

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

Chirasak Sutcharit

*Animal Systematics Research Unit, Department of Biology, Faculty of Science,
Chulalongkorn University, Bangkok, 10330, Thailand*

Fred Naggs

Department of Zoology, The Natural History Museum, Cromwell Road, London, SW7 5BD, UK

Somsak Panha

*Animal Systematics Research Unit, Department of Biology, Faculty of Science,
Chulalongkorn University, Bangkok, 10330, Thailand
Email: somsak.pan@chula.ac.th (Corresponding author)*

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 is 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 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 & Peile, 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, coll. 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 Sathitkhiriom, 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, Nakhonsritammarat: 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 those 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; spermiduct (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.

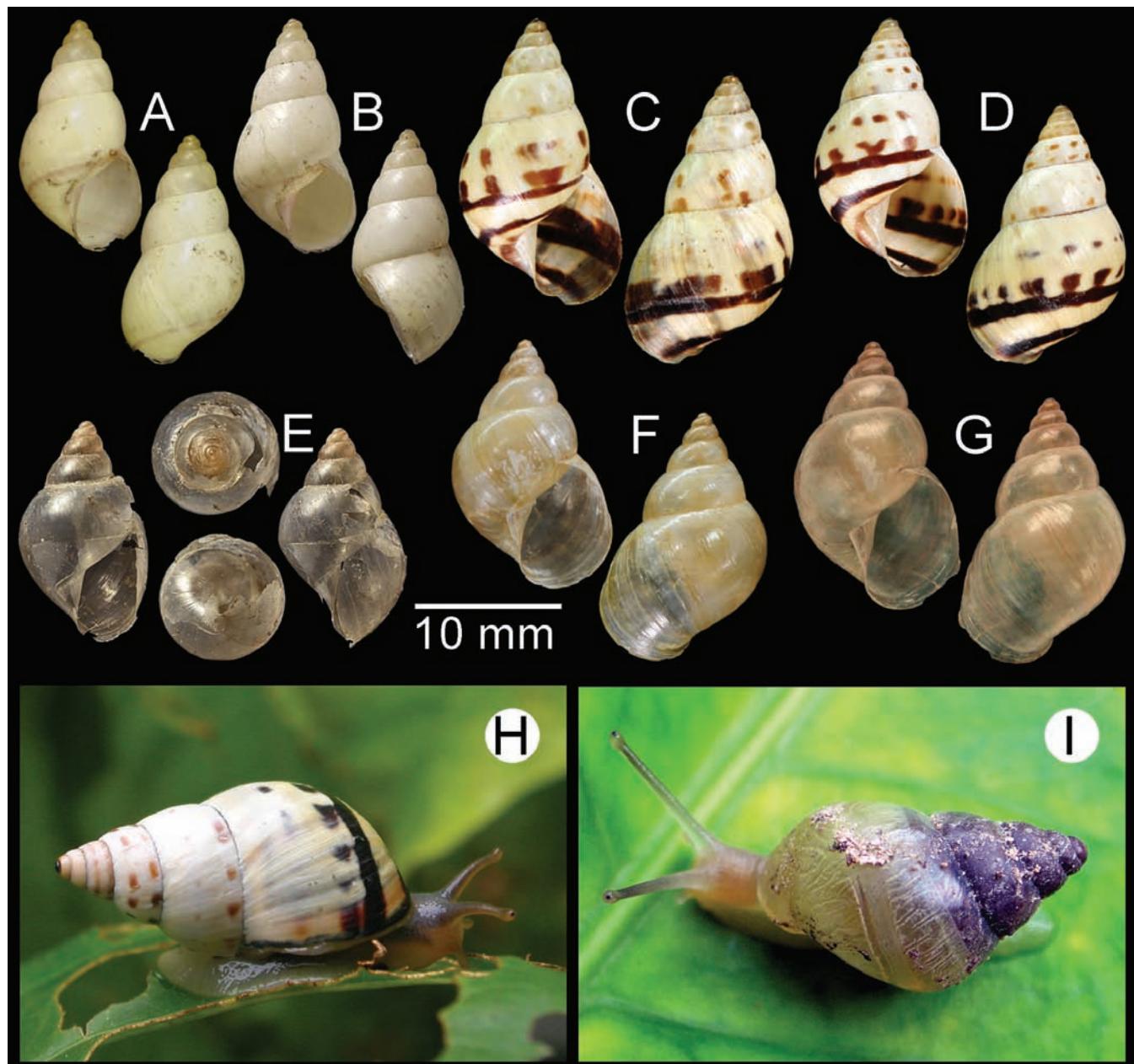


Fig. 1. Shell of *Rhachistia sulphurea*: A, lectotype NMW 1955.158.01155; B, paralectotype BMNH 1939.6.6.17. Shell of *Rhachistia conformalis* Sutcharit & Panha, new species: C, holotype CUMZ 3796; D, paratype CUMZ 3797. Shell of *Amimopina subangulatus*: E, lectotype BMNH 1986166; F, G, specimens from Jed Sao Noi Waterfall, Saraburi (CUMZ 3798, 3799). *Rhachistia conformalis* Sutcharit & Panha, new species: H, at type locality (shell height about 17 mm) CUMZ 3797. *Amimopina subangulatus*: I, 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 monocusp; broadly spatulate. Latero-marginal teeth (teeth number 1 to 15) bicuspid, endocone similar to central tooth; ectocone located at base of tooth and with two pointed cusps. Outermost teeth (teeth number 16 to 43 or 44) polycusp; endocone spatulate with slightly outward oblique cusp; ectocones located laterally and progressively divided up into six pointed cusps.

