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Taxonomic review of the tree snail genus *Amphidromus* Albers, 1850 (Pulmonata: Camaenidae) in Laos, with the description of two new species

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Abstract. The land snail genus *Amphidromus* Albers, 1850 and its subgenus *Syndromus* Pilsbry, 1900 (family Camaenidae) in Laos are revised. Fourteen species from various habitats of deciduous forest and limestone areas throughout Laos are confirmed. The classification is revised and discussed, based on material examined from Laos, Cambodia, Vietnam and Thailand and after comparison with the type specimens in many museums. Two new species, *A. (Amphidromus) syndromoides* Inkhavilay & Panha sp. nov., from central Laos, and *A. (Syndromus) xiengkhaungensis* Inkhavilay & Panha sp. nov., from northern Laos, are described and discussed.

Keywords. Limestone, *Amphidromus*, classification, systematics, Southeast Asia.

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Introduction

The Camaenidae family is comprised of some of the most fascinating land snails, and they occur in various habitat types in Southeast Asia. Many genera are ground dwellers but some are considered to be tree dwellers or arboreal snails, including those in the genus *Amphidromus* Albers, 1850. Members of *Amphidromus* have a conical shell (dextral and/or sinistral) and are very diverse in their shell color and banding patterns (Pilsbry 1900; Laidlaw & Solem 1961; Sutcharit & Panha 2006). Their distribution ranges from Assam in India to Indochina and to Sundaland, south of the Philippines, Wallacea, and a single species found in the Northern Territory of Australia (Solem 1959, 1983; Laidlaw & Solem 1961). There are about 95 recognized species, which are classified in two subgenera (Thach 2014, 2015; Thach & Huber 2014; Sutcharit *et al.* 2015 and references therein; Vermeulen *et al.* 2015). The nominotypical subgenus usually has a larger shell, is chirally dimorphic and has a long epiphallus and flagellum, whereas the smaller shells of the subgenus *Syndromus* Pilsbry, 1900 are mostly of the sinistral

type (except two species, the enantiomorphic *Amphidromus glaucolarynx* (Dohrn, 1861) and the dextral *Amphidromus kuehni* Möllendorff, 1902) with a short epiphallus and flagellum (Pilsbry 1900; Zilch 1953; Sutcharit & Panha 2006; Sutcharit *et al.* 2007, 2015).

Most members of the genus *Amphidromus* were named before the 20th century, based exclusively on shell characters, and many of them are known from only a single shell or a few type specimens with rough locality information (Sutcharit *et al.* 2015). Because *Amphidromus* exhibits a high degree of variation in shell color and banding patterns, its classification is very complicated and problematic. Although several efforts on the taxonomy of *Amphidromus* and catalogues and illustrations of the type specimens have been provided (Fulton 1896; Pilsbry 1900; Zilch 1953; Laidlaw & Solem 1961; Sutcharit *et al.* 2015), the wide range of morphological variation within *Amphidromus* raises doubt as to whether those previous revisionary works may be inapplicable for recent collections, especially since multiple names have been ascribed to single taxa, making species recognition confusing.

Laos is located near the center of the Indo-Burmese hotspots (Myers *et al.* 2000), which has a high diversity of forest types and pristine ecosystems that can potentially support a very high diversity of land snail fauna. Almost all the groups of land snails in Laos are poorly studied compared to other Indo-China countries. Only six species of *Amphidromus* have been reported so far from Laos: *A. flavus* (Pfeiffer, 1861), *A. xiengensis* Morlet, 1891, *A. haematostoma* Möllendorff, 1898, *A. laosianus* Bavay, 1898, *A. givenchyi* Geret, 1912 and *A. protania* Lehmann & Maassen, 2004, compared to, for example, 19 and 23 species in Thailand and Vietnam, respectively (Panha 1996; Schileyko 2011; Sutcharit *et al.* 2015). The present study focused on the basic taxonomy of the tree snail genus *Amphidromus* in Laos. Recently collected specimens were investigated together with reference materials in several museum collections. The previous uncertain recorded species and species of vague status in Laos are redescribed based on the type specimens and the genital characters. In addition, we propose a shell banding system for describing members of the subgenus *Syndromus* and describe the informative genitalia and radula characters of this subgenus based on the type species. Lastly, six new records and two new and endemic species are carefully described.

Material and methods

Empty shells and living specimens were collected throughout Laos from different elevations above mean sea level (amsl) and forest types and also from fruit orchards. Living specimens were photographed before preservation, initially at -20°C and subsequently in 95% (v/v) ethanol, prior to conducting the anatomical study. Genital morphology was critically examined. Intact adult shells were measured for whorl number, shell height (h) and major diameter or shell width (d) using digital Vernier calipers (Mitutoyo, CD-6 CS). The buccal masses were removed and soaked in 10% (w/v) potassium hydroxide solution for 3–5 hours before extracting the radula, which was then cleaned in distilled water and preserved in 95% (v/v) ethanol. Radulae were examined by scanning electron microscopy (SEM: JEOL, JSM-5410 LV), recording the formula and shape of the teeth.

The type locality is mentioned from the original publication in the original wording and language. If possible, the modern name and/or regional names of the type locality are provided in square brackets.

Abbreviations

The terms proximal and distal are used for the region closest to and furthest away from the genital orifice, respectively. New abbreviations are introduced for the vaginal stimulator pilaster (vsp) and vaginal pouch (vpo), but all others are as defined by Solem (1983) and Sutcharit & Panha (2006):

ag = albumen gland
ap = appendix

at	=	atrium
D	=	dextral
e	=	epiphallus
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 verg
S	=	sinistral
v	=	vagina
vd	=	vas deferens
vp	=	vaginal pilaster
vpo	=	vaginal pouch
vsp	=	vaginal stimulator pilaster

Institutional abbreviations

ANSP	=	Academy of Natural Science of Philadelphia, Drexel University, Philadelphia
CUMZ	=	Chulalongkorn University Museum of Zoology, Bangkok
MNHN	=	Muséum national d'Histoire naturelle, Paris
NHMUK	=	Natural History Museum, London
RBINS	=	Royal Belgian Institute of Natural Sciences, Brussels
RMNH	=	Naturalis Biodiversity Center, Rijksmuseum van Natuurlijke Historie, Leiden
SMF	=	Forschungsinstitut und Naturmuseum Senckenberg, Frankfurt am Main
ZMB	=	Museum für Naturkunde, Berlin

Results

Family Camaenidae Pilsbry, 1895
Genus *Amphidromus* Albers, 1850

Subgenus *Amphidromus* Albers, 1850

Amphidromus Albers, 1850: 138.

Amphidromus – Martens 1860: 184. — Fulton 1896: 66, 94.

Type species

Helix perversus Linnaeus, 1758 by subsequent designation of E. von Martens in Albers (1860).

Amphidromus (Amphidromus) roseolabiatus Fulton, 1896
Figs 1, 2A–B, 3A–B, 4A–F, 6A–B, 7A–C; Table 1

Amphidromus roseolabiatus Fulton, 1896: 89, pl. 6, fig. 8. Type locality: Siam [Thailand].

Amphidromus roseolabiatus – Pilsbry 1900: 188, pl. 60, fig. 36. — Laidlaw & Solem 1961: 527. — Richardson 1985: 42. — Schileyko 2011: 57. — Sutcharit *et al.* 2015: 88, fig. 13j–k.

Table 1 (continued on next page). Shell measurements of nine species of *Amphidromus* from Laos. Specimen catalogue numbers are indicated in parentheses.

Species, locality and CUMZ nos	No. of specimens	Range, mean \pm S.D. in mm of			Number of whorls
		Shell height	Shell width	H/W ratio	
<i>Amphidromus roseolabiatus</i> Fulton, 1896					
Ban Pha Vong, Khammouan (7011, 7012)	21	28.0–41.6 35.7 \pm 3.24	14.6–21.2 17.9 \pm 1.74	1.8–2.2 1.9 \pm 0.09	6–6½
Km 70 Lao-Vietnam border, Khammouan (7008)	4	28.0–35.3 33.4 \pm 3.57	15.5–19.0 17.1 \pm 1.48	1.4–2.2 1.9 \pm 0.34	6–6½
Tam Narng Lod, Khammouan (7009)	5	33.6–40.1 36.8 \pm 3.17	16.7–19.1 17.9 \pm 1.03	1.9–2.2 2.0 \pm 0.10	6–6½
Tam Mung Korn, Bolikhamxay (7004, 7005)	22	28.2–40.0 37.2 \pm 2.40	14.1–21.7 20.2 \pm 1.52	1.7–2.0 1.8 \pm 0.10	6–6½
Thad Khaungsy, Luang Phrabang (7013, 7047, 7048)	6	34.3–41.8 37.5 \pm 2.71	17.8–19.8 18.8 \pm 0.87	1.9–2.1 1.9 \pm 0.07	6–6½
Nam Turn Bridge, Khamkert (7006, 707)	9	26.1–34.2 30.3 \pm 2.31	15.2–17.5 16.3 \pm 0.75	1.6–2.0 1.8 \pm 0.14	6–6½
Ban Phone Can, Yommalat, Khammouan (7001)	8	27.2–33.8 30.4 \pm 2.39	13.4–15.9 14.1 \pm 0.91	1.9–2.3 2.1 \pm 0.11	6–6½
Wat Paphar, Khamkert (7002)	6	25.6–34.4 30.7 \pm 3.11	12.8–17.3 15.5 \pm 1.59	1.8–2.0 1.9 \pm 0.07	6–6½
Limestone Quarry, Bolikhamxay (4013)	6	26.9–40.7 30.2 \pm 5.25	13.3–19.3 15.4 \pm 2.08	1.8–2.1 1.9 \pm 0.12	6–6½
Ban Phahom, Vang Vieng (4017, 7049)	31	23.6–30.4 27.4 \pm 1.97	12.9–16.5 14.6 \pm 0.8	1.6–2.1 1.8 \pm 0.12	6–6½
<i>Amphidromus givenchyi</i> Geret, 1912					
Thad Lor, Salavan (7015, 7016)	110	23.3–43.6 36.5 \pm 3.7	11.8–22.9 19.6 \pm 2.26	1.7–2.1 1.8 \pm 0.09	7
Wat Phou, Salavan (7017, 7018)	44	27.1–37.8 33.1 \pm 2.44	15.6–21.2 18.1 \pm 1.35	1.6–2.1 1.8 \pm 0.08	6–6½
<i>Amphidromus syndromoideus</i> sp. nov.					
Tam Narng Ann, Khammouan (7019, 7020, 7021)	20	21.8–29.1 25.9 \pm 1.69	11.2–14.2 12.7 \pm 0.66	1.7–2.2 2.0 \pm 0.10	6
<i>Amphidromus pervariabilis</i> Bavay & Dautzenberg, 1909					
Ban Namly, Phongsaly (7014)	3	31.5–40.9 37.2 \pm 5.02	18.6–19.6 19.0 \pm 0.54	1.6–2.2 1.9 \pm 0.31	7½
<i>Amphidromus areolatus</i> (Pfeiffer, 1861)					
Thad Fek, Attapeu (7022, 7023)	33	13.3–21.8 16.9 \pm 2.19	7.1–10.2 8.5 \pm 0.74	1.5–2.2 1.9 \pm 0.13	6½
Thad Phasoam, Champasak (7024)	9	13.8–21.8 16.5 \pm 2.66	6.9–10.5 8.4 \pm 1.08	1.8–2.0 1.9 \pm 0.08	6½
<i>Amphidromus flavus</i> (Pfeiffer, 1861)					
Wat Phousy, Luang Phrabang (7025)	33	23.2–37.4 28.4 \pm 3.67	11.8–17.4 14.4 \pm 1.26	1.7–2.1 1.9 \pm 0.11	6½
Ban Na Deauy, Luang Phrabang (7026, 7027)	11	22.2–29.8 25.7 \pm 2.27	12.1–14.2 12.9 \pm 0.68	1.8–2.3 1.9 \pm 0.17	6½
Mouhot's Tomb, Luang Phrabang (7028)	5	24.4–29.0 27.6 \pm 1.88	13.1–13.9 13.5 \pm 0.36	1.7–2.2 2.0 \pm 0.17	6½
Tam Pou Kham, Vang Vieng (7029)	12	23.7–35.5 28.3 \pm 3.48	13.0–17.1 14.3 \pm 1.35	1.7–2.2 1.9 \pm 0.14	6½

<i>Amphidromus xiengensis</i> Morlet, 1891					
Ban Phon Pai, Champasak (7030)	33	21.4–36.2 31.0±3.04	13.4–16.9 15.1±0.96	1.4–2.3 2.0±0.14	6½–7
Ban Oudom limestone, Oudomxay (7032)	6	22.1–29.7 26.5±2.61	11.2–13.9 13.0±0.94	1.9–2.1 2.0±0.08	6½–7
Mouhot's Tomb, Luang Phrabang (7033)	5	21.9–35.2 28.1±5.03	12.0–14.8 13.2±1.43	1.8–2.3 2.1±0.21	6½–7
Thad Phasoam, Boloven Plateau, Champasak (7031)	10	17.4–34.4 29.9±5.87	8.7–15.9 13.8±2.46	2.0–2.2 2.1±0.07	6½–7
Ban Na Deauy, Luang Phrabang (7036, 7037)	4	22.4–29.4 26.7±3.32	11.4–13.9 13.1±1.16	1.8–2.1 2.0±0.15	6½–7
<i>Amphidromus fuscolabris</i> Möllendorff, 1898					
Ban Phone, Sekong (7040, 7041, 7042, 7043)	112	26.0–43.5 34.3±3.56	13.1–18.1 15.2±1.04	1.8–2.6 2.2±0.13	7
Ban Xai Na Pho, Champasak (7044)	3	26.0–43.6 34.8±4.06	13.1–18.1 15.3±1.20	1.8–2.5 2.2±0.14	7
<i>Amphidromus xiengkhaungensis</i> sp. nov.					
Nong Tang, Xieng Khaung (7045, 7046)	4	21.4–29.8 25.6±3.49	14.8–17.0 15.7±1.04	1.4–1.7 1.6±0.13	6

