	East Africa, Comores, Seychelles
Pseudelma	–			Mayotte, Comores
Gonospira	Yes	+	+	Mauritius, Réunion, Rodrigues
Microstrophia	No			Mauritius and Réunion
Gonidomus	Yes	+	+	Mauritius extinct
Plicadomus	No			Mauritius
Gibbus	Yes	+	+	Mauritius extinct
Gibbulinella	Yes	+	+	Canary Islands
Imperturbatia	Yes	+	+	Seychelles
Priodiscus	Yes	+	+	Seychelles
Gonaxis	Yes	+	+	Equatorial and South Africa.
Oophana	Yes	+	+	South-East Asia
Haploptychius	Yes	+	+	Andamans, south India, South-East Asia, southern and central China, North Sulawesi
Enneinae				
Ennea	Yes	+	?	Afrotropical
Maurennea	Yes	+	?	Mauritius, Comoros?
Indoennea	No			India, Malaya, Sumatra
Sinoennea	Yes	–	–	India, IndoChina, China, Malaysian Peninsula, Sumatra, Japan, South Korea
Diaphera	Yes	–	–	Philippines, Kalimantan, South-East Asia
Bruggennea	No			Kalimantan
Elma	No			Taiwan, Vietnam
Streptostele	Yes	+	+	Afrotropical, Gulf of Guinea islands, Seychelles, Comoros, Mascarenes
Varicostele	Yes	?	?	Central Africa, Congo Basin

Table 3. *Continued*

Taxa	Known anatomically	Penial hooks or spines	Penial sheath	Distribution
Ptychotrematinae				
Gulella	Yes	+	?	Afrotropical, Arabia, Madagascar, Comoros, Seychelles, Mauritius
Mirellia	No			East Africa
Huttonella	Yes	+	–	Tropical cosmopolitan 'weed' unknown origin but type locality India
Parennea	No			Afrotropical
Ptychotrema	Yes	+	?	Afrotropical
Sinistrexcisa	Yes	+	?	South-west Cameroon, Equatorial Guinea
Marconiinae				
Stenomarconia	Yes	+	+	Tanzania, Kenya
Marconia	Yes	+	+	Afrotropical, Comores
Macrogonaxis	No			East Africa, Seychelles
Odontartemoninae				
Somalitayloria	Yes	?	?	Somalia
Artemonopsis	No			Ivory Coast
Tayloria	Yes	?	?	East Africa
Pseudogonaxis	No			Congo Basin
Gigantaxis	No			East Africa
Afristreptaxis	Yes	?	+	Afrotropical and South Africa
Ondontartemon	Yes	+	–	West Africa

Global distributions, availability of anatomical data and presence/absence of penial hooks and sheath are shown (+, character present; –, character absent; ? character not described in the literature).
We include Myanmar and all Asian countries to the south and west as being South-East Asia and confine IndoChina to Laos, Vietnam, and Cambodia, but source references may have used these terms with different meanings.

Penial armature is not mentioned in the anatomical descriptions of four genera (Enneinae: *Varicostele*; Odontartemoninae: *Somalitayloria* Verdcourt, 1962, *Tayloria* Bourguignat, 1889, *Afristeptaxis* Thiele, 1932). There are only five streptaxoid genera (Table 3) for which penial armature is recorded as being absent (Streptaxinae: *Careoradula*, *Discartemon* Pfeiffer, 1856, *Augustula*; Enneinae: *Sinoennea*, *Diaphera*). *Careoradula*, *Discartemon*, and *Diaphera* lack any penial hard structures; *Sinoennea* and *Augustula* possess chitinized penial papillae.

Discartemon possesses a discoidal shell and a penial sheath. The enigmatic *Careoradula*, which is the only land snail recorded as lacking a radula (Gerlach & Bruggen, 1999), resembles *Imperturbatia constans* (Martens & Wiegmann, 1898) in possessing a depressed helicoid shell and in the absence of penial hooks, penial sheath and gametolytic sac. However, in *Imperturbatia violascens* (Martens & Wiegmann, 1898) the penis possesses spinules and both a penial sheath and gametolytic sac are present (Gerlach & Bruggen, 1999). Despite the similarity in shells it appears that the two species currently included in *Imperturbatia* Martens, 1898 might belong in different groups. The combination of these shared characters in *Diaphera, Careoradula*, and *I. constans* is quite remarkable. Schileyko's (2000: 794) figure of *I. constans*, which shows a penial sheath occupying half the length of the penis; large penial hooks, and a voluminous gametolytic sac is based on a misidentification. Justin Gerlach (unpubl. data) points out that the '*I. constans*' reported on by Schileyko was from Silhouette Island, Seychelles, where *Imperturbatia* does not occur and that it would be a *Silhouette* Gerlach & Bruggen, 1999 species. Whereas *Diaphera* and *Sinoennea* share high spired shell forms, *Sinoennea* possesses a distinct gametolytic sac that is absent in *Diaphera*, *Careoradula*, and *I. constans*. The systematic significance of the presence or absence of a distinct gametolytic sac is not clear. In addition, because the gametolytic sac may not be distinct in virgin individuals of some species when the gametolytic sac has not digested allospermatophores, the absence of a clearly defined gametolytic sac could be related to the state of reproductive development in examined specimens rather than being a species character. Although the presence or absence of a penial sheath is apparently of no value for identifying cur-

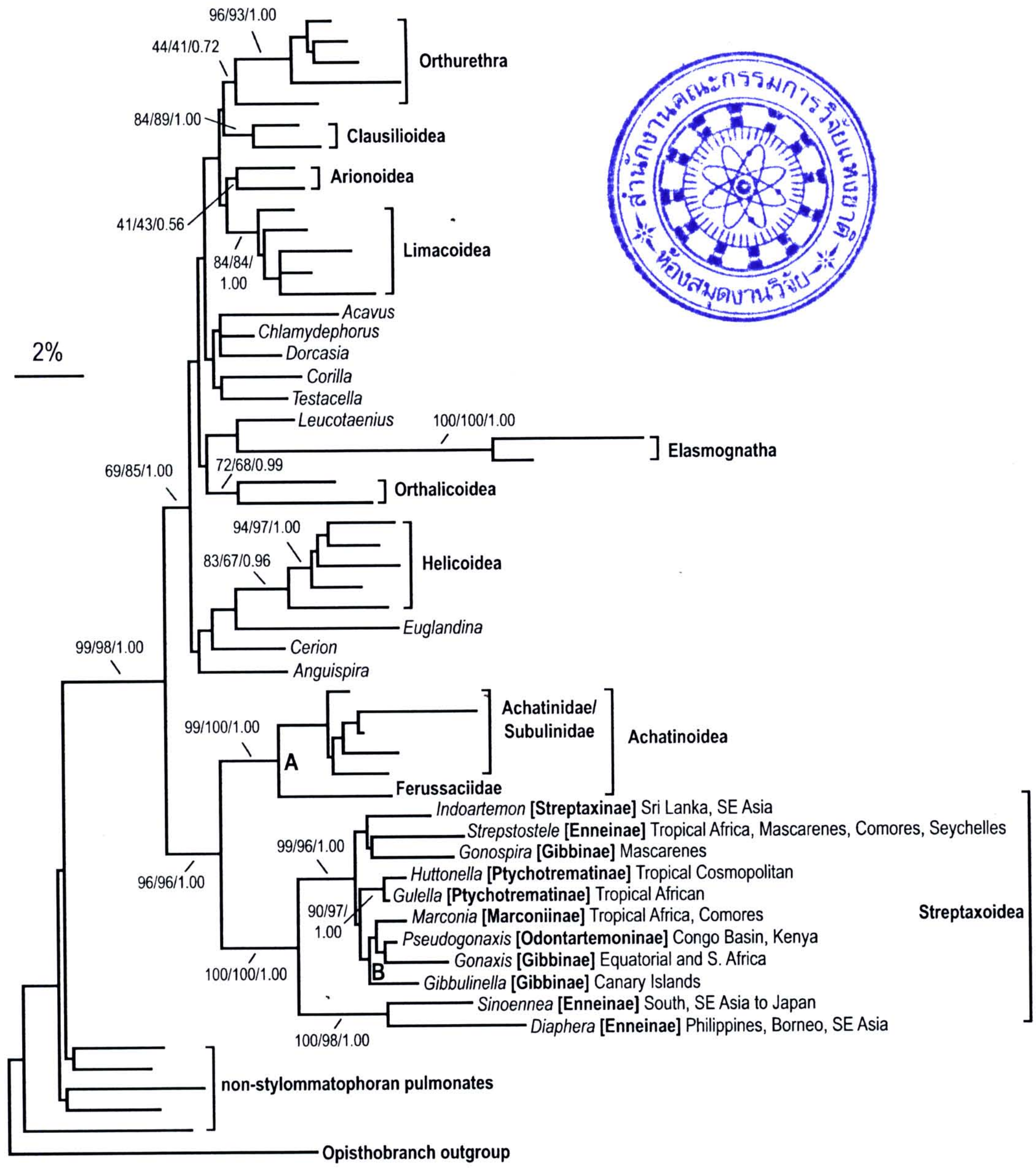

Figure 3. Neighbor-joining (NJ) phylogeny of the Streptaxoidea. The phylogeny includes representatives of the major stylommatophoran land snail groups and is rooted on the Opisthobranch *Aplysia*. The tree is based on 823 unambiguously aligned nucleotide sites with distances corrected for multiple hits using a GTR + Γ model (alpha = 0.197409). Bootstrap values [1000 NJ bootstraps and 1000 maximum likelihood (ML) bootstraps expressed as a percentage] and Bayesian posterior probabilities indicating support for individual branches are shown on the tree (NJ bootstraps/ML bootstraps/Bayesian inference posterior probabilities). The scale bar corresponds to a genetic distance of 2%. The geographical distribution of streptaxid genera and their current subfamily attributions are shown. A, first fossil record of achatinoid 140 Mya. B, minimum age 80 Mya based on fossil *Gibbulinella* from Portugal.

rently recognized subfamily groups within the Streptaxoidea, these subfamilies are unlikely to be natural groups. Thus the significance of *Discartemon* possibly belonging to a basal group in the Streptaxoidea and possessing a penial sheath is not clear.