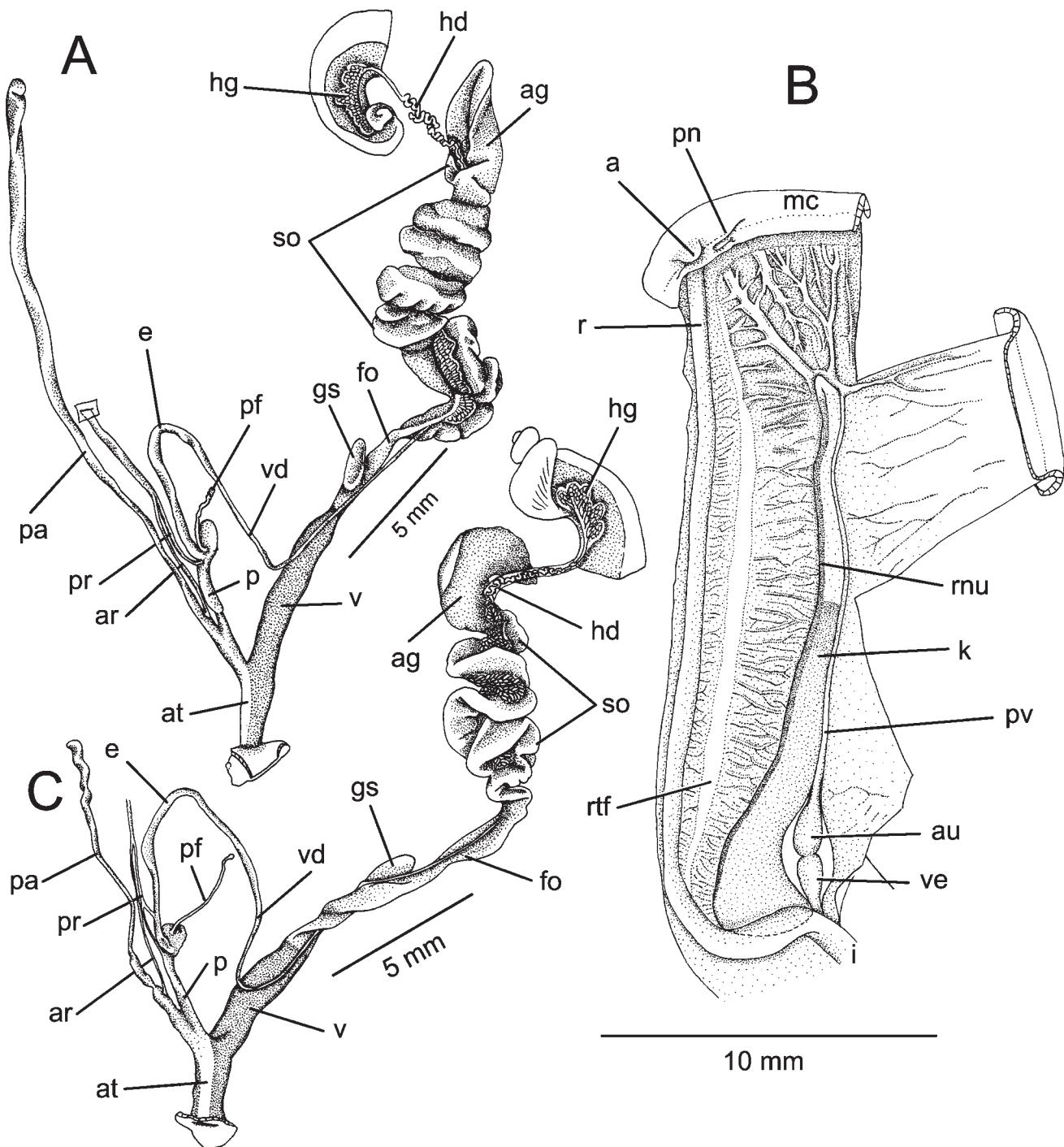


Fig. 2. Anatomy of *Rhachistia conformalis* Sutcharit & Panha, new species (Paratype CUMZ 3797): A, reproductive system; B, pallial system; C, genitalia of *Amimopina subangulatus* from Jed Saw Noi Waterfall, Saraburi (CUMZ 3798).

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

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.