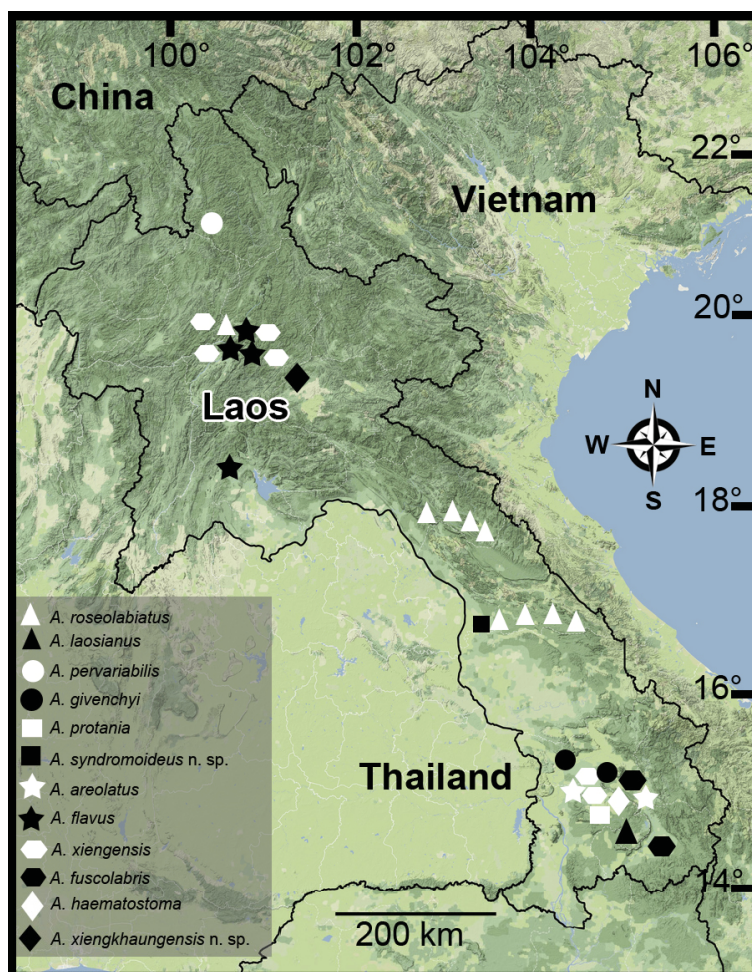


Fig. 1. Distribution map of *Amphidromus* spp. in Laos recognized in this study.

Material examined

Type material

THAILAND: Lectotype, NHMUK 19601462 (Sutcharit *et al.* 2015: fig. 13j); paralectotype, NHMUK 19601463 (1S shell, Sutcharit *et al.* 2015: fig. 13k).

Other material

LAOS: 5D + 3S shells, Ban Phone Can, Yommalat District, Khammouan (CUMZ 7001); 5D + 1S shells, Wat Paphar, Khamkert District, Bolikhamxay (CUMZ 7002); 2D + 1S shells, Thad Mouang, Khamkert District, Bolikhamxay (CUMZ 7003); 4D + 10S specimens, in ethanol (Fig. 4E–F, CUMZ 7004), 13S specimens in freezer (Fig. 2B, CUMZ 7005), Tam Mung Korn, Khamkert District, Bolikhamxay; 1D + 1S specimens, in ethanol (Fig. 4C–D, CUMZ 7006), 4D + 5S specimens in freezer (Fig. 3A–B, CUMZ 7007), Nam Turn Bridge, Khamkert District, Bolikhamxay; 8D + 6S shells, Limestone quarry, Bolikhamxay (CUMZ 4013); 4D + 3S shells, pink aperture, Km. 70 on the road from Laos to Vietnam border, Yommalat District, Khammouan (CUMZ 7008); 8D shells, pink aperture, Tam Nang Lod, Yommalat District, Khammouan (CUMZ 7009); 3D + 1S shells, pink aperture, Hany In River, Yommalat District, Khammouan (CUMZ 7010); 12D + 8S specimens, in ethanol, pink aperture (Fig. 4A–B, CUMZ 7011), 5D specimens, in ethanol (Figs 2A, 6A–B, 7A–C, CUMZ 7012), Ban Pha Vong, Yommalat District, Khammouan; 1D + 1S shells, pink aperture (CUMZ 7013), 6D specimens, in ethanol (CUMZ 7047), 4D specimens, in ethanol (CUMZ 7048), 1D + 1S shells, pink aperture (CUMZ 7035), Thad Khaungsy Waterfall, Luang Phrabang District, Luang Phrabang; 6D shells (CUMZ 40107), 10S + 21D shells (CUMZ 7049), Ban Phahom, Vang Vieng District, Vientiane.

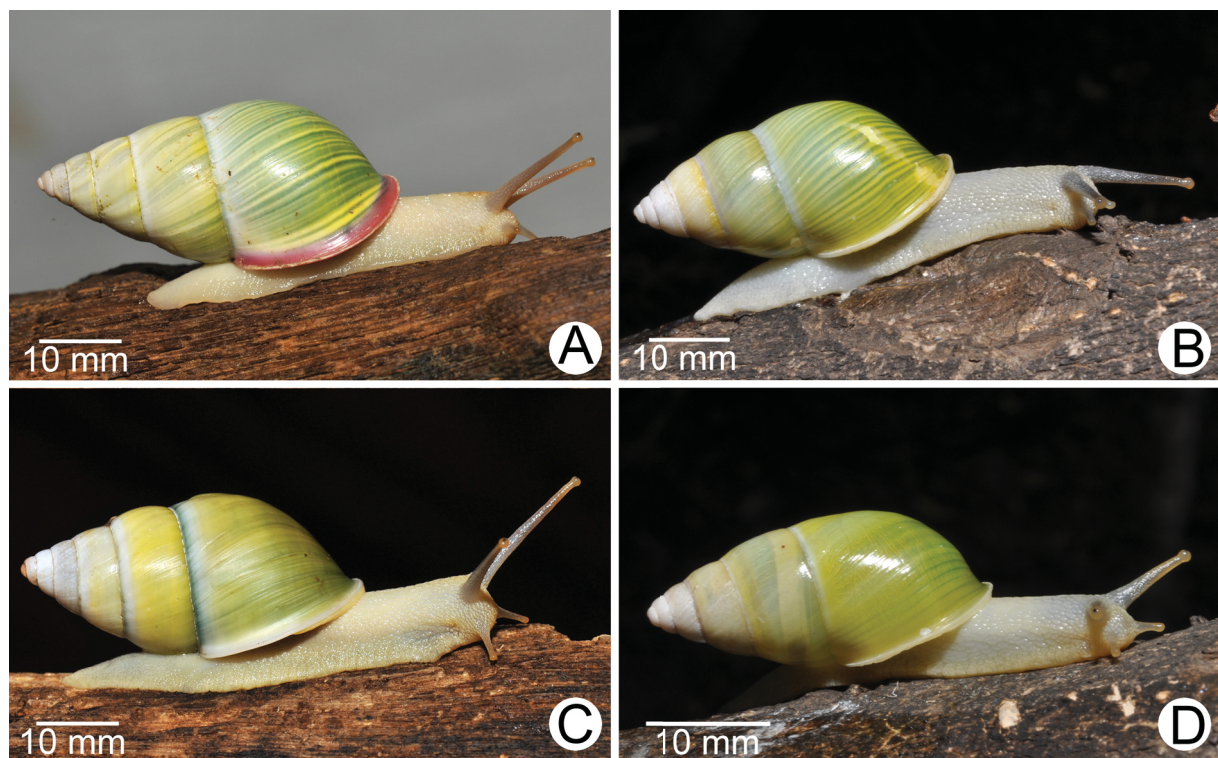


Fig. 2. Living snails. **A–B.** *Amphidromus roseolabiatius* Fulton, 1896. **A.** Typical form from Ban Phavong, Khammouan, Laos (CUMZ 7012). **B.** Form with white lip from Tam Mung Korn, Bolikhamxay, Laos (CUMZ 7005). **C.** *Amphidromus givenchy* Geret, 1912 from Thad Lor Waterfall, Salavan, Laos (CUMZ 7018). **D.** *Amphidromus syndromoideus* sp. nov., holotype from the type locality (CUMZ 7019).

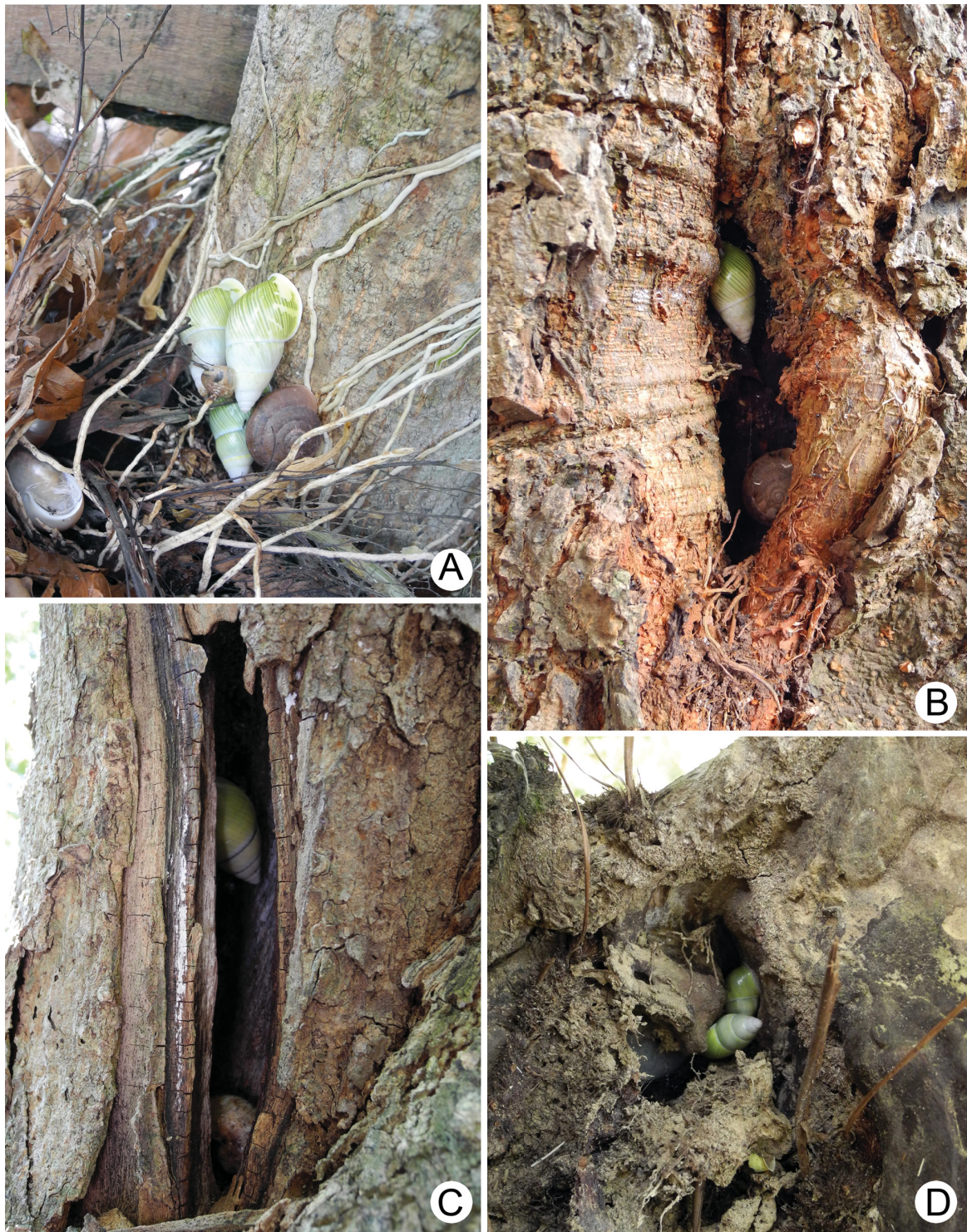


Fig. 3. Aestivation sites of *Amphidromus* species. **A–B.** *Amphidromus roseolabiatum* Fulton, 1896 (shell height about 34 mm) from NamTurn Bridge, Bolikhamxay, Laos, aestivated. **A.** Inside sterile fronds of stag horn ferns, *Platycerium* Desv. **B.** In a small hole on a Jackfruit tree trunk, *Artocarpus heterophyllus* Lam., with other snails, *Quantula* Baker, 1941 and *Durgella* Blanford, 1863. **C.** *Amphidromus givenchyi* Geret, 1912 (shell height about 43 mm), hiding in a small hole of a dipterocarpus tree shell. **D.** *Amphidromus syndromoides* sp. nov. (shell height about 28 mm) from the type locality, hiding in a hole of a tree, visible after removal of clusters of sterile fronds of the basket fern *Drynaria* (Bory) J. Sm .