Morphological characters have not provided a robust basis for recognizing higher level relationships in the Streptaxoidea and it seems likely that the extent of homoplasy and plesiomorphy in streptaxoid morphological characters will only be resolved when they are mapped on a molecular phylogenetic tree. Although described as a well-defined family (Bruggen, 1967), there is no identified apomorphy by which the group can be recognized. It is inherent in the molecular trees presented by Wade *et al.* (2001, 2006) that supposed streptaxoid affinity with other carnivorous stylommatophorans (Thiele, 1931; Zilch, 1960) is the result of homoplasies associated with specialized carnivory (Naggs, Raheem & Budha, 2008). Indeed, prior to our demonstration of the molecular relationship of *Diaphera* and *Sinoennea* being closer to streptaxoids than to achatinoids, inclusion of these genera within the Streptaxoidea was questionable.

Molecular phylogenetic trees are powerful tools for investigating evolutionary relationships and the relative chronologies of cladogenesis. In combination with the fossil record they provide a framework for developing testable hypotheses relating to calibrated chronologies and geographical distribution of taxa through time. Wade *et al.* (2001, 2006) reported molecular phylogenetic trees comprised of a large number of taxa in the major land snail group, the Stylommatophora. These support taxonomic relationships that had not been suspected on the basis of comparative morphology. Most notably, this includes a basal divergence within the Stylommatophora between a clade that includes the Achatinidae, Subulinidae, Ferussaciidae, Streptaxidae *sensu lato* (= Streptaxoidea = Streptaxidae + Diapheridae) and a clade that includes all other stylommatophoran groups. These two groups are currently referred to as the achatinoid and non-achatinoid clades. It appears likely that, in addition to the hierarchical position of the achatinoid group not being previously recognized within the Stylommatophora, that the degree of higher level diversity within the achatinoid group has also not been identified.

This investigation of *Diaphera* is an opportunity to present new molecular information on nine streptaxoid genera in addition to the two presented in Wade *et al.* (2006). Our molecular phylogenetic tree (Fig. 3) includes 11 streptaxoid species (Table 1) with at least one representative species from each of the six currently recognized subfamilies in the Streptaxidae (Table 3) (Schileyko, 2000; Bouchet & Rocroi, 2005). Current attribution of genera to subfamily categories and the subfamilies, which are also largely based on shell characters, is likely to require substantial revision and there is no merit in simply raising the status of current subfamily categories to family level in order to demonstrate the presence of higher level taxa. An indication of the extent to which current subfamily groups may be based on homoplasy is clear from the paraphyletic distribution of Enneinae *sensu* Schileyko in the tree (Fig. 3), which is represented in both the Streptaxidae *sensu stricto* and in the Diapheridae. The basal divergence of the Streptaxidae *sensu stricto* from the Diapheridae is strongly supported. There is little support for relationships within the Streptaxidae in the new restricted sense. However, there is strong support for *Gulella* and *Huttonella* as sister groups; a point of particular interest because of the tropical cosmopolitan distribution of *Huttonella* and doubts about its affinities and geographical origin (Naggs, 1989).

Here we use molecular information to clarify a high level systematic issue that the currently available morphological information cannot resolve. Although we have representatives of genera from all currently recognized subfamily groups, we are mindful of the limited geographical representation, most notably the absence of any South American taxa. The extent to which we are able to establish that taxonomic relationships correspond with geographical distribution is therefore limited (Fig. 3). In a group that has a fossil record extending deep into the Mesozoic (Zilch, 1960) this is a key issue. Because the group radiated through a period that corresponded with the major tectonic events associated with the break-up of Gondwana and possibly Pangaea, the extent of dispersal and vicariant distributions is central to understanding relationships and current distributions.

Supposed Palaeozoic stylommatophoran fossils (Solem & Yochelson, 1979) are of uncertain status (Naggs, 1997) and we have little idea of when stylommatophorans first appeared or when divergence of the achatinoid/streptaxoid and non-achatinoid clades may have taken place. There is both molecular and fossil evidence to support a long history for the streptaxoid clade but the occurrence of streptaxids on Atlantic and Indian oceanic islands of volcanic origin (Table 3) and the tropical cosmopolitan distribution of *Huttonella bicolor* is clear evidence of long distance dispersal in the group. The extent to which streptaxoids exhibit distributions based on Mesozoic vicariant events is unclear, unlike, for example, in the non-achatinoid acavoid groups, for which the extant species exhibit a classical Gondwanan distribution and occur only on continental tectonic plates or plate fragments. The earliest fossil record of what appears to be a subulinid member of the achatinoid/streptaxoid group was described from the Upper Jurassic/Early Cretaceous (about 140 Mya) of northwest Germany as *Hydrobia cypridae* Huckriede, 1967 (Huckriede, 1967; Naggs & Raheem, 2005). The first appearance of streptaxids was of *Gibbulinella* Wenz, 1920 recorded from the Late Cretaceous (about 80 Mya) of Portugal (Zilch, 1960). *Gibbulinella*, now restricted to the Canary Islands, is a possible survivor of the Continental European 'tropical' land snail taxa that become locally extinct in the Late European Eocene/Early Oligocene cooling (Preece, 1982).

However, the placement of *Gibbulinella* in the topology of our molecular tree (Fig. 3) indicates that a number of streptaxid clades had already diverged by the Late Cretaceous.

Solem (1978) gave a conservative estimate of 20 500 for the number of validly described stylommatophoran species. The approximately 18 000 non-achatinoid stylommatophorans have been split into 105 families (an average of some 170 species per family), whereas the approximately 2500 described achatinoid/streptaxoid species have been placed in five families, or six if the Glessulidae are recognized as a distinct family (Godwin-Austen, 1920; Schileyko, 1999), of which the about 1000 species in the Streptaxoidea are included in a single family and six subfamilies (Schileyko, 2000; Bouchet & Rocroi, 2005). That a taxon is species diverse is no justification in itself for classification into subgroups but, as an ancient group with few morphological characters that have proven to be of systematic value, higher level diversity within the streptaxoids may currently be underestimated. Although the molecular tree presented here gives strong support to the recognition of the Streptaxidae and Diapheridae it has not given strong support for groups with the Streptaxidae *sensu stricto*. A priority in studies of the achatinoid/streptaxoid clade is both to investigate the anatomy and molecular status of more species and to seek to establish categories at and above generic level.

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ภาคผนวก 3

New Subgenus and New Species of Amphidromus Albers, 1850 from Thailand (Pulmonata: Camaenidae)

INTRODUCTION

Many species of the tree snail genus Amphidromus Albers, 1850 have attractive shells exhibiting of especially diverse colour patterns and the polymorphic shell coiling (Schilthuizen & Davision, 2005; Schilthuizen et al. 2005, 2007; Sutcharit, 2006; Suitcharit & Panha, 2006b; Sutcharit et al., 2007). Most recent documents dealt with the systematic shown the well define characteristic of species in each subgenera (Sutcharit et al. 2007). Several workers (Pilsbry, 1900; Zilch, 1953; Laidlaw & Solem, 1961) have approved that the subgeneric classification of Amphidromus is satisfactory in almost species, but some of the species are still inadequate due to the low abundant and little information known. Previous conclusions on molecular phylogeny by Sutcharit et al. (2007) provided a new insight on the systematic knowledge of Amphidromus s. str.

Traditionally, a small and thin amphidromid shells were assigned to the subgenus Syndromus Pilsbry, 1900. However, it has been known or at least suspected that Amphidromus (Syndromus) s. l. is not monophyletic, which a number of species were assigned into uncertainty subgeneric classification (syndromus-like taxa) (see Laidlaw & Solem, 1961). Although, doubts having been expressed concerning the monophyly of the uncertain classified subgeneric species due to detailed studies on genital anatomy of them are still lacking. Though there have been contradicted, attempts to classify the subgeneric position within Amphidromus.

Most recent studies place A. glaucolarynx into syndromus-like taxa (Laidlaw & Solem, 1961). However, mitochondrial phylogeny of Amphidromus indicates a rather distant relationship, independent evolution of A. glaucolarynx to any other named subgenera and agrees on the monophyly of the lineages at the subgeneric level (Sutcharit et al. 2007). These species processes characters that allow the animals to be classified in the new subgenus closed to both subgenera. It was clear that of the shell variation revealed that there was one more addition species. As these two species, A. glaucolarynx (Dohrn, 1861) and this new species are most closely related. The description of the new subgenus offers new systematic insight, because it shows characteristics of the ancestor of the genus. Therefore, we proposed to classify the two species into a new subgenus. Amphidromus (Periallodromus) n. subgen. is sister taxa to both subgenera and this sister taxa relationship is strongly supported by conchological, anatomical and genetic data. This paper, we introduce and describes in morphological and anatomical detail of the new subgenus. The new subgenus is comprised of one new species and one other species, which all newly described anatomy and radula.