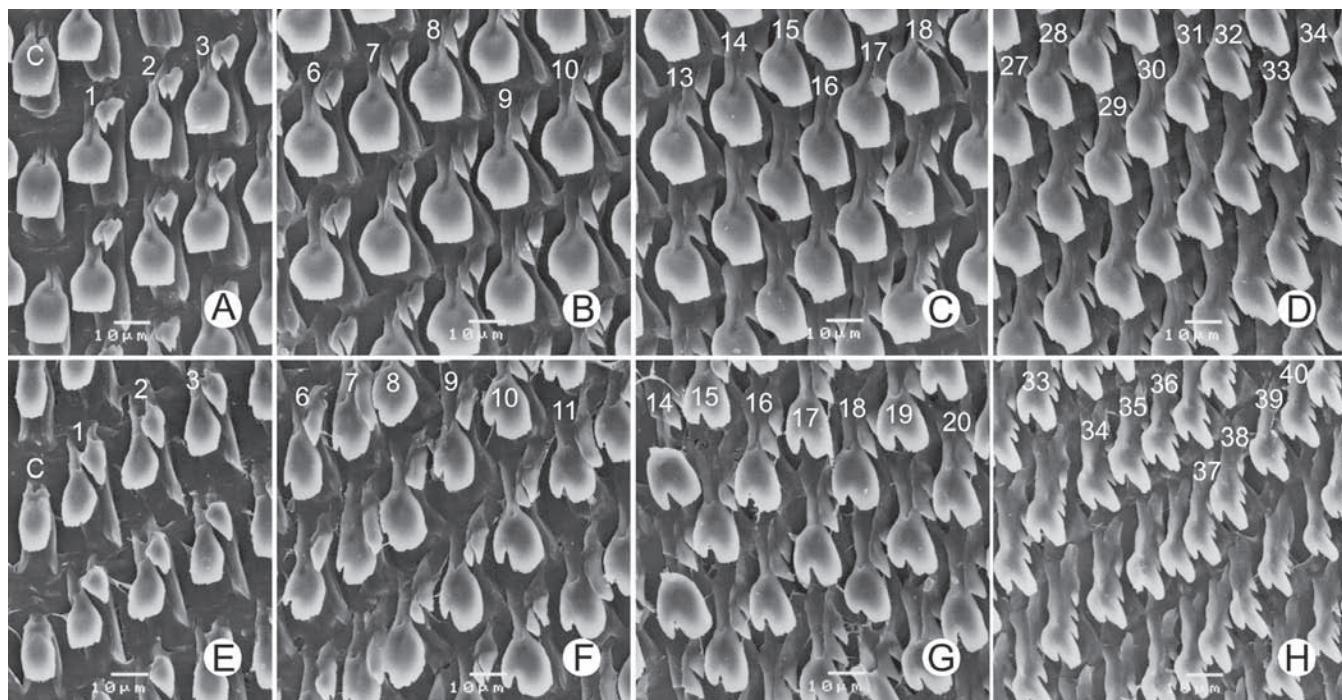


Fig. 3. Radula morphology. *Rhachistia conformalis* Sutcharit & Panha, new species (Paratype CUMZ 3797): A, central tooth with first to third lateral teeth; B, C, lateral teeth with bicuspid marginal teeth transition; D, outermost marginal teeth. *Amimopina subangulatus* (CUMZ 3798): E, central tooth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

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).

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. – *Amimopina 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. *Amimopina 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, southwestern 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 Storzewicz et al. (2009). However, molecular phylogenetic trees (Wade et al., 2006) have robustly demonstrated that the Orthurethra are 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.

ACKNOWLEDGEMENTS

We thank the staff of Kaeng Kracharn and Khao Nan National Parks for making the field work possible. We are also grateful to R. Janssen (SMF, Frankfurt), R. G. Moolenbeek (ZMA, Amsterdam), and H. Wood and J. Gallichan (NMW, Cardiff) for kindly permitting the authors to examine specimens and for providing access to literature resources. We are especially grateful to T. Asami, P. Tongkerd, A. Wiwegweaw, and the Animal Systematics Research Unit members for assistance in field collecting and providing key references. We also thank H. Taylor (NHM, London) for photographs of the type specimens. This project was supported by the TRF-MRG4980201, the BRT-R 252108, the CHE-RES-RG Limestone Biodiversity Project, the Darwin Initiative (project 15/018), the Natural History Museum, London, the RES-A1B1-7, and the SP2-TKK2555-PERFECTA and The Rachadapiseksompho Fund, Chulalongkorn University.