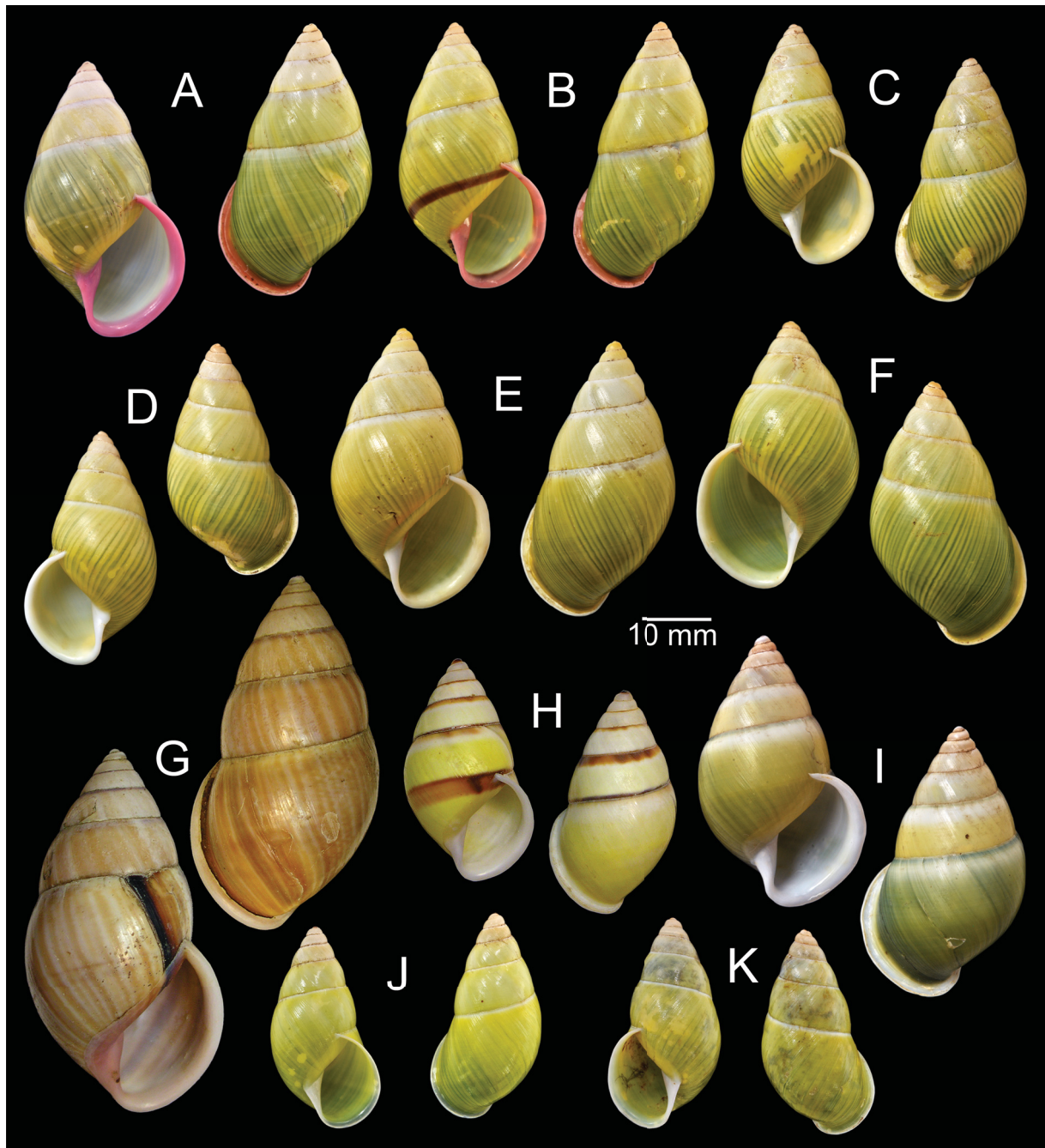


Fig. 4. Shells of *Amphidromus* (*Amphidromus*) spp. **A–F.** *Amphidromus roseolabiatum* Fulton, 1896. **A–B.** Typical form from Ban Phavong, Khammouan, Laos (CUMZ 7011). **C–D.** Form with white lip from Nam Turn Bridge, Bolikhamxay, Laos (CUMZ 7006). **E–F.** Form with white lip from Tam Mung Korn, Bolikhamxay, Laos (CUMZ 7004). **G.** *Amphidromus laosianus* Bavay, 1898 from Khone, Champasak, Laos (RMNH 101049). **H.** *Amphidromus protania* Lehmann & Maassen, 2004, holotype (RMNH 98143). **I.** *Amphidromus givenchy* Geret, 1912 from Thad Lor Waterfall, Salavan, Laos (CUMZ 7015). **J–K.** *Amphidromus syndromoideus* sp. nov. from the type locality. **J.** Holotype (CUMZ 7019). **K.** Paratype (CUMZ 7020).

VIETNAM: 2D+3S shells, Phong Nha National Park (CUMZ 7053).

THAILAND: 1D shell, Nan Province, Thailand (CUMZ 7054).

Description

Shell chirally dimorphic, elongate to ovate conical, rather thin and glossy. Spire conical; apex acute, light brown and without black spot on tip. Whorls 6 to 7 nearly smooth; suture wide and depressed; last whorl rounded. Periostracum usually deciduous to yellowish-green radial streaks, more conspicuous on last whorl and faded in previous whorls. Last whorl processes thin, whitish subsutural band, sometimes with one or two reddish-brown spiral bands below periphery but usually not reaching lip; varix absent. Parietal callus thin and transparent. Aperture ovate to elongate; peristome expanded and not reflected; lip usually purplish-pink or white. Columella straight, thickened, purplish-pink or white. Umbilicus narrowly opened.

Radula

Each row contains about 130 (66-(10-6)-1-(6-10)-63) teeth. Central tooth unicuspid and spatulate with curved cusp. Lateral teeth bicuspid. Endocone cylindrical, slightly oblique, with wide notch; ectocone large, with truncated to rounded cusp. Marginal teeth tricuspid, start around tooth number 6 to 10; endocone small; mesocone large, with rounded cusp, ectocone small, with sharp cusp. Outermost teeth with small and sharp cusp on endocone and extocone; mesocone large, with curved cusps (Fig. 7A–C).

Genital organs

Atrium (at) rather short ($n = 10$). Penis (p) long and stout. Epiphallus (e) long, about two times as long as penis; flagellum (fl) longer than epiphallus and terminated in folded coil. Appendix very small, extends from folded coil of flagellum, about same length as epiphallus. Penial retractor muscle (pr) short, thickened and inserted distally on penis. Vas deferens (vd) narrow tube connecting epiphallus and free oviduct (Fig. 6A).

Internal penial wall corrugated into series of thick penial pilasters (pp), which form a fringe around penial verge. Penial verge (pv) rather long and curved, conical, with smooth surface and orifice located at tip (Fig. 6B).

Vagina cylindrical, about two times as long as penis. Gametolytic duct very long, proximal to genital orifice large, coiled; distal to genital orifice tapering to small tube, short, about one-third length of proximal part and connected to enlarged gametolytic sac. Oviduct and albumin gland small (Fig. 6A).

Internally, vaginal wall performs longitudinal vaginal pilasters (vp); proximal to genital orifice with small corrugated continuous ridges, ridges distally becoming smooth (Fig. 6B).

Distribution

This species is distributed widely, from many localities in central and northern Laos. There are also records from Nan Province, Thailand and Phong Nha National Park, Vietnam.

Remarks

Amphidromus roseolabiatulus differs from *A. smithi* Fulton, 1896 and *A. ventrosulus* Möllendorff, 1900 (Zilch 1953; Sutcharit *et al.* 2015) in having an enantiomorphic shell coiling, purplish-pink lip and fine green streaks. In contrast, *A. smithi* has a sinistral shell, brownish lip with dark spot on the apex, and *A. ventrosulus* has a sinistral shell, uniform green color, elongate spire and more depressed suture.

Laidlaw & Solem (1961) recognized *A. roseolabiatus* as belonging to an uncertain subgenus that was probably close to the subgenus *Syndromus*. However, this species exhibits dimorphic shell coiling with a long flagellum and appendix, which are typical characters of the nominotypical subgenus (Fig. 6A). Two color forms were observed in the recently collected materials. The typical color form has a greenish radial streaked periostracum and pinkish apertural lip (Figs 2A, 4A–B). There are some specimens with the typical color form showing one or two additional reddish-brown lower, peripheral bands (Fig. 4B). The second, whitish form usually has a greenish periostracum, as in the typical color form, but a white apertural lip (Figs 2B, 4C–F). However, these two color forms have identical genital structures and sculptures inside the penis and vagina.

Amphidromus (Amphidromus) laosianus Bavay, 1898

Figs 1, 4G

Amphidromus laosianus Bavay, 1898: 15, 16, pl. 2, fig. 1, 1a. Type locality: Khône, sur les bords du Mékong [on the banks of the Mekong River, Khone, Champasak, Laos].

Amphidromus laosianus var. *albocaerulescens* Bavay, 1898: 16, pl. 2, fig. 2, 2a. Type locality: Khône, sur les bords du Mékong [on the banks of the Mekong River, Khone, Champasak, Laos].

Amphidromus laosianus – Pilsbry 1900: 183, 184, pl. 62, figs 60–61. — Laidlaw & Solem 1961: 526, 634.

Amphidromus laosianus var. *albocaerulescens* – Pilsbry 1900: 184, pl. 62, figs 62–63. — Laidlaw & Solem 1961: 526, 598.

Material examined

LAOS: 1D + 1S shells (Fig. 4G), Khone District, Champasak, South Laos (RMNH 101049); 1D + 2S shells, W.J.M. Maassen collection; 2D + 2D juveniles, Khone, South Laos, ZMB, Lehmann collection.

Remarks

Currently known only from the type locality. The unique shell characters are chirally dimorphic, conical to elongate conical; whorls weakly convex, with white subsutural band. Shell color with yellowish-brown or brownish radial streaks on pinkish to whitish ground color; dark varix present. Aperture elongated; peristome thickened, expanded and reflected; lip folded and pinkish. Parietal callus pinkish and thickened; columella pinkish and straight; umbilicus imperforated.

Laidlaw & Solem (1961) mentioned that this species is similar to the *A. atricallosus leucoxanthus* variety “*laidlawi*” (Solem 1965: pl. 1, fig. 3; Sutcharit & Panha 2006: fig. 4d–e). However, it differs in having a slender shell and pinkish peristome, parietal callus and inside of the aperture, while “var. *laidlawi*” has a white lip, parietal callus and inside aperture, and more depressed suture. Furthermore, *A. cambojiensis* (Reeve, 1860) can be distinguished from this species by having a very large and thickened shell, thickened and white parietal callus and lip, and purplish inside aperture (see Sutcharit *et al.* 2015).

Amphidromus (Amphidromus) pervariabilis Bavay & Dautzenberg, 1909

Figs 1, 5A–L; Table 1

Amphidromus pervariabilis Bavay & Dautzenberg, 1909b: 246–247. Type locality: Ban-Lao, Muong-Kong, Pha-Long, Pac Kha.

Amphidromus pervariabilis – Bavay & Dautzenberg 1909a: 279–281, pl. 9, figs 1–10, pl. 10, figs 1–8. — Laidlaw & Solem 1961: 527, 528. — Richardson 1985: 15.