MATERIALS AND METHODS

Specimens were collected from throughout Thailand as follow the previous records and included several additional localities. The living snails were drowned in water and fixed in 70% for anatomical purposes. The radula was examined using scanning electron microscope as follow Sutcharit and Panha (2006). Dissections were carrying out under binocular microscope. The number of whorls was estimated to the nearest eight of the whorl. Intact adult shells were measured for whorl number, shell height (h), major diameters or shell width (d) using digital vernier calipers (Mitutoyo, CD-6 CS). Shell height/shell width ratios (h/d ratio) were calculated as a measure of shape to reduce the dominating effects of overall size (Pilsbry, 1939; Kerney & Cameron, 1979).

We use the term "proximal" for the region, which closest to the genital orifice and "distal" for the region, which furthest away from genital orifice. The following abbreviations are used and as defined by Bishop (1977); Solem (1983) Sutcharit and Panha (2006b): ag, albumin gland; ap, appendix; at, atrium; e, epiphallus; ep, epiphallic pilaster; evd, fl, flagellum; fo, free oviduct; gd, gametolytic duct; gs, gametolytic sac; hd, hermaphroditic duct; hg, hermaphroditic gland; ov, oviduct; p, penis; pp, penial pilaster; pr, penial retractor muscle; pv, penial verge; pvo, penial verge opening; ta, talon; v, vagina; vd, vas deferens; vp, vaginal pilaster. The direction of shell coiling for the material examined is indicated by: D, dextral and S, sinistral

Institutional abbreviation: Registration numbers all refer to collections of the Chulalongkorn University, Museum of Zoology, Bangkok, Thailand (CUMZ), unless otherwise stated.
BMNH, The Natural History Museum, London;
MNHN, Muséum National d'Histoire Naturelle, Paris;
SMF, Forschungsinstitut und Naturmuseum Senckenberg, Frankfurt, a.m.;
RBINS, Royal Belgian Institute of Natural Sciences, Brussels;
RMNH, Nationaal Natuurhistorisch Museum Naturalis, Leiden;
UMZC, University Museum of Zoology Cambridge, Cambridge;
ZMB, Zoological Museum of Berlin, Berlin;
ZMUC, Zoological Museum, University of Copenhagen, Copenhagen.

SYSTEMATIC ACCOUNT

Genus Amphidromus Albers, 1850

Subgenus Amphidromus Albers, 1850

Type species: Helix perversus Linnaeus, 1758; by subsequent designation of Martens in Albers, 1860: 184.

The genitalia and radula morphology of A. (A.) perversus see Solem (1983: figs 8-13, 20, 21), and Sutcharit & Panha (2006b: figs 5, 6).

Subgenus Syndromus Pilsbry, 1900

Type species: Helix contraria Müller, 1774; by subsequent designation of Zilch, 1960: 623.

The genital anatomy and radula morphology of A. (S.) contrarius are examined herein (Figs 1A, B; 3A-C), and Wiegmann (1898: pl. 15, figs 12-17).

Subgenus Periallodromus n. subgen.

Type species: Bulimus glaucolarynx Dohrn, 1861

Etymology: The new subgeneric name is come from a combination of "*periallo*" (Greek) meaning "ancestor" and "*dromos*" (Greek) meaning "running". It is refer to the ancestor of it type species compared to other species in the genus Amphidromus.

Diagnosis: Shell thin, relatively small, conic or elongate conic, shell usually dimorphism or either dextral or sinistral. Apex acute with dark purplish or black spot. Genitalia amphidromus type with long epiphallic caecum (flagellum and appendix), appendix always presence; proximally of vaginal swollen with pouch. Radula with elongate and tricuspid central tooth and basal plate large.

External features: Living animals have a very long head-foot, undivided sole, brownish to light brown, and covered with light grayish reticulated skin. Mantle edge is blackish and mottle gray respectively. Foot broad and grayish with a light brownish margin. Eye tentacles dark brown at base and becoming lighter with black eye spots on the tips. Head, mouth and lower tentacles dark brown to blackish (Fig. 1M, N).

Remark: Comparing the genitalia and radula morphology of the new subgenus among nine species of the nominotypical subgenus (see Collinge, 1901, 1902; Bishop, 1977; Solem, 1983; Lehmann & Maassen, 2004; Sutcharit & Panha, 2006a, b), and 8 species of the subgenus Syndromus (Wiegmann, 1898, 1899; Haniel, 1921; Rensch, 1934; Minato, 1979; Solem, 1983; Sutcharit, 2006). A new subgenus, Periallodromus can be characterized by longer flagellum, appendix present and peculiar radula (longer than it width, and the lateral teeth with tricuspid cusp) morphology; while the subgenus Syndromus have short flagellum and appendix absent, and the nominotypical subgenus have longer flagellum and larger shell.

Key to subgenera of Amphidromus

1a. Shell small, thin and height usually less than 35 mm..........................2

1b. Shell large, solid, usually uniformly yellowish or greenish, height usually greater than 35 mm and h/d ratio less than 1.85; epiphallus and flagellum long; appendix usually present. .... Amphidromus

2a. Epiphallus and flagellum short; appendix absent; radula with bicuspid lateral teeth h/d ratio greater than 1.85 .... Syndromus

2b. Epiphallus and flagellum slightly long; appendix short; radula with tricuspid lateral teeth. h/d ratio less than 1.85 .... Periallodromus n. subgen.

Amphidromus (Periallodromus) glaucolarynx (Dohrn, 1861)
(Figure 1A-J, M; 2C, D; 3D-F; Table 1)

Bulimus glaucolarynx Dohrn, 1861: 207, pl. 26, fig. 7. Type locality: In regno Siam.

Bulimus schomburgki var. fasciata Martens, 1867: 80, pl. 21, figs la, 1b. Type locality: Petshaburi.

Amphidromus peerieri Rocherrune, 1882: 71. Type locality: Forést de Prek-Scholl, au sud de Cratate Cambodge. Laidlaw & Solem, 1961: 524-525, fig. 17.

Amphidromus glaucolarynx var. fasciata—Fulton, 1896: 90, pl. 7, fig. 3. Pilsbry, 1900: 181, pl. 60, figs 46-48.

Amphidromus glaucolarynx—Fulton, 1896: 90. Pilsbry, 1900: 180-182. Blandford, 1903: 278-279. Hass, 1952: 24. Zilch, 1953: 132. Laidlaw & Solem, 1961: 524, 525. Solem, 1965: 618, pl. 2, fig. 1.

Amphidromus glaucolarynx albicans Möllendorff, 1902: 157. Type locality: Siam. Zilch, 1953: 132, pl. 22, figs 2, 3. Laidlaw & Solem, 1961: 524, 525. Solem, 1965: 525, 598.

Amphidromus glaucolarynx var. perrieri—Pilsbry, 1900: 181-182.

Amphidromus glaucolarynx fasciata—Laidlaw & Solem, 1961: 524, 525, fig. 17.

Material examined: Lectotype of "glaucolarynx" BMNH 19601454 (Fig. 1A), and paralectotype BMNH 19601455 (2D, 1S; Fig. 1B). The figured specimen in Martens (1867, pl. 21, fig. 1a) is designated here as the lectotype of "fasciatus" ZMB 97685 (Fig. 1C). Holotype of "*perrieri*" MNHN (Fig. 1D). Specimen in Möllendorff collection having similar shell morphology to the original description is designated here as the lectotype of "albican" SMF 28259.1 (Fig.

1E), and paralectotype SMF 28259.2 (1D, 1S). Chieng Kong, LAOS: SMF 28260 (1D). Siam: RBINS Dautzenberg coll. (1D, 1S), BMNH MacAndrew coll. (3D, 2S), SMF 28261 (1D), ZMB Paetel coll. (1D, 1S), RMNH Frühstorfer coll. (1S). Pitsunaloke, Lampun, Siam: BMNH Blanford coll. (6D, 2S). Pitsunaloke, Siam: RBINS Dautzenberg coll. (1S). Near Um Pang, Siam: BMNH 1924.5.26.4 (1S). Kanburi, Siam: RBINS Dautzenberg ex. Frühstofer coll. (2D, 2S), BMNH 1902.9.17.13-14 (2D), BMNH 1910.12.30.23-25 (2D 1S). Near Ban Kao, Thailand: ZMUC Johnsèn coll. 3013 (2D). Petschaburi, Siam: ZMB 6392 (3D, 7S). Tam Tab Tao, Chaiprakarn, Chiengmai: 4689; Tam Lod National Park, Maehongsorn: 2243;Chao Por Pratupha, Ngao, Lampang: 4683;Tam Pha Bing, Wangsapung, Loei: 4518;Phu Luang Wildlife Sanctuary, Loei: 4686;Tam Pha Mak-hor, Wangsapung, Loei: 4523; Nam Nao National Park, Phetchaboon: 2265, 4517;Phu Wieng, Khonkaen: 4015;Wat Po Thikun, Maesod, Tak: 4690;Phra Wor, Maesod, Tak: 2239, 4692;Tam Singha Nang-non, Umpang, Tak: 2399; Tee Lor Zoo Waterfall, Umpang, Tak: 4694, 4695, 2254;Tam Ta-ko-bi, Umpang, Tak: 4693;Taksinmaharat National Park, Maesod, Tak: 4619;Pa Charoen National Park, Pobphra, Tak: 2247;Huy Hin Fon Village, Maesod, Tak: 2319; Wat Thepsathaporn, Banpotpisai, Nakhonsawan: 4697;Jedkot Waterfall, Muaklek, Saraburi: 4908, 4026, 4031;Erawan National Park, Kanchanaburi: 2244, 2253;Kanchanaburi: 2272, 4902, 2571;Saiyok Noi Waterfall, Kanchanaburi: 4684, 2532;Khao Dong Kamen, Saiyok, Kanchanaburi: 2267;Charoem Rattanakosin National Park, Kanchanaburi: 3506, 4901, 4062;Tam Sukho, Sangkhraburi, Kanchanaburi: 4696;Pong Pu Ron, Thong Phaphum National Park, Kanchanaburi: 4077, 4261, 2262, 2264, 2263, 2540;Pala-u Waterfall, Phetchaburi: 4079, 3501, 4078, 2242, 4522, 2652; Ban Krang Camp, Kaeng Kracharn National Park, Phetchaburi: 4515, 4685, 4501, 4516, 4513, 4514, 2241, 4501, 2259, 2238, 2266, 4909, 4521, 4520, 4524, 4525; Tam Na Kwang, Cha-am, Phetchaburi: 4688; Khao Nang Panthurat, Cha-am, Phetchaburi: 4912; Tam Rong, Bann-lad, Phetchaburi: 4910; Kuiburi National Park, Prachuapkhirikhan: 4262, 4512, 4009; Tam Khiriwong, Bangsaphan, Prachuapkhirikhan: 4088, 4519; Tam Phra Krayang, Kraburi, Ranong: 4006, 2260, 2537, 2246, 4687, 4029, 4047, 4911; Tam Khao Kriap, Langsuan, Chumporn: 4699; Suratthani: 4905; Tam Lord, Khao Nan National Park, Nakhonsrithammarat: 4084;