LITERATURE CITED

- Brazier, J., 1876. Descriptions of thirty-five new species of land shells from New Guinea, Australia, and islands in the Torres Straits, collected during the Chevert Expedition. *Proceedings of the Linnean Society of New South Wales*, **1**: 98–113.
- Connolly, M., 1925. The non-marine Mollusca of Portuguese East Africa. *Transactions of the Royal Society of South Africa*, **12**: 105–220.
- Dohrn, H., 1861. Descriptions of new shells from the collection of H. Cuming, Esq. *Proceedings of the Zoological Society of London*, **1861**: 205–207.
- Gray, J. E., 1825. A list and description of some species of shells not taken notice of by Lamarck. *The Annals of Philosophy (New Series)*, **9**: 407–415.
- Gude, G. K., 1914. Mollusca II (Trochomorphidae-Janellidae). In: Shipley, A. E. & G. A. K. Marshall (eds.), *The Fauna of British India, Including Ceylon and Burma*. Taylor and Francis, London. Pp. 1–520.
- Hemmen, J. & C. Hemmen, 2001. Aktualisierte liste der terrestrischen Gastropoden Thailands. *Schriften zur Malakozooologie aus dem Haus der Natur-Cismar*, **18**: 35–70.
- Hyatt, A. & H. A. Pilsbry, 1911. *Manual of Conchology, Structure and Systematic, with Illustrations of the Species*, 2nd Ser., Vol. 21. Academy of Natural Science Philadelphia, PA. Pp. 1–368.
- Martens, E. von, 1867. *Die Preussische Expedition nach Ost-Asien*. Verlag der Königlichen Geheimen Ober-Hofbuchdruckerei. 477 pp.
- Martens, E. von, 1869. Land- u. Süßwassermollusken. In: Peters, W. C. H., J. Cabanis, F. Hilgendorf, E. von. Martens & C. Semper (eds.), *Baron Carl Claus von der Decken's Reisen in Ost-Afrika, in den Jahren 1859–1865, Erste Abtheilung: Säugetiere, Vögel, Amphibien, Crustaceen, Mollusken und Echinodermen, Volume 3*. Leipzig und Heidelberg, Germany. Pp. 55–66, Pls. 1–3.
- Mordan, P. B., 1984. Taxonomy and biogeography of southern Arabian Enidae *sensu lato* (Pulmonata: Pupilliacea). In: Solem, A. & A. C. van Bruggen (eds.), *World Wide Snails: Biogeographic Studies on Non-marine Mollusca*. Leiden. Pp. 124–133.
- Mordan, P. B., 1986. A taxonomic revision of the southern Arabian Enidae *sensu lato* (Mollusca: Pulmonata). *Bulletin of the British Museum (Natural History), Zoology Series*, **50**: 207–271.
- Mordan, P. B., 1991. The phylogeny of the Cerastinae (Pulmonata: Pupilloidea): Its ecological and biogeographical significance. *Proceedings of the 10th Malacological Congress, (Tübingen 1989)*, **1991**: 561–563.
- Mordan, P. B., 1992. The morphology and phylogeny of the Cerastinae (Pulmonata: Pupilloidea). *Bulletin of the British Museum (Natural History), Zoology Series*, **58**: 1–20.
- Mordan, P. B., 1998. The anatomy and phylogeny of the African land snail *Limicena* Connolly, 1925 (Pulmonata: Cerastidae). *Zoologische Mededeelingen*, Leiden, **72**: 59–72.
- Morlet, L., 1884. Description d' especes nouvelles de coquilles recueillies, par M. Pavie au Cambodge. *Journal de Conchyliologie*, **32**: 386–403.
- Naggs, F. & D. Rhaheem, 2000. *Land Snail Diversity in Sri Lanka*. Department of Zoology, The Natural History Museum, London. Pp. i–xiv, Pls. 1–246.
- Nordsieck, H., 1985. The system of the Stylommatophora (Gastropoda), with special regard to the systematic position of the Clausiliidae, I. Importance of the excretory and genital systems. *Archiv für Molluskenkunde*, **116**: 1–24.
- Nordsieck, H., 1986. The system of the Stylommatophora (Gastropoda) with special regard to the systematic position of the Clausiliidae, II. Importance to the shell and distribution. *Archiv für Molluskenkunde*, **117**: 93–116.
- Pfeiffer, L., 1855. Descriptions of fifty-seven new species of Helicea from Mr. Cuming's collection. *Proceedings of the Zoological Society of London*, **1855**: 286–298.
- Pfeiffer, L., 1862. Description of thirty-six new land shells from the collection of H. Cuming, Esq. *Proceedings of the Zoological Society of London*, **1862**: 268–278.
- Pfeiffer, L., 1868. *Monographiae Heliceorum Viventium Supplementum*. Vol. **6**. Lipsiae: F.A. Brockhaus. 598 pp.
- Pfeiffer, L., 1877. *Monographiae Heliceorum Viventium Supplementum*. Vol. **8**. Lipsiae: F.A. Brockhaus. 729 pp.
- Pilsbry, H. A., 1900. On the Zoological position of *Partula* and *Achatinella*. *Proceedings of the Academy of Natural Sciences of Philadelphia*, **52**: 561–567.
- Pilsbry, H. A., 1919. A review of the land mollusks of the Belgian Congo chiefly based on the collections of the American Museum Congo expedition, 1909–1915. *Bulletin of the American Museum of Natural History*, **40**: 1–370.
- Schileyko, A. A., 1998. Treatise on recent terrestrial pulmonate molluscs, Part 2: Gastrocoptidae, Hypselostomatidae,