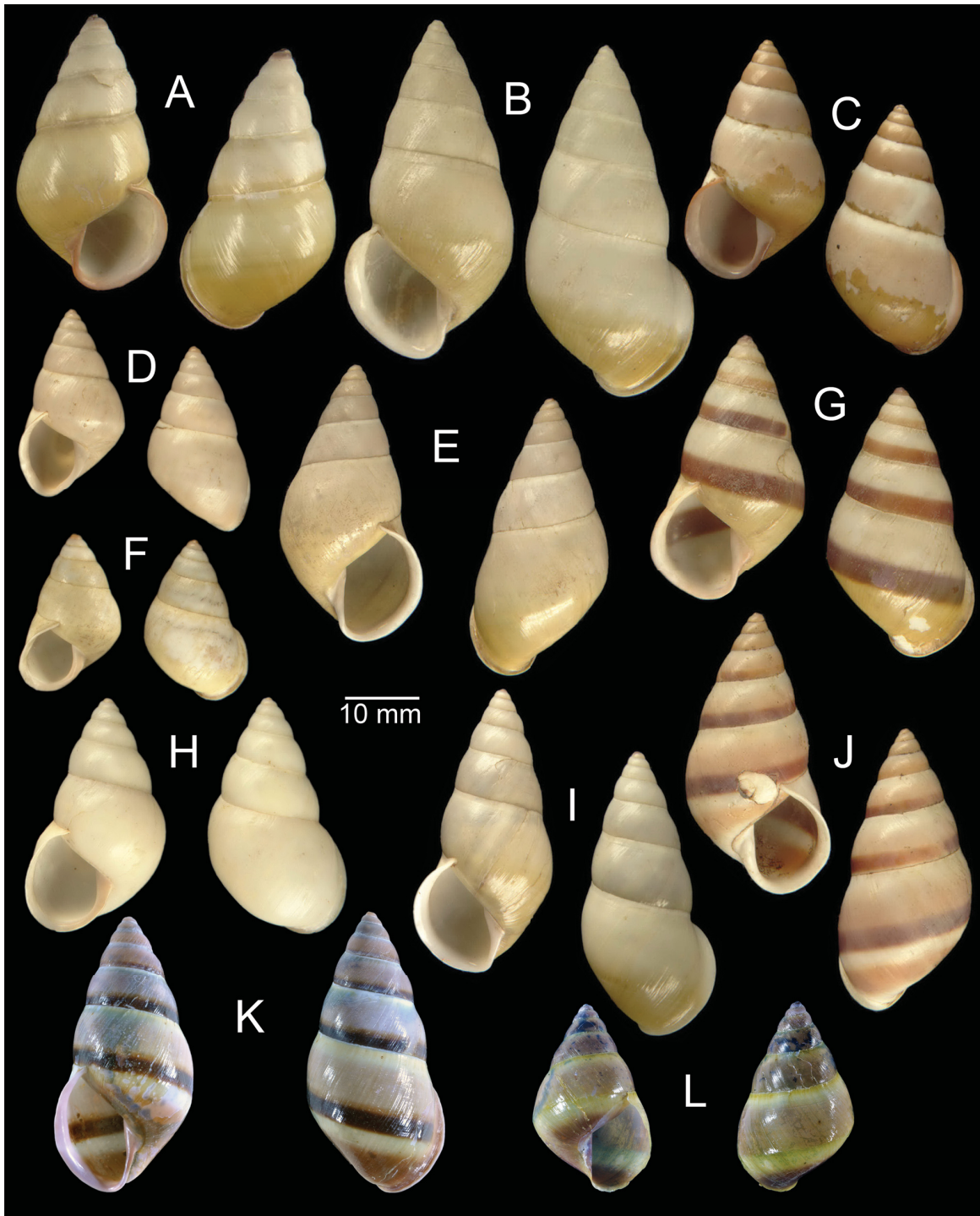


Fig. 5. Shells of *Amphidromus pervariabilis* Bavay & Dautzenberg, 1909. **A–B.** Syntype of the nominotypical form (MNHM-IM-2000-2049). **C.** Var. “*bifasciata*” Bavay & Dautzenberg, 1909, syntype (MNHM-IM-2000-2059). **D.** Var. “*goniostoma*” Bavay & Dautzenberg, 1909, syntype (MNHM-IM-2000-2058). **E.** Var. “*lilacina*” Bavay & Dautzenberg, 1909, syntype (MNHM-IM-2000-2052). **F.** Var. “*minor*” Bavay & Dautzenberg, 1909, syntype (MNHM-IM-2000-2050). **G.** Var. “*monozonalis*” Bavay & Dautzenberg, 1909, syntype (MNHM-IM-2000-2057). **H.** Var. “*obesa*” Bavay & Dautzenberg, 1909, syntype (MNHM-IM-2000-2053). **I.** Var. “*protracta*” Bavay & Dautzenberg, 1909, syntype (MNHM-IM-2000-2051). **J.** Var. “*tricolor*” Bavay & Dautzenberg, 1909, syntype (MNHM-IM-2000-2054). **K–L.** Specimens from Khua District, Phongsaly, Laos (CUMZ 7014).

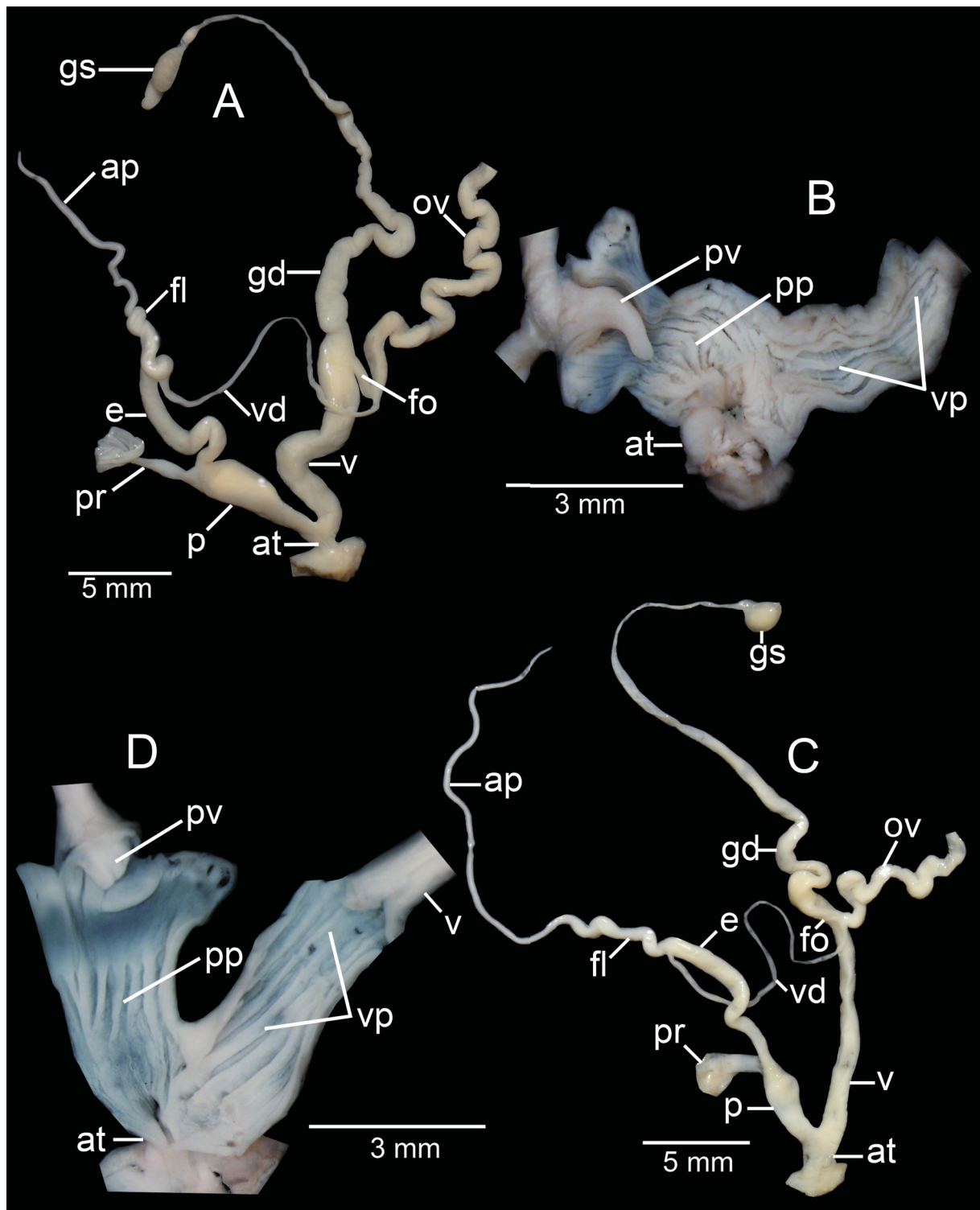


Fig. 6. Genitalia of *Amphidromus* spp. **A–B.** *Amphidromus roseolabiatum* Fulton, 1896 from Ban Phavong, Khammouan, Laos showing reproductive system and interior structures of penis and vaginal chamber (CUMZ 7012). **C–D.** *Amphidromus syndromoideus* sp. nov., holotype, showing general characteristics of the genital system and interior structures of penis and vagina chamber (CUMZ 7019).

Material examined

Type material

VIETNAM: 2 shells (Fig. 5A–B), syntypes of *A. pervariabilis* s.str. MNHM-IM-2000-2049, from Ban-Lao [19° 39' N, 103° 19' E], Muong-Kong [19° 33' N, 104° 44' E], Pha-Long [22° 48' N, 104° 14' E], Pac Kha [21° 00' N, 104° 35' E].

VIETNAM: 2 shells (Fig. 5C), syntypes of *A. pervariabilis* var. “*bifasciata*”, from Ban-Lao, Muong-Kong, Pha-Long, Pac Kha (MNHM-IM-2000-2059).

VIETNAM: 1 shell (Fig. 5D), syntype of *A. pervariabilis* var. “*goniostoma*”, from Phong-Tho, 22°34' N, 103°22' E (MNHM-IM-2000-2058).

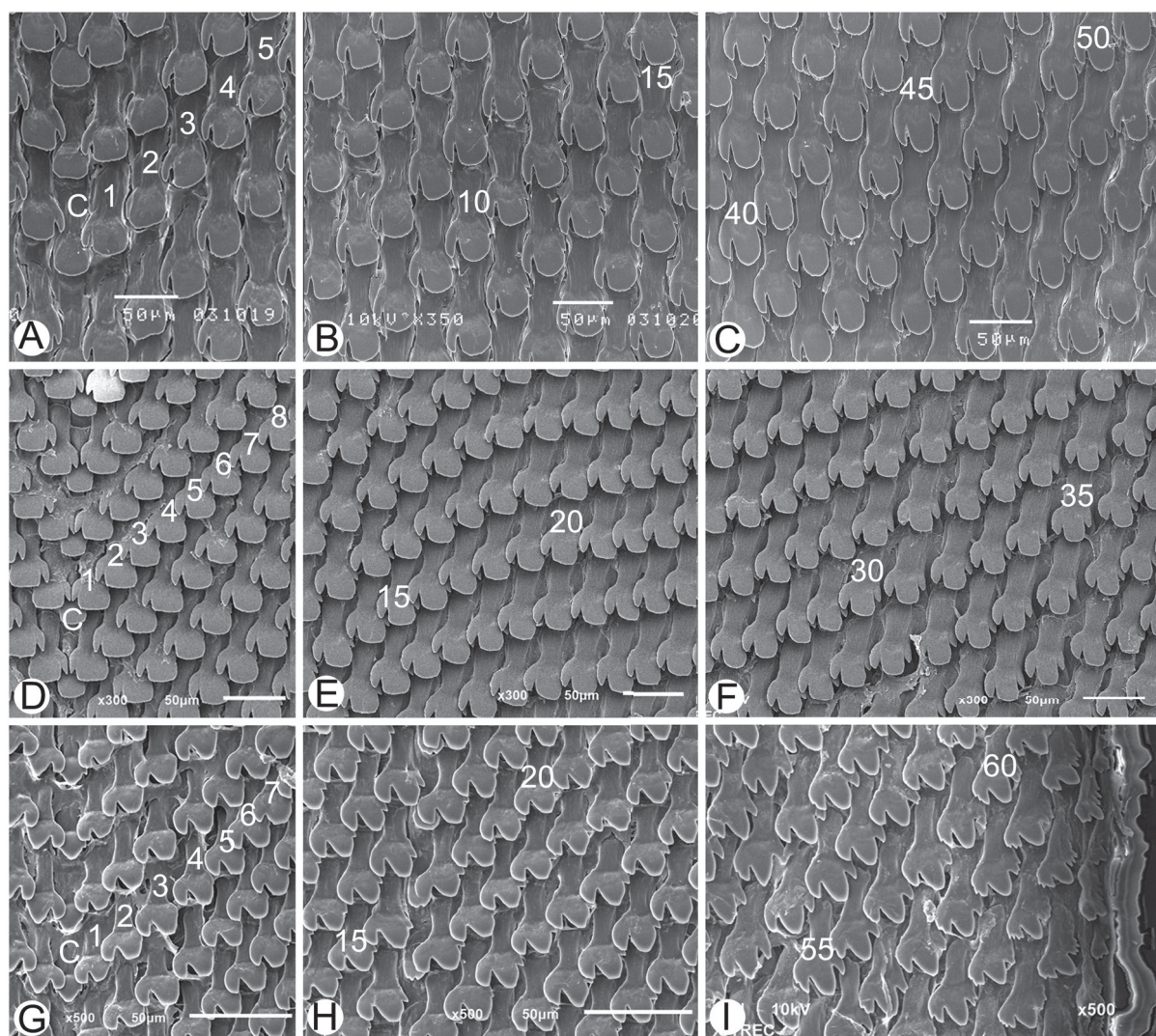


Fig. 7. SEM images of the radula. **A–C.** *Amphidromus roseolabiatus* Fulton, 1896 from Ban Phavong, Khammouan, Laos (CUMZ 7012). **D–F.** *Amphidromus syndromoideus* sp. nov., holotype (CUMZ 7019). **G–I.** *Amphidromus areolatus* (Pfeiffer, 1861) from Thad Fek, Attapue, Laos (CUMZ 7023). A, D, G = central tooth with the first to fifth to eighth lateral teeth; B, E, H = lateral teeth with the tricuspoid marginal teeth transition; C, F, I = outermost marginal teeth. Numbers indicate the order of the lateral and marginal teeth. Central tooth indicated by ‘C’.

VIETNAM: 2 shells (Fig. 5E), syntypes of *A. pervariabilis* var. “*lilacina*”, from Ban-Lao (MNHM-IM-2000-2052).

VIETNAM: 1 shell (Fig. 5F), syntype of *A. pervariabilis* var. “*minor*”, from unknown locality (MNHM-IM-2000-2050).

VIETNAM: 2 shells (Fig. 5G), syntypes of *A. pervariabilis* var. “*monozonalis*”, from Ban-Lao (MNHM-IM-2000-2057).

VIETNAM: 1 shell (Fig. 5H), syntype of *A. pervariabilis* var. “*obesa*”, from Muong-Bo, 22°24' N, 102°49' E (MNHM-IM-2000-2053).

VIETNAM: 1 shell (Fig. 5I), syntype of *A. pervariabilis* var. “*protracta*”, from Ban-Lao, Muong-Kong, Pha-Long, Pac Kha (MNHM-IM-2000-2051).

VIETNAM: 2 shells (Fig. 5J), syntypes of *A. pervariabilis* var. “*tricolor*”, from Ban-Lao (MNHM-IM-2000-2054).

Other material

LAOS: 3 shells (Fig. 5K–L), Km 34, road to Ban Namly, Khua District, Phongsaly, 21°11'55.5" N, 102°6'40.2" E, 834 m amsl (CUMZ 7014).

Description

Shell chirally dimorphic, elongate conical, rather thick and glossy. Spire elongate conical; apex acute, with or without black spot on tip. Whorls 6 to 7 convex to smooth; suture wide and shallow; last whorl rounded to well rounded. Periostracum thin corneous; varix usually absent. Shell color varies from uniform white, yellowish to reddish brown or with narrow to wide brownish peripheral and umbilical bands. Parietal callus thin and transparent. Aperture ovate to oblique elongated; peristome expanded and not reflected; lip white, brownish or purplish. Columella straight, thick or thin and white or brownish. Umbilicus imperforated.

Remarks

This species tend to have a high diversity of shell colors, with eight infra-specific names being provisionally proposed to distinguish the distinct shell shape and color patterns. We examined all the type specimens and recognized them as subspecific entities of one species.