Shell: Shell elongate conic, rather thin, usually dimorphic coiling, and umbilicus rimate. Apex acute with blackish or dark purplish, one to two following whorls with tinted pink. Whorl little convex; last whorl rounded; suture wide and shallow. Subsutural band narrow with greenish colour, and usually paler to disappear on upper whorl. Shell colour with brown or dark brown blotch or streaks, and sometime interrupted in middle with whitish band. Umbilical area whitish and with greenish inside umbilicus. Aperture ovate to little elongate; lip thicken, expanded, and with purplish colour. Parietal callus thick or thin and purplish colour; columella straight and with purplish (Figs. A-J).

Genitalia: Atrium (at) short (n=10). Penis (p) long slender with cylindrical shaped. Eiphallus (e) smaller than penis and as long as penis length; flagellum (fl) short and with short appendix (ap). Vas deferens (vd) narrow tube extending from free oviduct (fo) and connected to end of epiphallus. Penial retractor muscle (pr) relatively long, thick and inserts near distal end of penis (Fig. 2C).

Internal wall of the penis with corrugated into a series of thickened and swollen penial pilasters (pp), which form a fringe around the fleshy penial verge. Penial verge (pv) small, truncate and with irregular surface (Fig. 2D).

Vagina (v) with cylindrical, longer than penis, and series of held in position with series of thin muscles originating from foot floor. Proximal end enlarged and perform vaginal pouch (vpo). Gametolytic duct (gd) long and slender, and distally connected to swollen gametolytic sac (gs). Oviduct (ov) and albumen gland (ag) enlarged, hermaphroditic gland (hg) contracted, and convoluted hermaphroditic duct (hd) connected at tip of talon (ta) (Fig. 2C).

Internally, proximal to genital orifice, vaginal pouch perform irregular and enlarged pilaster, which line transverse compare to vaginal pilaster. Vagina wall possesses longitudinal vaginal pilasters (vp). Proximally with slightly smooth and continuous ridges, and distally pilasters interrupted by transverse divisions (Fig. 2D).

Radula: Radula teeth arranged in anteriorly wide pointed V-shaped rows, each row contains about 136 (67-1-68) teeth. Central tooth monocuspid and narrowly spatulate shaped. Inner lateral teeth tricuspid; endocone and ectocone very small with pointed cusp; mesocone large, spatulate shaped and with truncate cusp (Fig. 3B). Lateral and marginal teeth undivided; outer most teeth (near radula edge) with tricuspid in structure, endocone and ectocone cusps usually split into two or more pointed cusps, and mesocone large with curved cusp (Fig. 3C, D).

Distribution: Amphidromus (P.) glaucolarynx was primary recorded from Thailand, with some museum specimens labeled in Laos and Cambodia boundary. The previous recorded of this species were from Thailand: Lampang, Lumpun, Kampaengpet, Pistsunaloke, Pak Chong of Nakornratchasrima, Srakeo and Phetchaburi; Cambodia: Perk Scholl (Fulton, 1896; Pilsbry, 1900; Haas, 1952; Laidlaw & Solem, 1961; Solem, 1965). The recent study, however, this species tended to have chiefly wider distributed than previous records, which ranged from Tak, Kampengpet and Kanchanaburi Provinces in the western Thailand; Phetchaburi, Prachuapkhirikhan, Ranong and Suratthani Provinces in the southern peninsular Thailand.

Remark: Large set of specimens from entire there distribution range, and type specimens of the nominal species group names, which has been associated with A. glaucolarynx were critically examined. Three nominal species group names: "fasciatus Martens, 1867", "perrieri Rocherrune, 1882" and "albicans Möllendorff, 1902" had been considered to be the subspecies or infra-subspecies of A. glaucolarynx (Fulton, 1896; Pilsbry, 1900; Laidlaw & Solem, 1961). The type specimens of those three nominal group names are almost identical to the typical A. glaucolarynx, only little differences as shell size and colour pattern are observed. This differences still in the variation range of A. glaucolarynx, which we synonymies those three nominal species-group names to A. glaucolarynx.

There were 15 populations of the species were explore throughout Thailand. Normally, this species perform dimorphic shell coiling, however, only 2 populations from Jed Kot Waterfall, Saraburi (370 specimens) (Fig. 1I) and Tam Prakayang, Ranong (400 specimens) (Fig. 1J) tended to have strongly bias with dextral and sinistral shell respectively. However, there shell morphology and colour patterns show indifferences from the typical A. glaucolarynx.

Amphidromus (Periallodromus) spirularis n. sp.
(Figures 1K, L, N; 2E, F; 3G-I; Table 1)

Type material: Holotype (CUMZ xxxx); type locality: Wat Thathungna Rittharam, Saiyok, Kanchanaburi Province. Paratype: CUMZ xxxx; BMNH xxxx; SMF xxxx.

Other material: Tubsathorn: 2240, 2248, 2252, 2258, 2257, 2249, 2270, 2255, 2398, 2250, 2251, 2396, 2269, 2618, 4097; Sai Yok Yai N.P., Kanchanaburi: 4698; Saiyok: 4700, 2256; Erawan waterfall, Kanchanaburi: 2245; Kanchanaburi: 4906, 4904; Wat Thathungna Rittharam, Saiyok, Kanchanaburi: 4903;

Etymology: The specific epithet comes from a Latin world "*spirula*" meaning spiral. It is referring to the prominent brownish spiral band on the last whorl of this species.

Diagnosis: Amphidromus (P.) spirularis n. sp. differs from A. (P.) glaucolarynx by having ovate last whorl, pale yellowish green subsutural band and with unique continuously brownish spiral bands on last whorl. The genitalia with slightly large

In addition, this new species differs from A. mouhoti (Pfeiffer, 1861) in shell, genitalia and radular morphology. The latter species tended to have greenish radial streaks and conic shell, genitalia with long epiphallus and flagellum, and radular with unicuspid central tooth and bicuspid lateral teeth (Panha unpub. data).

Shell: Shell slightly small, dimorphic coiling, oblong-conic, rather thin, umbilicus wide. Apex acute without black spot, suture shallow and wide, whorls slightly flatten and smooth, and last whorl angular at periphery. Ground colour is yellowish. Last whorls covered with closer oblique green radial streaks and the greenish pattern usually faded on spire. Subsutural band is absent or some time with dark green. Aperture is ovate to elliptical shaped, columella perpendicular and straight. Parietal callus thin, lip white, peristome widely expanded and little reflected.

Genitalia: The atrium (at) is long (n=10). The penis (p) is short with swelling at penial verge base. The distinguish characters are the long eiphallus (e), flagellum (fl) and a long narrow appendix (ap) present. The vas deferens (vd) is a narrow tube, extending from the free oviduct (fo) to epiphallus. The penial retractor muscle (pr) is relatively long and inserts near the distal end of penis (Fig. A). External morphology of female genitalia and internal sculpture of penis vagina, and epiphallus closely resemble to those of nominotypical subspecies (Fig. 2E, F).

Radula: Each row contains about 132 (66-1-65) teeth. Central, lateral and latero-marginal teeth similar to those of A. glaucolarynx (Fig. 3G-I).

Distribution: This new species is known from many localities in Kanchanaburi province western Thailand.

Remark: This new species is mainly differed from A. (P.) glaucolarynx having much smaller shell, last whorl large and ovate, and colour pattern with spiral band instead of blotch band as in the A. glaucolarynx.