- Vertiginidae, Truncatellinidae, Pachnodidae, Enidae, Sagdidae. *Ruthenica, Supplement*, **2**: 129–261.
- Smith, B. J. & J. Stanisic, 1998. Pulmonata. In: Beesley, P. L., G. J. B. Ross, & A. Wells (eds.), *Mollusca: The Southern Synthesis*. Fauna of Australia Vol. 5. CSIRO Publishing, Melbourne. Pp. 1037–1125.
- Solem, A., 1959a. On the family position of some Palau, New Guinea, and Queensland land snails. *Archiv für Molluskenkunde*, **88**: 151–158.
- Solem, A., 1959b. Systematics of the land and fresh-water Mollusca of the New Hebrides. *Fieldiana: Zoology*, **43**: 1–238.
- Solem, A., 1964a. *Animopina*, an Australian Enid land snail. *The Veliger*, **6**: 115–119.
- Solem, A., 1964b. New records of new Caledonian non-marine mollusks and an analysis of the introduced mollusks. *Pacific Science*, **18**: 130–137.
- Solem, A., 1973. Convergence in pulmonate radulae. *The Veliger*, **15**: 165–171.
- Solem, A., 1979. A theory of land snail biogeographic patterns through time. In: Van der Spoel S., A. C. Van Bruggen & J. Lever (eds.), *Pathways in Malacology: 6th European Malacological Congress, Amsterdam, 1977*. Dr W. Junk b.v. Publishers, The Hague. Pp. 225–249.
- Solem, A., 1988. Non-camaenid land snails of the Kimberley and Northern Territory, Australia. I. Systematics, affinities and ranges. *Invertebrate Taxonomy*, **2**: 455–604.
- Solem, A. & E. Yochelson, 1979. North American palaeozoic non-marine snails. *United States Geological Survey, Professional Paper*, **1072**: 1–42.
- Storzewicz, E., J. Szulc, & B. M. Pokryszko, 2009. Late paleozoic continental gastropods from Poland: systematic, evolutionary and paleoecological approach. *Journal of Paleontology*, **83**: 938–945.
- Sutcharit, C. & S. Panha, 2006. Taxonomic review of the tree snail *Amphidromus* Albers, 1850 (Pulmonata: Camaenidae) in Thailand and adjacent areas: Subgenus *Amphidromus*. *Journal of Molluscan Studies*, **72**: 1–30.
- Sutcharit, C. & S. Panha, 2008. Taxonomic revaluation of *Sarika diaedema* (Dall, 1897) and *S. asamurai* (Panha, 1997), two endemic land snails from Thailand (Pulmonata: Ariophantidae: Macrochlamydinae). *Raffles Bulletin of Zoology*, **56**: 95–100.
- Sutcharit, C., 2004. *Taxonomic revision and phylogenetic analysis of the tree snail genus Amphidromus Albers and implication for biogeography of Thai species*. Ph.D. Thesis, Faculty of Science, Chulalongkorn University, Thailand. Pp. 168.
- Sutcharit, C., F. Naggs, & S. Panha, 2007. Systematic review of the land snail genus *Neocepolis* Pilsbry, 1891 (Pulmonata: Camaenidae) from North Vietnam. *Journal of Natural History*, **41**: 619–631.
- Tillier, S. & P. B. Mordan, 1995. Anatomy and systematics of the New Caledonian land snail genus *Draparnaudia* Montrouzier, 1859 (Pulmonata: Orthurethra). *Zoological Journal of the Linnaean Society*, **113**: 47–91.
- Tillier, S., 1989. Comparative morphology, phylogeny and classification of land slugs and snails (Gastropoda: Pulmonata: Stylommatophora). *Malacologia*, **30**: 1–303.
- Tomlin, J. R. le B. & A. J. Peile, 1930. *Eorrhachis* a new genus of bulimoid snails. *Proceedings of the Malacological Society of London*, **19**: 153–154.
- Vaught, K. C., 1989. *A classification of the living Mollusca*. American Malacologists, Inc., Florida, USA. Pp. 1–189.
- Verdcourt, B., 1961. Notes on east African Enidae. *Journal of Conchology*, **25**: 9–14.
- Wade, C. M., P. B. Mordan, & F. Naggs, 2006. Evolutionary relationships among the pulmonate land snails and slugs (Pulmonata, Stylommatophora). *Biological Journal of the Linnean Society*, **87**: 593–610.
- Zilch, A., 1959. Gastropoda, Euthyneura. In: Schindewolf, O. H. (ed.), *Handbuch der Paläozoologie, Volume 6*. Gebrüder Borntraeger, Berlin. Pp. 1–400.