Laidlaw & Solem (1961) recognized this species as a synonym of *A. dautzenbergi* Fulton, 1899. The latter species exhibits a thin shell, yellowish with a thin faded greenish streak near the umbilicus, a white subsutural band and an elongated ovate aperture, while *A. pervariabilis* has a thick shell, monochrome or with dark brown spiral band and ovate aperture. However, the type locality of *A. dautzenbergi* was “Tonkin”, the historical political division during the French colonial period, and it still is an uncertain boundary. The species is known from the holotype only (Sutcharit *et al.* 2015: fig. 6g), no specimen was found in the present study, and, therefore, the taxonomic status of *A. dautzenbergi* and *A. pervariabilis* remains to be confirmed.

Amphidromus (Amphidromus) givenchy Geret, 1912

Figs 1, 2C, 3C, 4I; Table 1

Amphidromus givenchy Geret, 1912: 55–56, pl. 2, figs 21–22. Type locality: Unknown.

Amphidromus givenchyi – Laidlaw & Solem 1961: 526, 621. — Richardson 1985: 43. — Sutcharit & Panha 2006: 26–28, figs 4n–q, 18–19.

Material examined

LAOS: 120D + 18D juveniles (Figs 3C, 4I, CUMZ 7015), 7D specimens, in ethanol (Fig. 2C, CUMZ 7016), Thad Lor Waterfall, Salavan District, Salavan; 61D + 8D juveniles (CUMZ 7017), 2D specimens, in ethanol (CUMZ 7018), Wat Phou (Temple on the mountain), Khong Xédon District, Salavan.

Remarks

The species description, as well as the morphology of the genitalia and the radula, have been carefully presented in Sutcharit & Panha (2006), which allows an unambiguous recognition of this species. The unique characters are a relatively medium sized (compared to other members of this genus, as shown in Table 1), ovate-conical and dextral shell; apex with black spot; aperture oblique; peristome expanded and not reflected; parietal callus thin and transparent to slightly thickened and white; shell color uniform greenish with pale to yellowish color on earlier whorl, and greenish subsutural band; genitalia contain long and slender penis, short and curved epiphallus of equal length to flagellum; proximal to enlarged and coiled appendix epiphallus; appendix short.

The early records of this species were from the Ubon Ratchathani and Kalasin Provinces of Thailand, and the Luang Phrabang and Savannakhet Provinces of Laos (Sutcharit & Panha 2006). Here, two more localities from Salavan Province, Laos are added. All of the records are from dry dipterocarp to deciduous forests with sandstone hills. The snails were found in small holes on branches or tree trunks during the aestivation period (Fig. 3C).

Amphidromus (Amphidromus) protania Lehmann & Maassen, 2004
Figs 1, 4H

Amphidromus (Amphidromus) protania Lehmann & Maassen, 2004: 17–20, figs 1–4. Type locality: South Laos, Salavan Province, near Ban Donxé Village, E bank of Se Don River.

Material examined

LAOS: Dextral, holotype (RMNH 98143, Fig. 4H); 4D shells, paratypes (RMNH 98144).

Remarks

No specimen was found in this survey. *Amphidromus protania* has a very similar shell shape to that the dipterocarp forest species *A. givenchyi*. The genitalia contain a long and coiled proximal part of the epiphallus, with a relatively short appendix, as in *A. givenchyi* (Lehmann & Maassen 2004; Sutcharit & Panha 2006). However, the characters distinguishing it from *A. givenchyi* are the relatively smaller shell (height 26–31 mm in *A. protania*; Table 1), the yellowish shell color as well as the brownish subsutural and spiral bands on the periphery. Moreover, Lehmann & Maassen (2004) mentioned that the brownish banding pattern had less variation. However, a brownish spiral band on the periphery can also be observed in juvenile *A. givenchyi* (see Sutcharit & Panha 2006: fig. 4o). Moreover, this species occurs in dipterocarp forest within the range of *A. givenchyi*; therefore, it is possibly a shell color variant of *A. givenchyi*. Additional specimens for further anatomical and molecular study are desirable to test this hypothesis.

Amphidromus (Amphidromus) syndromoideus Inkhavilay & Panha sp. nov.
[urn:lsid:zoobank.org:act:26B7BD0E-55D1-494B-B057-6D7986EB36DA](https://doi.org/10.21203/rs.3.rs-1444441/v1)

Figs 1, 2D, 3D, 4J–K, 6C–D, 7D–F; Table 1

Diagnosis

The new species differs from all other known *Amphidromus (Syndromus)* species in having a long epiphallus and flagellum and very long appendix, both being unique characters of the nominotypical subgenus (Solem 1983; Sutcharit & Panha 2006). The new species differs from *A. roseolabiatus* in having a small and thin shell, inconspicuous greenish radial streaks and about two times longer appendix. In contrast, *A. roseolabiatus* has a larger solid shell, conspicuously greenish radial streaks in fresh specimens, sometimes with a single brownish spiral band below the periphery, purplish-pink apertural lip, and a short appendix.

Etymology

The specific epithet ‘*syndromoideus*’ is from ‘*syndromus*’, an *Amphidromus* subgeneric name, and the suffix ‘*-oideus*’, meaning ‘like or resembling’. This name refers to the resemblance in shell morphology of the new species with members of the subgenus *Syndromus*.

Type material

Holotype

LAOS: dextral, shell height 28.2 mm, shell width 13.4 mm, with 6½ whorls (CUMZ 7019, Figs 2D, 3D, 4J, 6C–D, 7D–F).

Paratypes

LAOS: 22D + 9S shells (Fig. 4K, Table, CUMZ 7020 (1); 1S specimen, in ethanol (CUMZ 7021); 1D + 1S shells (NHMUK); 1D + 1S shells (SMF).

Type locality

LAOS: Tam Nang Ann (cave), Thakhek District, Khammouan, 17°26′39.2″ N, 104°56′54.8″ E, 163 m amsl.

Description

Shell chirally dimorphic, thin, rather small, elongate conical and glossy. Spire conical; apex acute, brownish and without black spot on tip. Whorls 5 to 6 weakly convex; suture depressed; last whorl rounded. Periostracum thin and transparent. Last whorl with narrow white subsutural band and shell color uniform yellowish with green radial streaks on last whorl (pale to inconspicuous in older whorls and empty shells); varix absent. Parietal callus thin and transparent. Aperture wide ovate; peristome weakly expanded; lip whitish or transparent. Columella straight, thickened and white. Umbilicus narrowly opened.

Radula

Each row contains about 105 (54-(3-5)-1-(3-5)-50) teeth. Central tooth small, unicuspid, with spatulo-truncated cusp. Lateral teeth bicuspid; endocone cylindrical, with wide notch; ectocone large, with truncated cusp. Marginal teeth tricuspid, starting around tooth number 3 to 5; endocone small, with sharp cusp; mesocone large, with truncated cusp; ectocone smallest. Outermost teeth with curved and pointed cusp of endocone; mesocone large, with curved cusp; ectocone of triangular shape, with pointed cusp (Fig. 7D–F).

Genital organs

Atrium (at) rather short (n = 10). Penis (p) short and conic-shaped. Epiphallus (e) long, slender and two times longer than penis. Flagellum (fl) short, about half length of epiphallus and terminated in folded

coil. Appendix very long, small tube extends from folded coil of flagellum, about three times as long as epiphallus. Penial retractor muscle (pr) short, thickened and inserted distally on penis. Vas deferens (vd) narrow tube connecting epiphallus and free oviduct (Fig. 6C).

Internal penial wall, proximal to genital orifice, corrugated into series of thick penial pilasters (pp) form fringe; distal to genital orifice smooth around penial verge. Penial verge (pv) small, conical and smooth-surfaced (Fig. 6D).

Vagina cylindrical, about four times as long as penis. Gametolytic duct very long, proximal to genital orifice large, coiled; distal to genital orifice tapering to small tube and connected to ovate gametolytic sac. Oviduct and albumin gland very small (Fig. 6C).

Internally, vaginal wall shows longitudinal vaginal pilasters (vp); proximal to genital orifice with smooth, thickened and continuous ridges, and distally pilasters thinner, with smooth ridges (Fig. 6D).

Distribution

This new species is currently known from the type locality only, a dry evergreen forest with limestone outcrops in the central part of Laos at Thakhek District, Khammouan Province.

Remarks

Two living snails were found during the aestivation period in a small tree hole a height of 5 m (Fig. 3D).

Subgenus *Syndromus* Pilsbry, 1900

Amphidromus (*Syndromus*) Pilsbry, 1900: 184.

Type species

Helix contraria Müller, 1774 by subsequent designation in Zilch (1960: 623).

Diagnosis

Shells mostly sinistral, conical to elongate conical and rather small (height 25 to 40 mm), varices absent and varying in color pattern. Genital characteristics show camaenid type with short epiphallus and flagellum, appendix absent, vaginal pouch and vaginal stimulator pilaster sometimes present. Radula teeth with spatulate shape.

The subgenus *Syndromus* was first nominated as “Sinistral Division” for *Amphidromus* with a relatively smaller sinistral coiling shell (Pilsbry 1900). Until now, the genital characters of the type species have never been examined; only Wiegmann (1894) briefly reported on the radular and jaw structures of the type species. To clarify the genitalia and radula characters of the subgenus, spirit preserved specimens in the Zoological Museum of Amsterdam (ZMA) collection were examined and are described below.

Amphidromus (*Syndromus*) *contrarius* (Müller, 1774)

Fig. 8A–B, E–G

Helix contraria Müller, 1774: 95. Type locality: Unknown.

Amphidromus contrarius – Wiegmann 1894: 208–210, pl. 15, figs 12–17. — Fulton 1896: 77– 8. — Pilsbry 1900: 210–212, pl. 65, figs 22–27. — Haniel 1921: 1–88, pls 1–5. — Zilch 1960: 623, fig. 2183. — Laidlaw & Solem 1961: 570, 612.

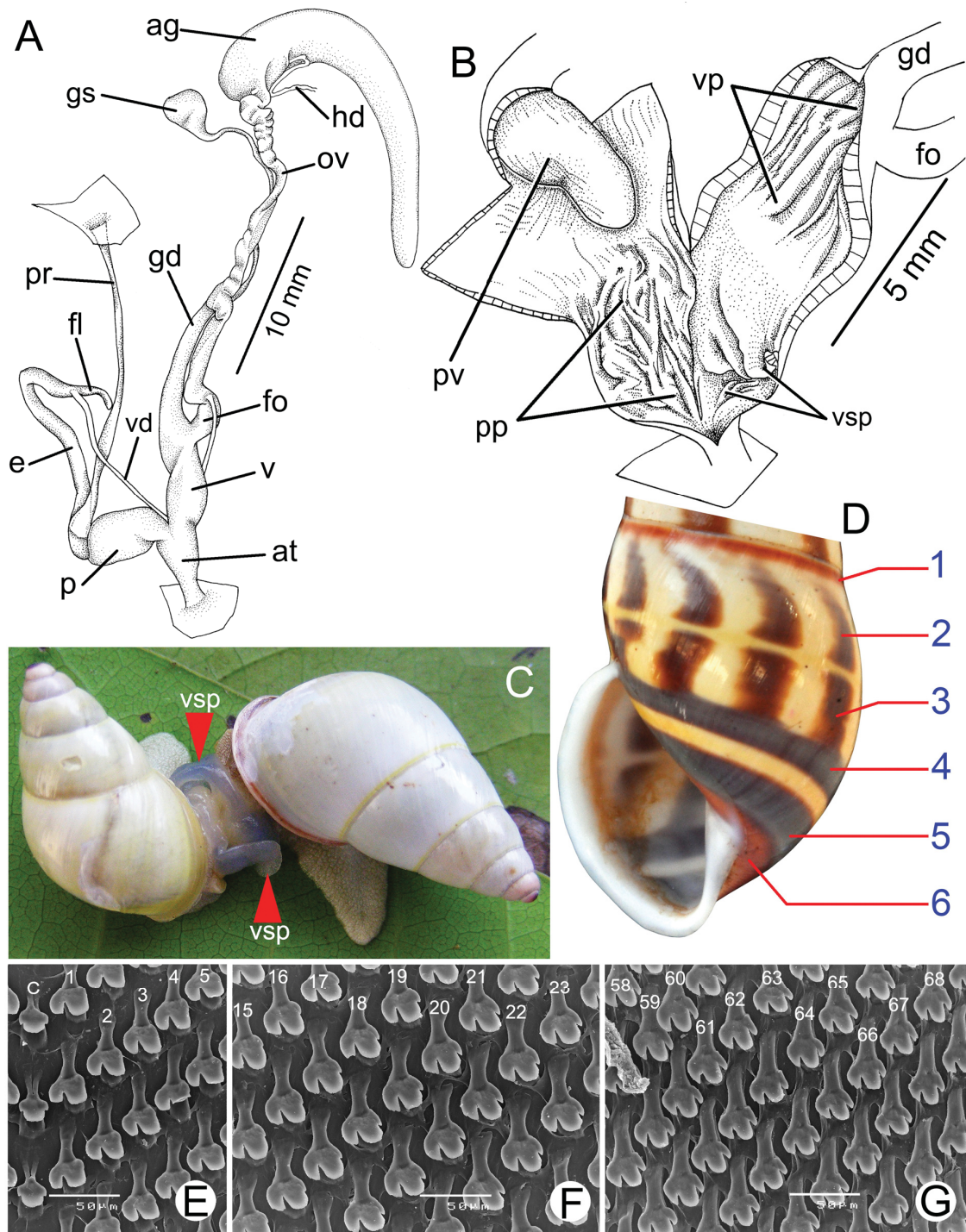


Fig. 8. Genitalia, mating pairs, shell banding formula and radula morphology. **A–B.** *Amphidromus (Syndromus) contrarius* (Müller, 1774) from Timor (ZMA). **A.** Genital system. **B.** Internal structures of penis and vagina. **C.** Mating pair of *Amphidromus (Syndromus)* sp., showing the protruded vaginal simulator pilaster (vsp, red arrows) and its possible function as a stimulating organ. **D.** Schematic drawing of shell banding, where the numbers 1 to 6 on the last whorl indicate the position of each band. **E–G.** Radula morphology of *Amphidromus (Syndromus) contrarius* (Müller, 1774) from Timor (ZMA). **E.** Central tooth, with the first to fifth lateral teeth. **F.** Lateral teeth with the tricuspid marginal teeth transition. **G.** Outermost marginal teeth. Numbers indicate the order of the lateral and marginal teeth. Central tooth indicated by ‘C’.