The snail in this subgenus and the subgenus Syndromus (Panha, personal observation) having similar strategy on laying eggs in the hole. While, the nominotypical subgenus such as A. (A.) atricallosus and A. (A.) palaceus lay there eggs in the nest, which the snail can build the nest by glued two leaves to make a nest (Palavicini, 1921; Sutcharit & Panha, 2006b). Two cases of laying snail were observed after the heavy rain. Snail lays eggs by inserted the anterior body in the hole of the tree or loose bark (Fig. 1N). Eggs are globular, whitish, with soft and flexible shells, 2-3 mm in diameter and glued to each other in the socket of nest site with mucus. The number of eggs in the cult is about 20-30 eggs, although the nominotypical subgenus produced eggs 100-230 eggs in single cult, however, the cults size is proportionated to snail size.

CONCLUSION

Systematic affinity of Amphidromus (Periallodromus) n. subgen.

The genus Amphidromus was proved to be monophyletic, which consisted of three major distinct lineages. Two of them are clearly corresponded with the traditional subgeneric division: the nominotypical subgenus and the subgenus Syndromus (see Sutcharit et al., 2007). The last one fall into an independent clade that included only A. glaucolarynx s. l., which now recognized here as independent subgenus Periallodromus. The mtDNA 16S rRNA gene phylogeny by Sutcharit et al. (2007) and recent anatomical data showed that the subgenus Periallodromus is derived from the most common ancestors of the genus Amphidromus, and could not placed in neither nominotypical nor the subgenus Syndromus.

The systematic position of the subgenus Periallodromus within the genus Amphidromus is possibly the most basal to those other two clades. Traditionally Amphidromus (P.) glaucolarynx, type species of this new subgenus, have been associated to the subgenus Syndromus s. l., because of the similarity of there shell morphology (Pilsbry, 1900; Laidlaw & Solem, 1961). However, the shell morphology and the genital characteristics were applied to distinguish between the subgenus Syndromus s. l. and the nominotypical subgenus as well. In contrast, the nominotypical subgenus has larger and thick shell, varix usually present, and genitalia with long epiphallic caecum (Pilsbry, 1900; Laidlaw & Solem, 1961; Sutcharit & Panha, 2006b). In consideration to the subgeneric relationship, the elongate conic and variegated shell colour pattern, arboreal habitat, spatulate shaped of radula, and chirally dimorphism could be common characters among those three subgenera of the genus Amphidromus. The gouge shape with wide central teeth of radula and much interval of the lateral teeth in the subgenera Amphidromus and Syndromus may support their having a close relationship. The medium length of epiphallic caecum, long gouge radula shape, and much closer of lateral teeth are possibly the distinctive characters of the subgenus Periallodromus. The large shell size, monochrome colour, long flagellum, thick shell, varix usually present and the parietal callus usually thickened are probably the unique characters of the subgenus Amphidromus. With the anatomy of the type species of the subgenus Syndromus examined here, the difference of the subgenus Syndromus from the subgenus Periallodromus are the secondary derivation of sinistral shell coiling, with short flagellum, and missing appendix. These support the distinct subgeneric position of the Periallodromus from other two subgenera, Amphidromus and Syndromus. The characters of shell coiling, genitalia and radula structure are considered as apomorphies supporting a distinct lineage of the subgenus Periallodromus. Shell coiling of the subgenus Periallodromus show the coexisted of left- and right-handed individual in every population, a feature not found in the subgenus

Syndromus. The fixed with left-handed shell coiling, and the very short terminal part of male organ (epiphallic caecum) seem to be there apomorphy.

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Table 1. Comparative characters among those three gubgenera of the genus Amphidromus, and it type species are indicated in parentheses. Superscript numbers indicate the sources of information: [1][Jacobi (1898), Collinge (1901, 1902, 1903), Lehmann & Maassen (2004), and Sutcharit & Panha (2006a, b)]; [2][Wiegmann (1894, 1899), Sarasin & Sarasin (1899), Haniel (1921), Rensch (1934), and Minato (1979)]; [3][Pilsbry (1900), Laidlaw & Solem (1961), Bishop (1977), and Solem (1983)]; [4]Sutcharit (2006).

Characters	Amphidromus [1, 3, 4] (Helix perverfa Linnaeus, 1758)	Syndromus [2, 3, 4] (Helix contraria Müller, 1774)	Periallodromus [4] (Bulimus glaucolarynx Dohrn, 1862)
Shell shape and colour	elongate conic, h/d ratio less than 1.85; usually monochrome colour, varix usually present	elongate conic, h/d ratio grater than 1.85; usually variegated colour and pattern, varix absent	elongate conic to ovate, h/d ratio less than 1.85, variegated colour and pattern, varix absent
Shell size and thickness	medium to large (height 35-75 mm); thicken	small to medium (height 20-40 mm); thin and fragile	small (height 20-30 mm); thin and fragile
Shell coiling	usually dimorphic coiling	sinistral coiling	usually dimorphic coiling
Genitalia	very long epiphallic flagellum	very short epiphallic flagellum	intermediate length of epiphallic flagellum
Radula teeth shaped	central tooth broad, inner lateral teeth bicuspid	central tooth broad, inner lateral teeth bicuspid	central tooth narrow, inner lateral teeth tricuspid
Lateral and marginal teeth	wide gap in lateral and marginal teeth	wide gap in lateral and marginal teeth	teeth closed in lateral and marginal teeth

Table 2. Shell size variation in A. (P.) glaucolarynx and A. (P.) taeniochlorus n. sp. Catalogue numbers of specimens are indicated in parentheses.

Species, Locality and CUMZ nos.	Number of adult shell examined	Ranges, Mean ± SD in mm			Whorl Ranges
		Shell Height	Shell Width	h/d Ratio	
A. (P.) glaucolarynx					
Jedkot Waterfall, Saraburi (4031, 4908)	87	24.46-30.66 27.65±1.34	14.41-17.72 15.57±0.61	1.54-1.94 1.78±0.08	6¼-7
Tam Rong, Phetchaburi (4910)	20	25.62-36.39 31.73±2.52	15.64-19.91 17.71±1.15	1.6-1.96 1.79±0.09	6¾-7¼
Kaeng Kracharn N. P., Phetchaburi (2241, 2259, 2266, 4501, 4513, 4514, 4515, 4516, 4521, 4524, 4685, 4909,)	225	23.24-33.35 28.16±2.27	13.49-18.82 15.92±1.03	1.34-1.91 1.77±0.07	6¼-7
Tam Phra Krayang, Ranong 4911, 4029	72	21.13-28.64 24.80±1.63	13.56-15.90 14.69±0.56	1.49-1.88 1.69±0.08	6 ¼ -7
Tam Na Kwang, Phetchaburi (4688)	12	25.57-38.56 33.33±3.72	16.17-20.67 18.18±1.38	1.58-1.96 1.83±0.12	6¾-7¼
Pong Pu-Ron, Kanchanaburi (2261, 2263, 2264, 2328, 2540, 4077, 4261)	36	20.90-28.68 24.75 ±1.86	12.48-16.14 14.45±0.91	1.58-1.90 1.71±0.07	6¼-7
A. (P.) spirularis n. sp.					
Sai Yok Yai Waterfall, Kanchanaburi (2256, 4698, 4700)	13	17.14-22.77 19.86±1.63	11.50-14.29 12.49±0.79	1.43-1.72 1.59±0.10	5¾-6¾
Tubsathorn, Kanchanaburi (2230, 2239, 2240, 2248, 2249, 2252, 2255, 2258, 2257, 2270, 2398, 4906, 4907)	158	18.26-25.49 21.24±1.31	11.35-15.01 13.26±0.65	1.40-1.77 1.60±0.07	5¾-7

Figure 1. A-J. Shell of Amphidromus (Periallodromus) glaucolarynx: (**A**) lectotype BMNH 19601454, (**B**) paralectotype BMNH 19601455, (**C**) lectotype of "fasciatus" ZMB 97657, (**D**) holotype of "perrieri" MNHN, (**E**) lectotype of "albicans" SMF 28259, (**F**) specimen from Mae Sod, Tak (CUMZ xxxx), (**G**) specimen from Thong Phaphum, Kanchanaburi (CUMZ), **(H)** specimen from Kaeng Kracharn, Phetchaburi (CUMZ xxxx), (**I**) specimen from Jed Kot waterfall, Saraburi (CUMZ xxxx), and (**J**) specimen from Tam Prakrayang, Ranong (CUMZ xxxx). Shell of Amphidromus (Periallodromus) spirularis n. sp.: (**K**) holotype CUMZ xxxx, and (**L**) paratype CUMZ xxxx. **M.** An intrachiral copulation of Amphidromus (Periallodromus) glaucolarynx (shell height ~25 mm) from Kaeng Kracharn, Phetchaburi (August, 2004). **N.** Eggs, and eggs laying behavior of Amphidromus (Periallodromus) spirularia n. sp. (shell height ~20 mm) from Kanchanaburi (October, 2007). Snail used the loose bark of the tree trunk to rearing their eggs, which blue arrow indicates head of snail and red arrow indicate the eggs.