Material examined

INDONESIA: ZMA collection from Niki Niki, central Timor, collected by M.E. Walsh, Mar.–Apr. 1929 [Niki Niki, Central Amanuban District, South Timor Tengah Regency, East Nusa Tenggara Province, Indonesia].

Description

Shell

Shell morphology was completely described in Pilsbry (1900: 212–213).

Radula

Teeth arranged in V-shaped rows, each row contains about 170 (83-(11-14)-1-(12-14)-86) teeth. Central tooth unicuspid, with spatulate shape. Lateral teeth bicuspid, endocone small, ectocone large, with truncated cusps, gradually transformed to tricuspid marginal teeth from about tooth number 11 to 14 outwards. Marginal teeth tricuspid, endocone with curved shape, mesocone largest, with long and obtuse cusp, and ectocone smallest, with pointed cusp (Fig. 8E–G).

Genital organs

Atrium (at) long, conical ($n = 3$). Penis (p) short and swollen distally. Epiphallus (e) about two times as long as penis; flagellum (fl) very short and smaller than epiphallus. Appendix absent. Penial retractor muscle (pr) thin and long. Vas deferens (vd) narrow tube extending from end of epiphallus to free oviduct (Fig. 8A).

Internal penial wall, proximal to genital orifice, corrugated with obliquely penial pilasters (pp), forming fringe around penial verge; distal to genital orifice smooth. Penial verge (pv) enlarged, elongated, elliptical, with smooth surface (Fig. 8B).

Vagina (v) short, cylindrical, about same length as penis and proximal to genital orifice weakly swollen; vaginal pouch (vpo) present. Gametolytic duct (gd) long, cylindrical, almost same diameter as vagina; distally tapering to small tube and connected to spherical gametolytic sac (gs). Free oviduct (fo) short; oviduct (ov) and albumin gland very small (Fig. 8A).

Internally, vaginal wall possesses rather smooth longitudinal pilasters (vp); distally showing weak crenulation pilasters to smooth surface. Vaginal stimulator pilaster (vsp) located close to atrium, with swollen and curled shape (Fig. 8B–C).

Remarks

Approximately 45 species are currently recognized in this subgenus. Laidlaw & Solem (1961) divided those recognized species into six supraspecific groups based on geographic distribution. All of the Indochina forms (six species) were assembled into the *A. xiengensis* group (Group XIV). However, the members exhibit diverse shell color patterns. Their genital characters have not yet been described. Here, we attempt to clarify those described specific entities and color forms with distinct reproductive characters and shell banding pattern.

Most of the species of the subgenus *Syndromus* exhibit diverse shell banding, which can be characterized in terms of five banding systems. The definitions of those five bands and description of shell color forms follow the conventional procedures used in *Euhadra* (Pilsbry 1928), *Cepaea* (Cain & Sheppard 1950; Cain & Currey 1963), *Partula* (Murray & Clarke 1966), *Theba pisana* (see Cowie 1984) and *Satsuma* (Wu *et al.* 2008). The syndromid species complex maintains a polymorphic color pattern of varied width, shape and coloration. We simplify the banding pattern systems by modifying that outlined above

and dividing them into six sections or six banding systems (Fig. 8D), starting from the uppermost of the last whorl to the lowermost near the umbilicus. They are:

Band 1 (subsutural band) just below or in contact with the suture, usually thin and sometimes omitted in some species or populations.

Bands 2 and 3 (supra-peripheral bands) begin from below Band 1 to the posterior angle of aperture. These two bands are usually separated with a narrow gap in the middle. Band 2 is located just below Band 1, and Band 3 is placed above the posterior angle of the aperture. These two bands are usually modified as dotted, blotched or divided into several thinner bands.

Bands 4 and 5 (sub-peripheral bands) located below the posterior angle of the aperture or below the periphery of the umbilicus. These two bands are usually separated by a narrow to wide gap of ground color. Band 4 normally contacts the bottom of Band 3. Band 5 is located just around the umbilicus.

Band 6 usually covers the entire umbilical area between the umbilicus and Band 5.

Amphidromus (Syndromus) areolatus (Pfeiffer, 1861)

Figs 1, 7G–I, 9A, 10A–C, 11A–B; Table 1

Bulimus areolatus Pfeiffer, 1861a: 194. Type locality: Siam [Thailand]. Pfeiffer 1861b: 172, pl. 46, figs 11–12.

Amphidromus areolatus – Fulton 1896: 81. — Pilsbry 1900: 198–199, pl. 63, figs 85–86. — Laidlaw & Solem 1961: 564. — Solem 1965: 624–625, pl. 1, figs 4–7. — Sutcharit *et al.* 2015: 58, fig. 3j–k.

Material examined

Type material

THAILAND: Lectotype NHMUK 19601430 (Sutcharit *et al.* 2015: fig. 3j); paralectotype NHMUK 19601431 (1 shell).

Other material

LAOS: 20 shells (Fig. 10A–C, CUMZ 7022), 17 specimens in freezer (Figs 7G–I, 9A, 11A–B, CUMZ 7023), Thad Fek, Sammakeexay District, Attapeu; 8 shells, Thad Phasoam, Paksong District, Champasak (CUMZ 7024).

Description

Shell sinistral, elongate conical, rather small, thin and glossy. Spire conical; apex acute, with black spot on tip. Whorls 5 to 6 slightly convex; suture depressed; last whorl rounded. Periostracum transparent to thin corneous. Last whorl process, with yellow to absent Band 1; Bands 2 to 4 (sometimes Bands 2 to 5) usually merge and become brownish slanted blotches with flame shape; Band 6 yellowish or roseate. Parietal callus thin and transparent. Aperture auriform; peristome expanded to weakly expanded; lip white to transparent. Columella straight and white. Umbilicus narrowly opened.

Radula

Teeth arranged in V-shaped rows, each row contains about 126 (62-(13-9)-1-(9-13)-63) teeth. Central tooth tricuspid, with triangular shaped mesocone, ectocones very small, with pointed cusp. Lateral teeth bicuspid, endocone small, with curved cusp; ectocone large, with truncate or curved cusps, gradually transformed to tricuspid marginal teeth. Tricuspid marginal teeth start around tooth number 9 to 13 outwards; endocone curve shaped; mesocone of largest size, with long and obtuse cusp; ectocone

smallest, with pointed cusp. Outermost teeth with small serrated endocone and extocone; mesocone large, with curved cusps (Fig. 7G–I).

Genital organs

Atrium (at) rather long (n = 10). Penis (p) long, cylindrical and enlarged. Epiphallus (e) short, of about same length as penis; flagellum (fl) short and terminated in pointed tip. Appendix absent. Penial retractor muscle (pr) thin and relatively long. Vas deferens (vd) narrow tube connecting epiphallus and free oviduct (Fig. 11A).

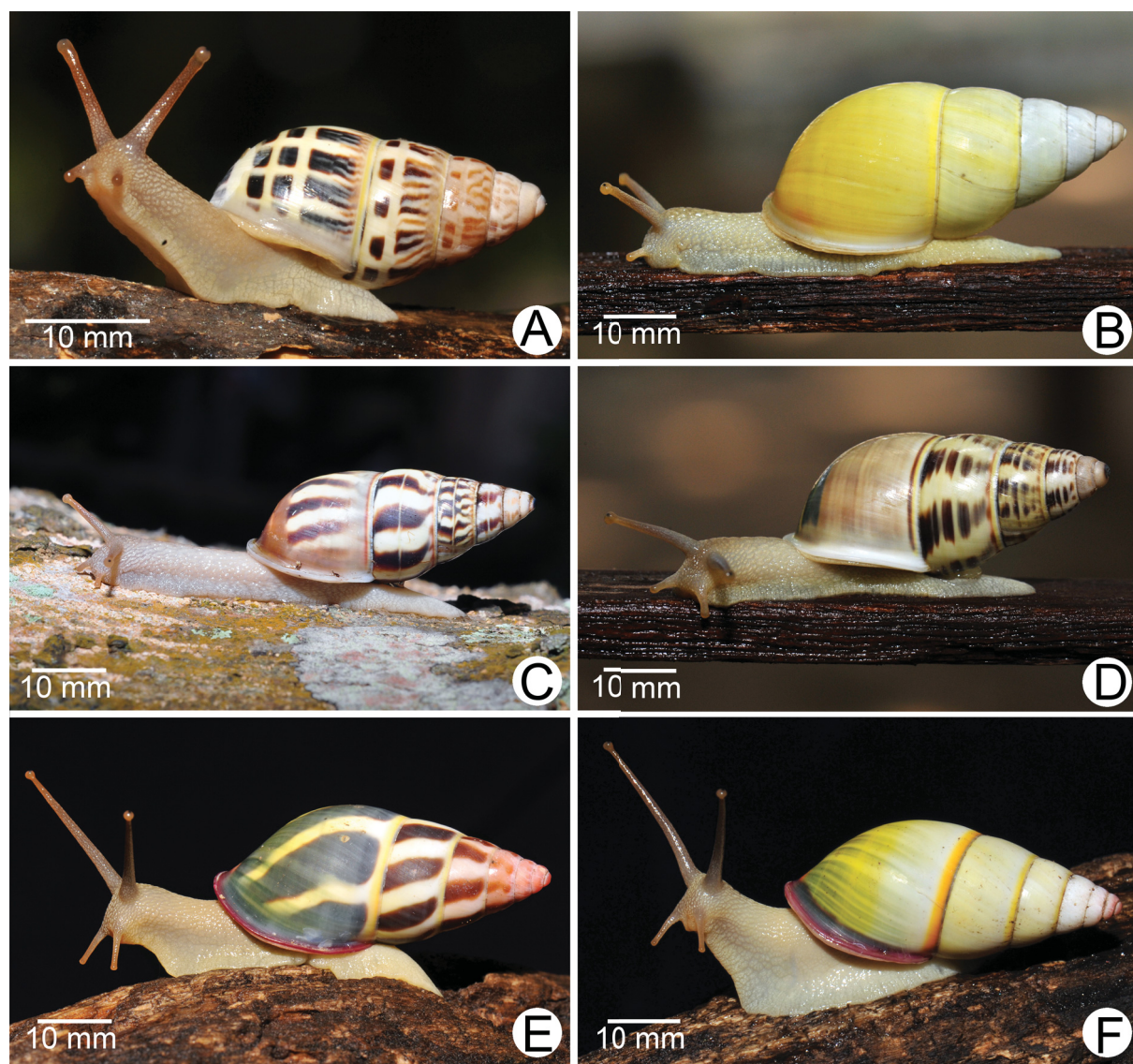


Fig. 9. Living snails of *Amphidromus* (*Syndromus*) spp. **A.** *Amphidromus areolatus* (Pfeiffer, 1861) from Thad Fek, Attapeu, Laos (CUMZ 7023). **B.** *Amphidromus flavus* (Pfeiffer, 1861) from Ban Na Deay, Luang Phrabang, Laos (CUMZ 7027). **C–D.** *Amphidromus xiengensis* Morlet, 1891 from Thad Kacham, Luang Phrabang, Laos (CUMZ 7035), the typical form, and var. “*multifasciata*” Fulton, 1896, respectively. **E–F.** *Amphidromus fuscolabris* Möllendorff, 1898 from Ban Phone, Sekong, Laos (CUMZ 7041–7042). **E.** Typical color form. **F.** Monochrome yellowish color form.

Internal penial wall nearly smooth and corrugated into thin penial pilasters, which form fringe around penial verge. Penial verge rather small, conical, with smooth surface (Fig. 11B).

Vagina cylindrical, of about same length as penis. Gametolytic duct long, proximal to genital orifice, of larger diameter than vagina and coiled; distal to genital orifice tapering to small tube of about same length as proximal part and connected to gametolytic sac. Oviduct and albumin gland very small (Fig. 11A).