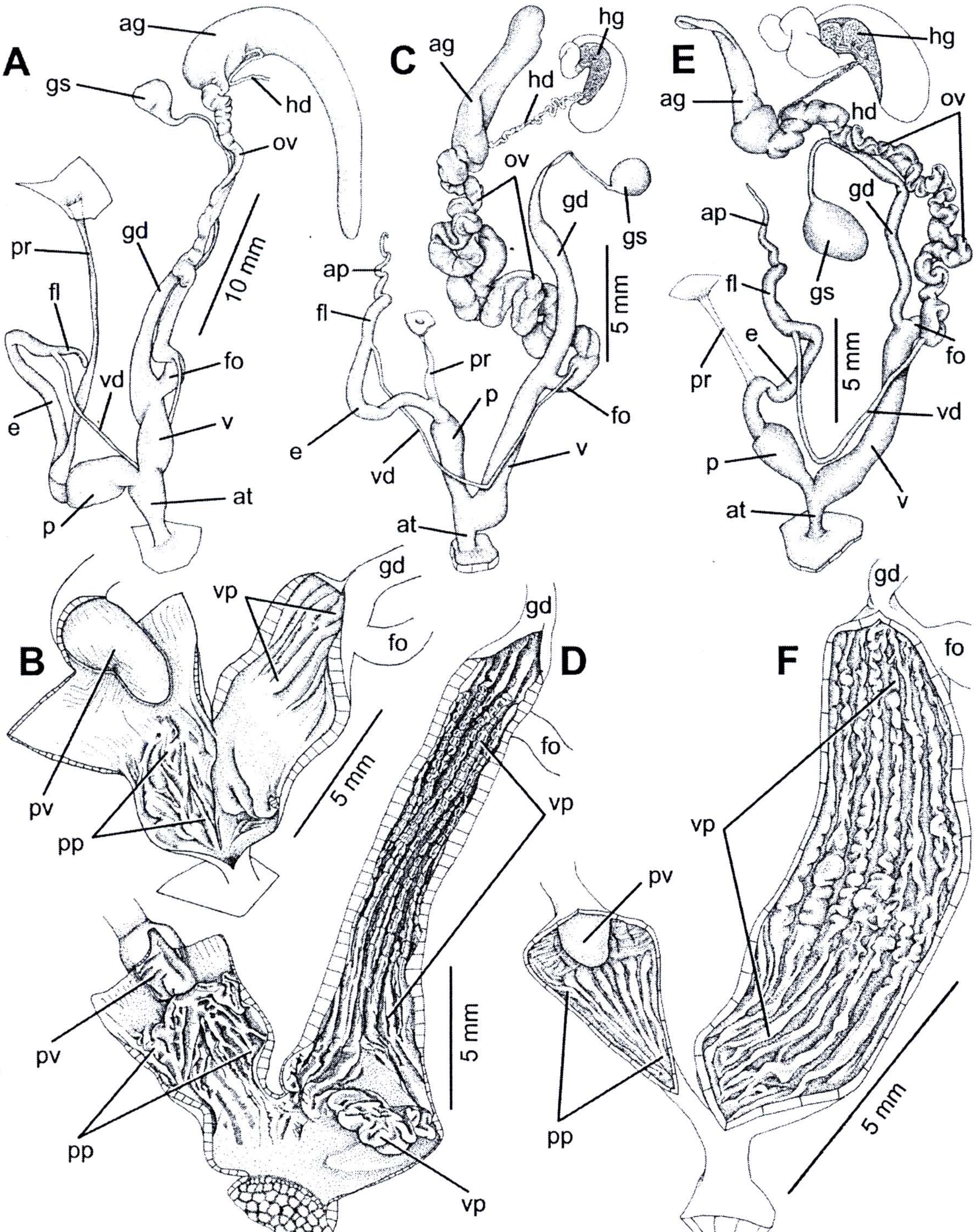

Figure 2. Reproductive system. **A, B.** Amphidromus (S.) contrarius from Niki Niki, Central Timor. **C, D.** Amphidromus (P.) glaucolarynx from Kaeng Kracharn National Park, Phetchaburi (CUMZ xxxx). **E, F.** Amphidromus (P.) spirularis n. sp. (paratype CUMZ xxxx). (**A, C, E**) whole genital system; (**B, D, F**) interior structure of atrium, penis, and vagina chamber.

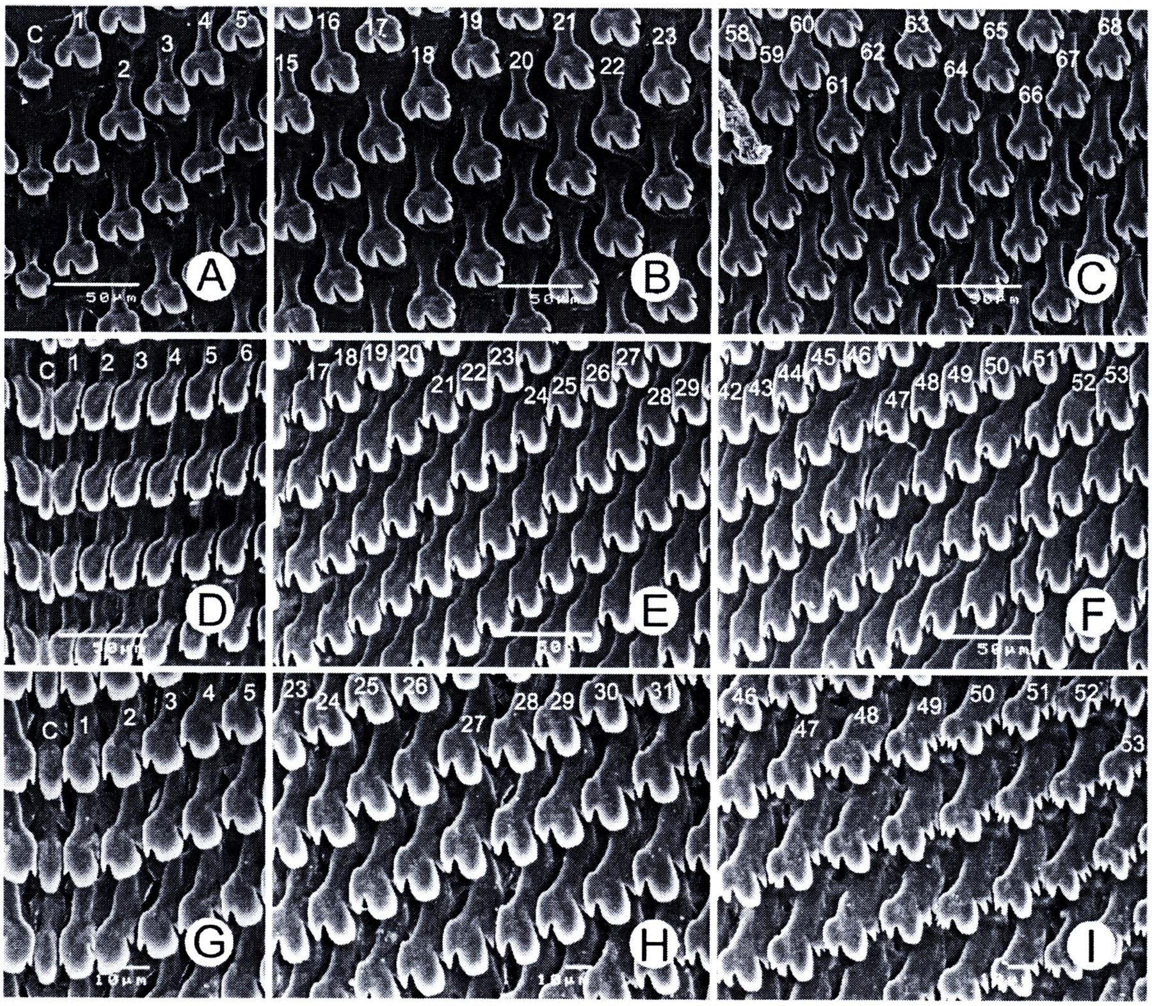

Figure 3. SEM images of the radula. **A-C.** Amphidromus (S.) contrarius from Niki Niki, Central Timor. **D-F.** Amphidromus (P.) glaucolarynx from Kaeng Kracharn N.P., Phetchaburi (CUMZ xxxx). **G-I.** Amphidromus (P.) spirulus n. sp., paratype CUMZ xxxx. (**A, D, G**) central tooth with the first to the fifth lateral teeth; (**B, E**) lateral teeth; (**C, F, I**) outermost marginal teeth; (**H**) lateral teeth with the tricuspid marginal teeth transition. Numbers indicated order of lateral and marginal teeth. Central tooth indicated by 'C'.

ภาคผนวก 4

Neotype Designation and Redescription of the Vanishing Tree Snail, Amphidromus (Amphidromus) mundus (Pfeiffer, 1853) (Pulmonata: Camaenidae)

ABSTRACT

A population of Amphidromus (Amphidromus) mundus (Pfeiffer, 1853) was recently discovered on a Malaysian island. Here we investigate and describe the internal anatomy for the first time and re-describe the shell. The small white chirally dimorphic shells with reflected lip not attached to the outer wall, and pale brown body colour allow clear discrimination from the related species A. (A.) perversus, A. (A.) inversus albulus, and A (A.) atricallosus. The distinctively long epiphallic caecum provides a clear discriminating character based on internal anatomy. The syntype cannot be traced and a neotype is designated herein for the stability of the nominal species.

INTRODUCTION

Amphidromus Albers, 1850, is a genus of tree dwelling snails that range from Indochina to the Philippines and the Sunda Islands (Pilsbry, 1900; Laidlaw & Solem, 1961). About 90 species are recognized (Laidlaw & Solem, 1961; Richardson, 1985; Lehman & Maassen, 2004; Dharma, 2007). Most nominal species were based on few individuals, often with poor locality information, leading to much subsequent confusion.