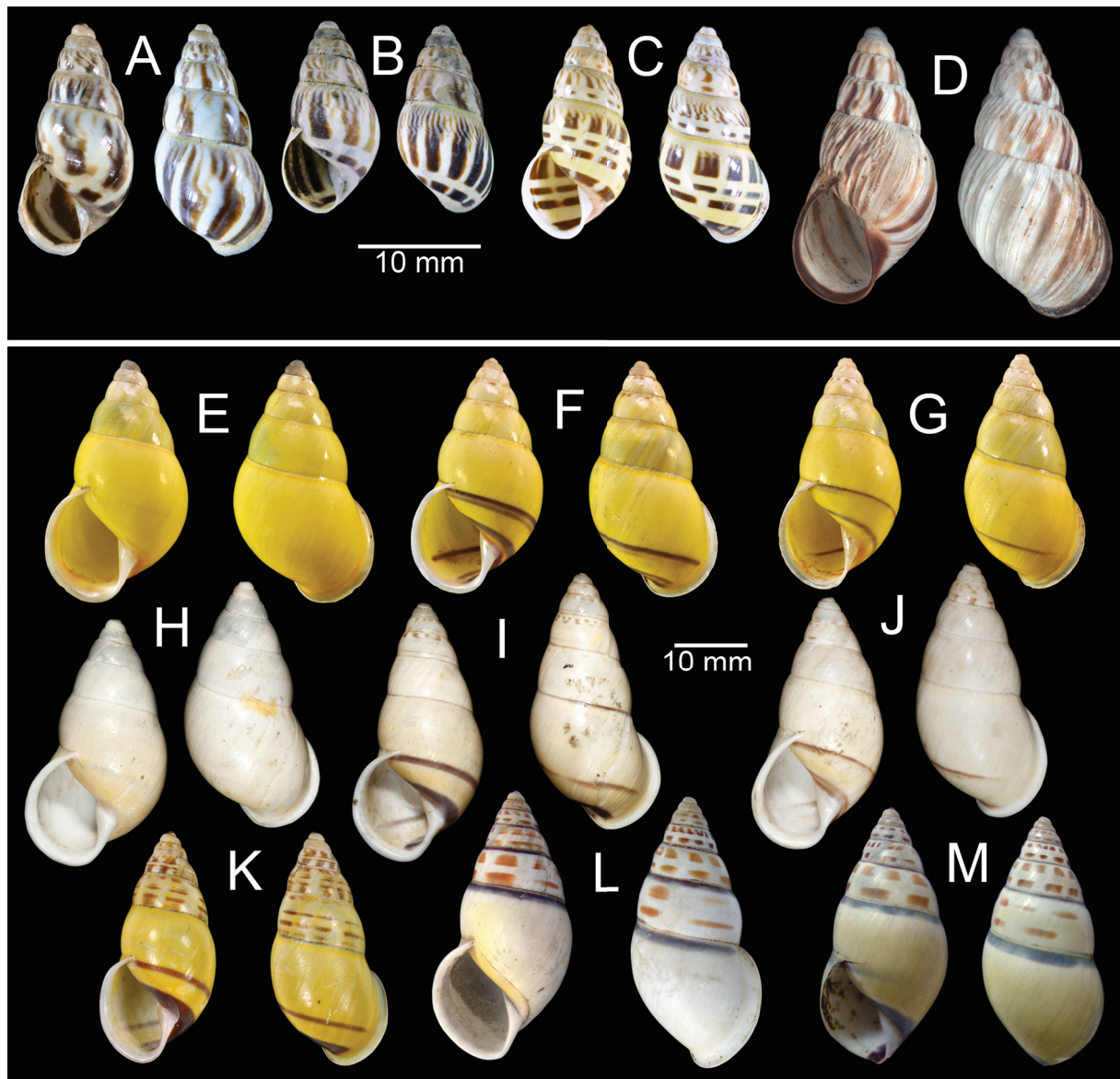


Fig. 10. Shells of *Amphidromus* (*Syndromus*) spp. **A–C.** *Amphidromus areolatus* (Pfeiffer, 1861) from Thad Fek, Attapeu, Laos (CUMZ 7022). **D.** *Amphidromus begini* (Morlet, 1886), syntype from Strung-Trang, Cambodia (MNHN-IM-2000-1832). **E–G.** *Amphidromus flavus* (Pfeiffer, 1861) from Tam Pou Kham, Vientiane, Laos (CUMZ 7029). **H.** *Amphidromus flavus* var. “*indistinctus*” Pilsbry, 1900, holotype (ANSP 31486). **I–K.** *Amphidromus flavus* var. “*tryoni*” Pilsbry, 1900. **I.** Lectotype (ANSP 31488). **J.** Paralectotype (ANSP 252745). **K.** Specimen from Ban Na Deauy, Luang Phrabang, Laos (CUMZ 7026). **L–M.** *Amphidromus semitessellatus* (Morlet, 1884). **L.** Lectotype (MNHN-IM-2000-1985). **M.** Specimen from Cambodia (NHMUK).

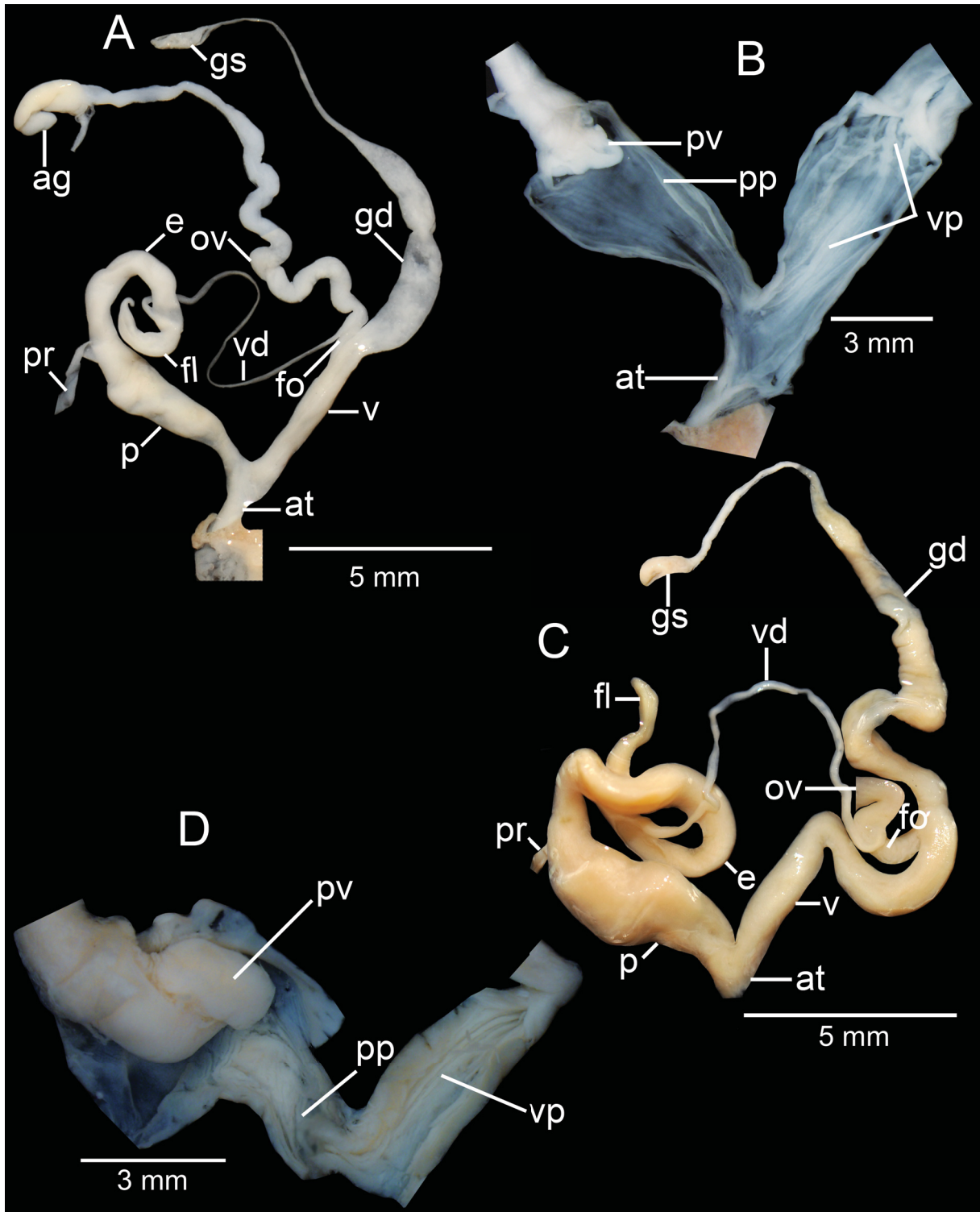


Fig. 11. Genitalia of *Amphidromus (Syndromus)* spp. **A–B.** *Amphidromus areolatus* (Pfeiffer, 1861) from Thad Fek, Attapeu, Laos showing the reproductive system and interior structures of the penis and vaginal chamber (CUMZ 7023). **C–D.** *Amphidromus flavus* (Pfeiffer, 1861) from Ban Na Deauy, Luang Phrabang, Laos showing the general characteristics of the genital system and the interior structures of the penis, atrium and vagina chamber (CUMZ 7027).

Internal wall of vagina shows longitudinal vaginal pilasters (vp); proximal to genital orifice with nearly smooth surface for about half of its length, distally pilasters become corrugated ridges (Fig. 11B).

Distribution

The species is known from southern Laos, where the specimens were collected at Thad Fek, Sammakeexay District, Attapue and Thad Phasoam, Paksong District, Champasak in a dry dipterocarp forest.

Remarks

This species can be distinguished from *A. zebrinus* (Pfeiffer, 1861) and *A. begini* (Morlet, 1886) by its having a smooth shell surface and brownish spiral Bands 4 and 5 present, with white lip. In contrast, *A. zebrinus* (see Sutcharit *et al.* 2015: fig. 15k) has an elongate conical shell shape, Band 1 absent, Bands 2 to 5 merged and developing slanted radial streaks, as well as a reddish band between Bands 5 and 6. *Amphidromus begini* exhibits strong radial ridges, Bands 2 to 6 merged and developing slanted brownish radial streaks, and brownish ribs (Fig. 10D, syntype MNHN-IM-2000-1832).

Amphidromus (Syndromus) flavus (Pfeiffer, 1861)

Figs 1, 9B, 10E–K, 11C–D, 12A–C; Table 1

Bulimus flavus Pfeiffer, 1861a: 194. Type locality: Siam [Thailand].

Amphidromus flavus var. *proxima* Fulton, 1896: 81, pl. 6, fig. 4. Type locality: Unknown. Sutcharit *et al.* 2015: 85, fig. 13c.

Amphidromus xiengensis var. *tryoni* Pilsbry, 1900: 196–197, pl. 63, fig. 78. Type locality: Laos Mountains, Cambodia.

Amphidromus sinensis var. *indistinctus* Pilsbry, 1900: 192, pl. 62, fig. 70. Type locality: Laos Mountains, Cambodia.

Bulimus flavus – Pfeiffer 1861b: 171, pl. 46, figs 7–8. — Morelet 1875: 265.

Amphidromus flavus – Fulton 1896: 81. — Ancey 1898: 134. — Pilsbry 1900: 197–198, pl. 63, figs 92–93. — Laidlaw & Solem 1961: 563–564, 619.

Amphidromus flavus var. *proximus* – Pilsbry, 1900: 198, pl. 63, fig. 94.

Amphidromus xiengensis var. *proxima* – Laidlaw & Solem 1961: 565, 652.

Material examined

Type material

THAILAND: Lectotype, NHMUK 19601436 (Sutcharit *et al.* 2015: fig. 7i); paralectotype, NHMUK 19601437 (1 shell).

UNKNOWN LOCALITY: Holotype of var. “*proxima*” Fulton, 1896, NHMUK 1896.6.13.48 (Sutcharit *et al.* 2015: fig. 13c).

CAMBODIA: Holotype of var. “*indistinctus*” Pilsbry, 1900, ANSP 31486 (Fig. 10H).

CAMBODIA: Lectotype of var. “*tryoni*” Pilsbry, 1900, ANSP 31488 (Fig. 10I); paralectotypes, ANSP 252745 (2 shells, Fig. 10J).

Other material

LAOS: 5 shells, park at the temple mountain, Luang Phrabang (NHMUK ex. Brandt collection No. 17320); 20 shells, Tempelberg (Temple Mount), Luang Phrabang (ZMB ex. Lehmann collection); 33 shells, Wat Phousy (temple), Luang Phrabang (CUMZ 7025); 3 shells (Fig. 10K, CUMZ 7026), 7 specimens, in ethanol (Figs 9B, 11C–D, 12A–C, CUMZ 7027), Ban Na Deauy, Luang Phrabang

District, Luang Phrabang; 5 shells, Mouhot's Tomb, E bank of Kan River, Luang Phrabang District, Luang Phrabang (CUMZ 7028); 16 shells (Fig. 10E–G), Tam Pou Kham, Vang Vieng District, Vientiane (CUMZ 7029).

Description

Shell sinistral, small, ovate conical, small, thin and glossy. Spire conical; apex acute yellowish, with black spot on tip. Whorls 5 and 6 convex; suture depressed; last whorl rounded to well rounded. Periostracum transparent to thin corneous. Last whorl processes uniform yellowish; Bands 1 to 3 usually absent; Bands 4 and 5 absent or present with indistinct bands; Band 6 usually absent or sometimes present as scanty reddish band. Parietal callus thin and transparent. Aperture ovate to sub-ovate; peristome weakly thickened and shortly expanded; lip whitish. Columella straight and white. Umbilicus opened to narrowly opened.