Seven nominal species of `Amphidromus have been recorded from peninsular Malaysia (Fulton, 1896, 1901; Pilsbry, 1900; Laidlaw & Solem, 1961; Maassen, 2001). One of these, Bulimus mundus Pfeiffer, 1853, has been regarded as being of uncertain taxonomic status, primarily because of the dubious locality records given in the original description (Laidlaw & Solem, 1961; Richardson, 1985) and a few recorded occurrences from disparate localities left the taxonomic status and distribution of this species uncertain (Laidlaw & Solem, 1961).

In February 2008, approximately 30 living land snails were collected from Pulau Bersa, a small island off peninsular Malaysia in the South China Sea. Among these specimens, some were provisionally identified as Amphidromus s.s. species. After comparison with material in reference collections and examination of Pfeiffer's example of Bulimus mundus var. β, cited in Pfeiffer's original description, we conclude that A. (A.) mundus has been rediscovered. However, in the absence of type material, doubt will remain about the identity of this species and in our opinion stability will best be served by the designation of a neotype and redescription under the terms of reference provided by ICZN (1999, Article 75).

MATERIALS AND METHODS

Shell height (H) and shell diameter (D) were measured in mm, and the whorl count and H/D ratios were recorded. The radula was examined under a Scanning Electron Microscope. In descriptions of the genitalia, we used 'proximal' to refer to the region closest to the genital orifice and 'distal' to refer to the region furthest away from the genital orifice. D = dextral; S = sinistral.

Institutional abbreviations: **BMNH**, The Natural History Museum, London; **CUMZ**, Chulalongkorn University, Museum of Zoology, Bangkok; **RBINS**, Royal Belgian Institute of Natural Sciences, Brussels; **RMBR**, Raffles Museum of Biodiversity Research, Singapore; **RMNH**, Nationaal Natuurhistorisch Museum Naturalis, Leiden; **ZMB**, Museum für Naturkunde, Humboldt University, Berlin; **ZMUC**, Zoological Museum, University of Copenhagen, Denmark.

SYSTEMATIC ACCOUNT

Genus Amphidromus Albers, 1850
Subgenus Amphidromus Albers, 1850

Amphidromus (Amphidromus) mundus (Pfeiffer, 1853)

Bulimus mundus Pfeiffer, 1853a: 57 (Type locality: Sincapore (= Singapore)). Pfeiffer, 1853b: 651. Pfeiffer, 1856: 261, 262, pl. 70, figs. 21 & 22.
Bulimus mundus var. β Pfeiffer, 1853a: 57 (Locality: Borneo ?). Pfeiffer, 1853b: 651.
Amphidromus mundus—Morgan, 1885: 387. Fulton, 1896: 71. Pilsbry, 1900: 174, pl. 61, figs 57-59. Laidlaw & Solem, 1961: 589, 590, 642, 643, fig. 38. Richardson, 1985: 31. Maassen, 2001: 119.
Amphidromus atricallosus form mundus—Yan et al., 1995: 4 (with figure of shell).

Designated Neotype CUMZ 4917 (Fig. 1A, height 35.3 mm, width 21.3 mm, 5¾ whorls, h/d ratio 1.66). Based on the neotype, the type locality is Pulau Besar, Mersing, Johor, Malaysia (2° 26' 7.02" N, 103° 58' 38.59" E). Additional material from the type locality CUMZ 4913 (Fig. 1B) (14D, 19S, height 35.6 ± 1.69 mm, width 21.6 ± 0.93 mm, 5½ - 6 whorls, h/d ratio 1.65 ± 0.06), 4914 (7D, 6S, height 35.6 ± 1.25 mm, width 21.4 ± 0.90 mm, 5½ - 6 whorls, h/d ratio 1.66 ± 0.05); BMNH xxxx, RMBR xxxx, SMF xxxx.

After a long investigation the original type series of "Bulimus mundus" from "Gruner's collection" has not been located, and is presumed to be lost (M. Glaubrecht, R. Janssen, B. Hausdorf, R. Seemann and S. Stoll, personal communication). The absence of type material of the nominate form has been the cause of doubt about the identity and status of this species (Laidlaw & Solem, 1961). We consider that the specimen of Bulimus mundus var. β cited by Pfeiffer 1853 from the Cuming collection, is an example of this species but having been identified by Pfeiffer as a variant form it is excluded from the original type series of Bulimus mundus. Because the recorded locality Borneo? and China? , which is added to the label of the form β render the origin of this lot uncertain, it is deemed unsuitable for designation as a neotype and an example has been selected from our Pulau Besar collection.

Other material examined: Pfeiffer's examined specimens from Borneo (?) or China (?): BMNH 19601542.1 (Fig. 1C-E). Singapore: ZMB, Paetel coll. (1S); RMNH #19a (1D). BMNH 98.10.25.131 (2S). Singapore or Borneo: RBINS, Dautzenberg ex. Crosse coll. (1D), Dautzenberg coll. 6990 (1D). Java: ZMB, Seckendorf coll. (1D). Unknown locality: ZMB, Büxger coll. (1S), Wallenberg coll. (1S); RBINS, Dautzenberg coll. #6990α (1S); ZMUC #295 (2S).

Description (Fig. 1A): Shell medium to small for genus, white, solid, ovate conic; umbilicus perforate; chirally dimorphic. Apex acute; spire short; suture depressed. Whorls slightly convex; last whorl round to ovate. Dark varix absent; periostracum thin and transparent. Aperture broadly ovate; lip thickened, expanded and reflexed but not attached externally to last whorl. Parietal callus thickened; columella twisted.

Living specimens (Fig. 1B): Animals possess a pale brown body, covered with darker recessed reticulations on skin. Foot broad and long with pale margin, extended across posterior tail. Upper tentacles drumstick shaped, orange-brown, with dark eyespots on tentacular tips. Lower tentacles short, orange to pale orange; head and mouthparts brown. Mantle edge light orange; mantle cavity with dark pigmentation.

Genitalia (Fig. 2A, B): Atrium (at) relatively short (n = 5). Penis (p) cylindrical, about ¾ of vagina length, and enlarging slightly distally. Epiphallus (e) long and slightly smaller in diameter than penis. Flagellum (fl) almost the same length as epiphallus with coiled distal portion. Appendix (ap), located beyond coiled portion of flagellum, nearly same length as flagellum. Vas deferens (vd), a narrow tube, extending from free oviduct ending at epiphallus. Penial retractor muscle (pm) inserting to near distal end of penis (Fig. 2A).

Internal wall of penis corrugated, exhibiting series of thickened swollen longitudinal penial pilasters (pp), which form a fringe around conical penial verge. Penial verge (pv) short, conic with smooth surface (Fig. 2B).

Vagina (v) long, slender and cylindrical. Gametolytic duct (gd) extends from vagina, proximally enlarged cylindrical tube, abruptly tapering to small tube distally, terminally connected to gametolytic sac (gs). Free oviduct (fo) short, oviduct compact and enlarged to form lobule alveoli. Prostate gland ventrally fused with oviduct. Albumen gland (ag) large and lingulate (Fig. 2A). Hermaphroditic gland (hg) contracts from numerous small lobules; narrow and convoluted hermaphroditic duct (hd) connects to middle of talon (Fig. 2A).

Internally the vagina possesses longitudinal vaginal pilasters (vp). Pilasters have continuous ridges with short smooth ridges near genital orifice; extends to slightly swollen portion with irregular shaped deep crenellations (Fig. 2B).

Radula and jaw (Fig. 2C-F): Jaw light brown and corneous with strong vertical ridges (Fig. 2C). Teeth arranged in anteriorly pointed V-shaped rows, each row containing about 204 teeth (102-(17-15)-1-(15-17)-103). Central tooth tricuspid, spatulate, with small ectocones (Fig. 2D). Lateral teeth bicuspid, endocone large with truncated cusp, ectocone larger with curved cusp. From tooth 15 to 17 outwards lateral teeth gradually transformed to tricuspid marginals (Fig. 2E). Marginal teeth asymmetric, endocone medium; mesocone large with curved margins and ectocone small (Fig. 2F).

Distribution: Based on the neotype designation herein, the confirmed distribution of this species is currently restricted to the type locality,Pulau Besar, Johor, Malaysia. Museum collections recording this species from a diverse range of localities such as Singapore, the Philippines, Borneo and Java (Laidlaw & Solem, 1961: 589; S. Panha, personal observation in collections) need to be verified. The possibility of China as a locality, as given on the label cited above, can be discounted because China is beyond the geographic range of Amphidromus (Solem, 1959, 1983; Laidlaw & Solem, 1961; Sutcharit & Panha, 2006b).

DISCUSSION

Because of the absence of type material and uncertainty about its distribution, the status of Amphidromus (A.) mundus has long been uncertain. With only the shell morphology available, Laidlaw and Solem (1961) considered that Bulimus mundus Pfeiffer, 1853 probably came within the wide range of shell variation exhibited by A. (A.) perversus (Linnaeus, 1758). From this study, A. (A.) mundus can be distinguished from the former species by possessing a smaller, white shell, short spire, globose last whorl and a reflected lip that does not attach to the outer wall. In addition, the genitalia of A. (A.) mundus exhibits a slightly longer epiphallic caecum and a corrugated vaginal pilaster (Fig. 2A, B) (Solem, 1983; Sutcharit & Panha, 2006b).

Two Amphidromus taxa from peninsular Malaysia, A. (A.) atricallosus perakensis Fulton, 1901 and A. (A.) inversus albulus Sutcharit & Panha, 2006, are similar but distinct from A. (A.) mundus. The differences from A. (A.) atricallosus perakensis are a smaller, stout and white shell, short spire, and a much shorter appendix (Collinge, 1902; Sutcharit & Panha, 2006b). A. (A.) atricallosus exhibits a white shell morph (Sutcharit & Panha, 2006b, figs 3, 4), however, the pale brown body with pale orange on the tentacles in A. (A.) mundus (Fig. 1B) are clearly distinct from the white to yellowish body with a bright orange head and stripes along the foot and sole of A. (A.) atricallosus (Fig. 1C). A. (A.) mundus is clearly distinguished from A. (A.) inversus albulus; most notably, A. (A.) mundus possesses a long penial appendix, which is almost absent in A. (A.) inversus albulus. In addition, the dark pigment of the lung cavity and the pale orange tentacles and mantle collar of A. (A.) mundus are clearly distinct from those of A. (A.) inversus albulus (see also Sutcharit & Panha, 2006a for comparison).

We consider that Amphidromus (A.) mundus is a robustly defined species that differs from the three adjacent species A. (A.) perversus (Linnaeus, 1758), A. (A.) atricallosus perakensis and A. (A.) inversus albulus, in its shell, genital morphology and the soft body pigmentation.

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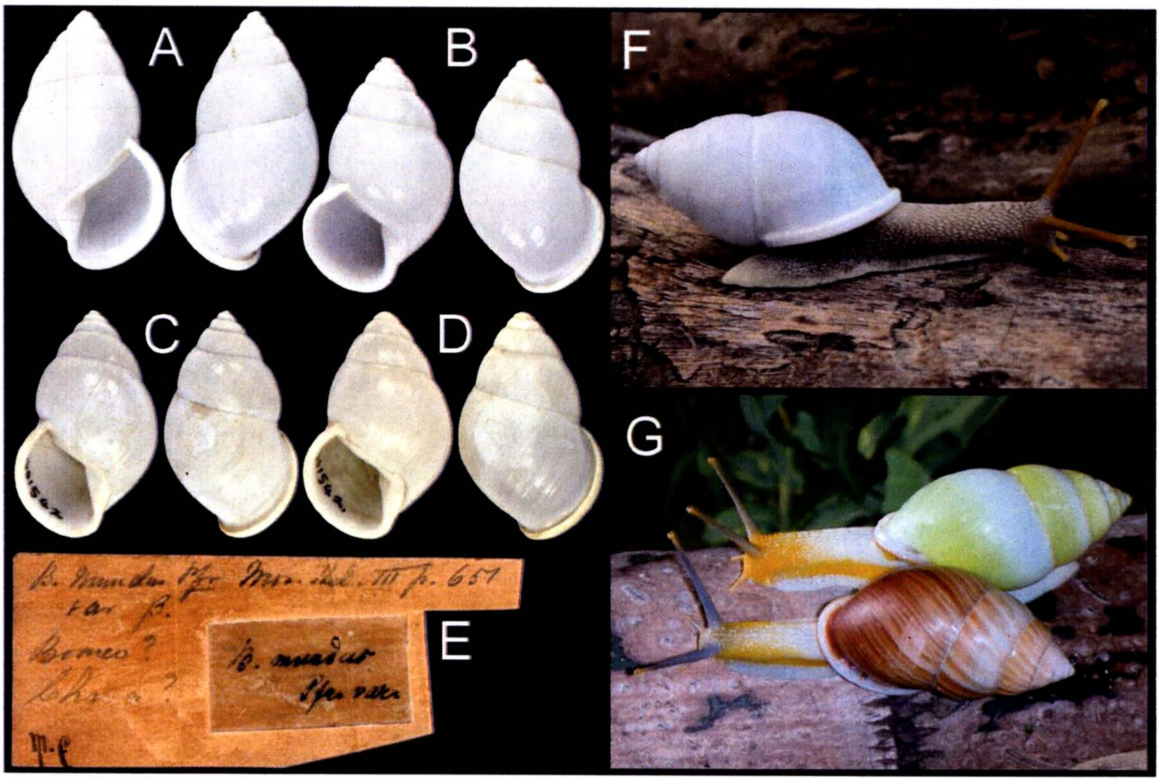

Figure 1. A-B. Amphidromus (Amphidromus) mundus, (**A**) neotype CUMZ 4917 and (**B**) additional material CUMZ 4914 from the type locality Pulau Bersa, Johor, Malaysia. **C, D.** Original Pfeiffer's specimens of Bulimus mundus var. β BMNH 19601542. **E.** Pfeiffer's original handwritten label on the small label attached to the bottom left of a larger lable that gives the locality as 'Borneo?/China?. "M. C.", is an acronym identifying the material as coming from the Hugh Cuming collection Acc. No. 1829. **F.** Living specimen of A. (A.) mundus (shell height about 35 mm). **G.** Living specimens of A. (A.) atricallosus leucoxanthus from Makham District, Chanthaburi, Thailand; the lower snail is the '*laidlawi*' form (both have shell heights of about 45 mm).

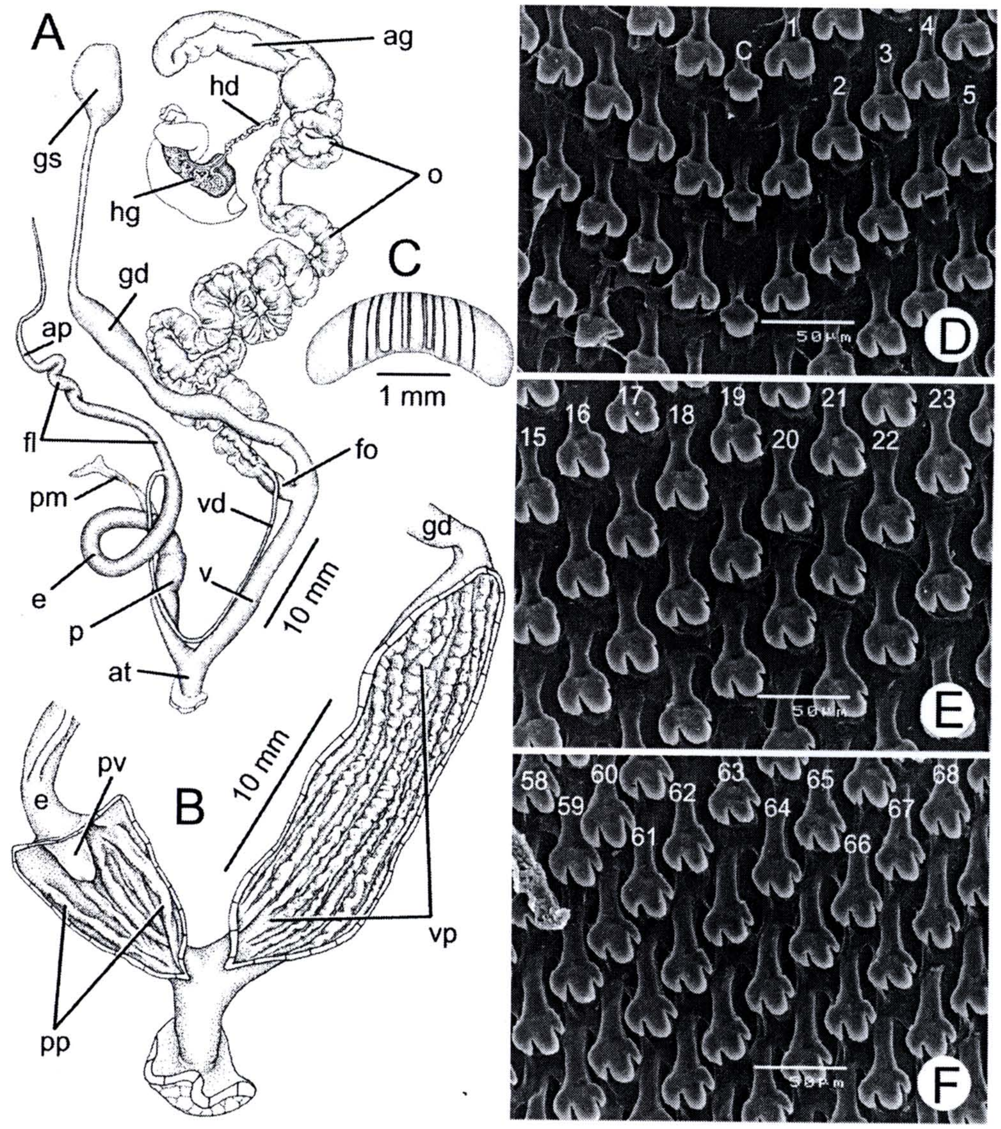

Figure 2. Genitalia, jaw and SEM radula images of A. (A.) mundus. **A.** Reproductive system. **B.** Interior structures of penis and vaginal chamber. **C.** Jaw. **D.** Central teeth with the first to the forth lateral teeth. **E.** Lateral teeth with the tricuspid marginal transition. **F.** Marginal and outermost marginal teeth. Anatomical abbreviation as described in Sutcharit & Panha (2006b): ag, albumin gland; ap, appendix; at, atrium; e, epiphallus; fl, flagellum; fo, free oviduct; gd, gametolytic duct; gs, gametolytic sac; hd, hermaphroditic duct; hg, hermaphroditic gland; o, oviduct; p, penis; pp, penial pilaster; pm, penial retractor muscle; pv, penial verge; v, vagina; vd, vas deferens; vp, vaginal pilaster. Central tooth is indicated by 'C' and the other numbers indicate the order of lateral and marginal teeth.