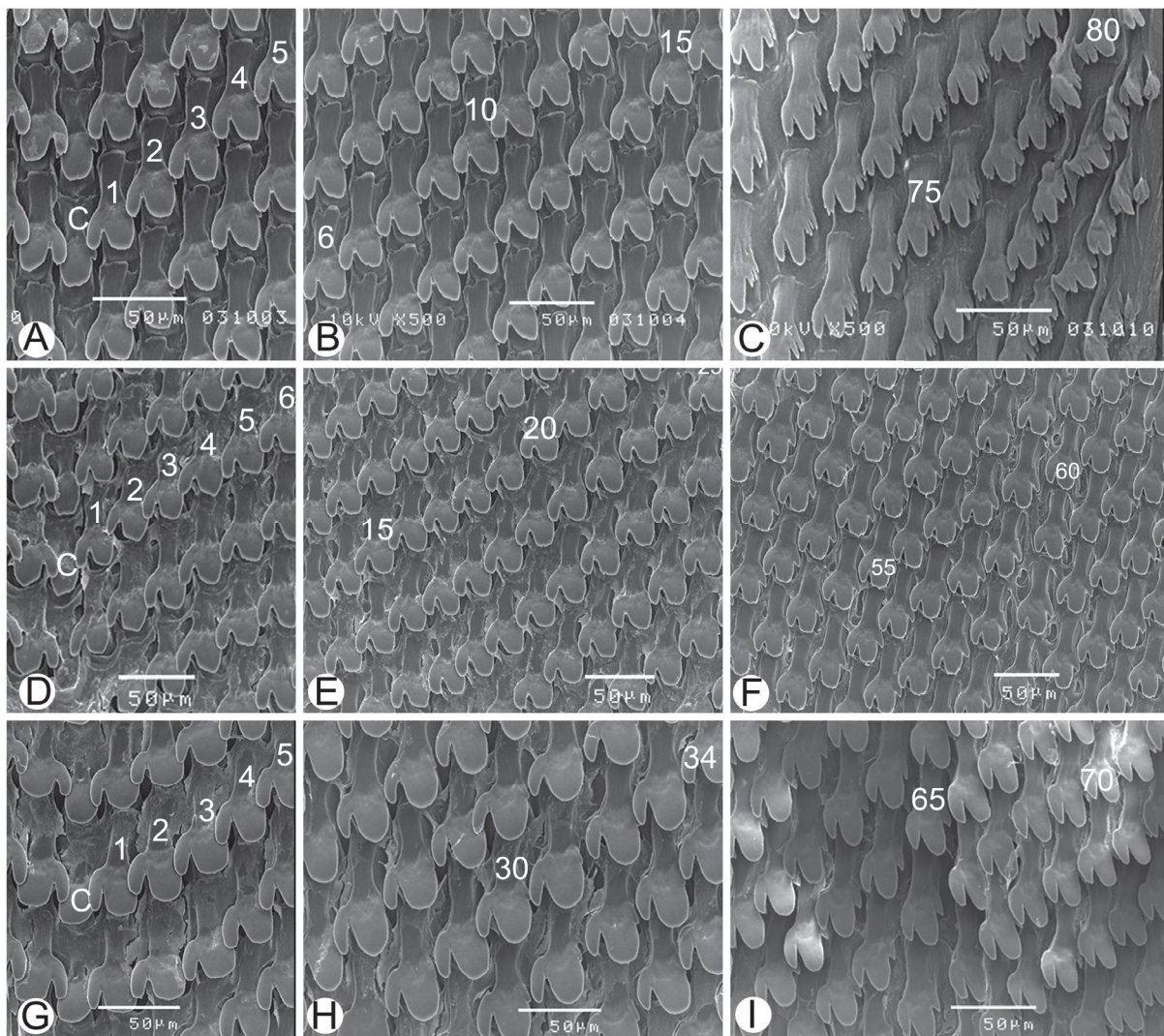


Fig. 12. SEM images of the radula. **A–C.** *Amphidromus flavus* (Pfeiffer, 1861) from Ban Na Deauy, Luang Phrabang, Laos (CUMZ 7027). **D–F.** *Amphidromus xiengensis* Morlet, 1891 from Ban Na Deauy, Luang Phrabang, Laos (CUMZ 7037). **G–I.** *Amphidromus fuscolabris* Möllendorff, 1898 from Ban Phone, Sekong, Laos (CUMZ 7041). A, D, G = central tooth with the first to fifth or sixth lateral teeth; B, E, H = lateral teeth with the tricuspid marginal teeth transition; C, F, I = outermost marginal teeth. Numbers indicate the order of the lateral and marginal teeth. Central tooth indicated by ‘C’.

Radula

Teeth arranged in V-shaped rows, each row contains about 166 (84-(7-10)-1-(8-12)-81) teeth. Central tooth tricuspid; mesocone of triangular shape; ectocones small, with pointed cusp. Lateral teeth tricuspid; endocone small and rounded cusps; mesocone large and truncated cusp; ectocone very small, pointed cusp and located at base of teeth. Lateral teeth gradually transformed to elongated marginal teeth. Marginal teeth tricuspid, start around tooth number 8 to 12; endocone elongate with dull cusps and separated from mesocone by wide notch; mesocone large, elongate and curved cusps; ectocone small, with pointed cusps or sometimes serrated shape (Fig. 12A–C).

Genital organs

Atrium (at) rather long ($n = 5$). Penis (p) long, cylindrical and enlarged from middle to end. Epiphallus (e) cylindrical, length longer than that of penis; flagellum (fl) short and one fourth as long as epiphallus; appendix absent. Penial retractor muscle (pr) thickened and relatively short. Vas deferens (vd) small tube, connecting epiphallus and free oviduct (Fig. 11C).

Internal penial wall corrugated into thin penial pilasters, which form fringe around penial verge. Penial verge conical, with smooth surface and orifice open near tip (Fig. 11D).

Vagina cylindrical, long, slender about two times as long as penis length. Gametolytic duct long, proximal to genital orifice almost same diameter as vagina, distally tapering; distal to genital orifice small tube of about same length as proximal part and connected to gametolytic sac. Oviduct and albumin gland small (Fig. 11C).

Internally, vaginal wall shows longitudinal vaginal pilasters (vp); pilasters very narrow and thin (Fig. 11D).

Distribution

The distribution range of the species is from Vientiane to Luang Phrabang Provinces.

Remarks

Amphidromus flavus differs from *A. sinensis* (Benson, 1851) in having a smaller shell, the spire more ovate and conical, with a single reddish band on the penultimate whorl. It can be distinguished from *A. xiengensis* in having a smaller shell, ovate conical, without any band on yellowish ground color or on shell sculpture. It differs from *A. globonevilli* Sutcharit & Panha, 2015 by having a larger shell size, and it is smaller than *A. principalis* Sutcharit & Panha, 2015. In comparison, *A. globonevilli* has an elongate conical shell and a faint yellow spiral band below the periphery, while *A. principalis* has a more elongate conical shell, last whorl without any band, aperture ovate. In our collection we found two types identified as *A. flavus* and *A. flavus* var. “*proxima*”, living sympatrically at Luang Phrabang and Vang Vieng.

Three subspecific entities have been proposed; however, we recognize them as a single biological species, *A. flavus*.

1. Typical form: monochrome yellowish shell and Bands 1 to 6 absent (Sutcharit *et al.* 2015: fig. 7i–j, for the lectotype and paralectotype).

2. var. “*proxima*” Fulton, 1896: monochrome yellowish shell, Bands 4 and 5 are indistinct pale brownish bands (Sutcharit *et al.* 2015: fig. 13c, for the holotype).

3. var. “*tryoni*” Pilsbry, 1900: Band 1 yellowish, Bands 2 and 3 absent, Bands 4 and 5 brownish and Band 6 absent. In some specimens, brownish blotches of Bands 2 and 3 present in the earlier whorls and disappeared in the penultimate and last whorls (Fig. 10I–K).

4. var. “*indistinctus*” Pilsbry, 1900: identical to var. “*proxima*” Fulton, 1896” (Fig. 10H).

***Amphidromus (Syndromus) roemeri* (Pfeiffer, 1863)**

Bulimus roemeri Pfeiffer, 1863a [1862]: 274, pl. 36, fig. 4. Type locality: Laos Mountains, Camboja [sic].

Amphidromus roemeri – Pfeiffer 1863b (1860–1866): 217, pl. 57, figs 10–11.— Fulton 1896: 80. — Pilsbry 1900: 192–193, pl. 63, figs 95–96. — Laidlaw & Solem 1961: 654. — Sutcharit *et al.* 2015: 87, fig. 13e–f.

Material examined

CAMBODIA: Lectotype, NHMUK 19601450 (Sutcharit *et al.* 2015: fig. 13e); paralectotype, NHMUK 19601451 (1 shell).

Remarks

The type specimens have recently been figured in Sutcharit *et al.* (2015: fig. 13e–f). The unique characters of this species are the sinistral, ovate conical shell; spire with a brownish color; last whorl well rounded. Shell whitish ground color, Bands 1 to 3 and 6 absent and Bands 4 and 5 perform reddish brown bands. Aperture ovate; peristome weakly expanded; lip white.

Amphidromus roemeri was described based on specimens collected by H. Mouhot with the type locality “Laos Mountains, Camboja”. This collection locality is a historical geographic name with an uncertain boundary. So far, this species is known only from the type specimens and an uncertain record from Laos by Laidlaw & Solem (1960: 654). However, no specimens were found in the present study; therefore the records from Laos still remain to be confirmed.

Laidlaw & Solem (1961) placed *A. roemeri* as a junior synonym of *A. sinensis* (Benson, 1851) from S China. We have examined the type specimens of both species and found that *A. roemeri* differs from *A. sinensis* by having an ovate conical, whitish shell, aperture ovate, spire short and conical, last whorl well rounded (see Sutcharit *et al.* 2015: fig. 13e–f). In contrast, *A. sinensis* (see Sutcharit *et al.* 2015: fig. 16g–i) has a yellowish shell, elongate conical spire, aperture auriform and the last whorl rounded. Furthermore, *A. globonevilli* differs by having a larger, spired conical, yellowish shell and an oblique aperture.

***Amphidromus (Syndromus) semitessellatus* (Morlet, 1884)**

Fig. 10L–M

Bulimus (Amphidromus) semitessellatus Morlet, 1884: 387, 388, pl. 11, figs 2, 2a. Type locality: “Les montagnes qui bordent le grand fleuve au delà de Stung-Treng. Les forêts et les montagnes de Kampot à Campong-Som” (Mountains along the great river behind Stung-Treng. Forests and mountains of Kampot and Sihanoukville Provinces, Cambodia).

Amphidromus semitessellatus – Morlet 1889: 128. — Fulton 1896: 87. — Pilsbry 1900: 194, pl. 60, figs 41–44. — Laidlaw & Solem 1961: 564. — Solem 1965: 625–626, pl. 2, fig. 2. — Richardson 1985: 43. *Bulimus (Amphidromus) semitessellatus* – Fischer-Piette 1950: 153.

Material examined

This species was described from specimens collected by A. Pavie from the L. Morlet collection. The original description includes an illustration of a single shell, one set of shell measurements, and a species description that may be based on one unknown specimen. There is a single specimen of L. Morlet in the MNHN collections, with an original label stating “Type”. Fischer-Piette (1950: 153) wrote the “holotype, 35 mm”, which we consider to be an inadvertent lectotype designation (ICZN 1999: Art.

74.5). Therefore, lectotype MNHN-IM-2000-1985 (Fig. 10L) was designated by Fischer-Piette (1950: 153) to stabilise the name.

CAMBODIA: 3 shells (RBINS Dautzenberg collection); 1 juvenile (Fig. 10M) (NHMUK).

Description

Shell sinistral, elongate conical, thickened and glossy. Spire conical; apex acute, with brown or black spot on tip. Whorls 6 to 7 slightly convex; suture depressed; last whorl rounded. Periostracum thin. Last whorl monochrome whitish, with black Band 1 and Bands 2 to 6 absent; spire with concurrent brownish blotches of Bands 2 and 3. Parietal callus thickened and transparent or white. Aperture sub-ovate; peristome rather thickened, expanded and weakly reflected; lip whitish. Columella thickened, perpendicular and white. Umbilicus narrowly opened to perforate.

Remarks

Previous records of this species were from the type locality in Stung Treng Province in the north and Kampot and Sihanoukville Provinces in the south of Cambodia, and later from Sraokeo Province, Thailand. Laidlaw & Solem (1961: 658) mentioned that the distribution range of this species was in Laos. However, no specimens were collected and, therefore, new records of this species in Laos are required to confirm its precise distribution.

Amphidromus semitessellatus can be distinguished from *A. flavus* and *A. xiengensis* by having a solid shell, with black Band 1, last whorl monochrome whitish, Bands 2 to 6 absent, and spire with concurrent brownish blotches of Bands 2 and 3. In comparison, *A. flavus* has a yellowish and thin shell, Bands 1 to 6 usually absent, but sometimes Bands 4 and 5 present and with scanty reddish Band 6. Meanwhile, *A. xiengensis* exhibits a yellowish ground color, thinner shell, reddish Band 1, Bands 2 and 3 with concurrent brownish slanted blotches, dark brown Bands 4 and 5, and yellowish or reddish Band 6.

Similar to the previous species, color variation occurs in this species in having concurrent brownish blotches of Bands 2 and 3 on the first half of the last whorl and blackish spiral Bands 4 and 5 present, but not continuing to the lip, and a black Band 6.

Amphidromus (Syndromus) xiengensis Morlet, 1891

Figs 1, 9C–D, 12D–F, 13A–H, 14A–B; Table 1

Amphidromus xiengensis Morlet, 1891a: 27. Type locality: “Xieng-Mai et les forêts des bords du Ménam Pinh, Laos occidental” (banks of Ping River, Chiang Mai Province, Thailand).

Amphidromus contrarius var. *multifasciata* Fulton, 1896: 78, pl. 7, fig. 5. Type locality: Cambodia.

Amphidromus xiengensis var. *clausus* Pilsbry, 1900: 195–196, pl. 63, figs 79–82. Type locality: Laos Mountain, Cambodia.

Amphidromus porcellanus var. *xiengensis* – Fulton 1896: 79.

Amphidromus xiengensis – Morlet 1891b: 232, 240–241, pl. 5, fig. 4. — Ancey 1898: 134. — Pilsbry 1900: 194–195, pl. 63, figs 75–76. — Fischer-Piette 1950: 159. — Laidlaw & Solem 1961: 564–565. — Solem 1965: 626–627, pl. 2, figs 7–13.

Amphidromus xiengensis var. *clausus* – Solem 1965: 626, pl. 2, figs 11–13.

Amphidromus xiengensis var. *multifasciatus* – Pilsbry 1900: 195, pl. 63, fig. 77. — Solem 1965: 626.

Material examined

The species was described based on material from Muséum (MNHN) ex. A. Pavie Collection and did not include an illustration. Morlet (1891b) subsequently re-published the description and illustrated a

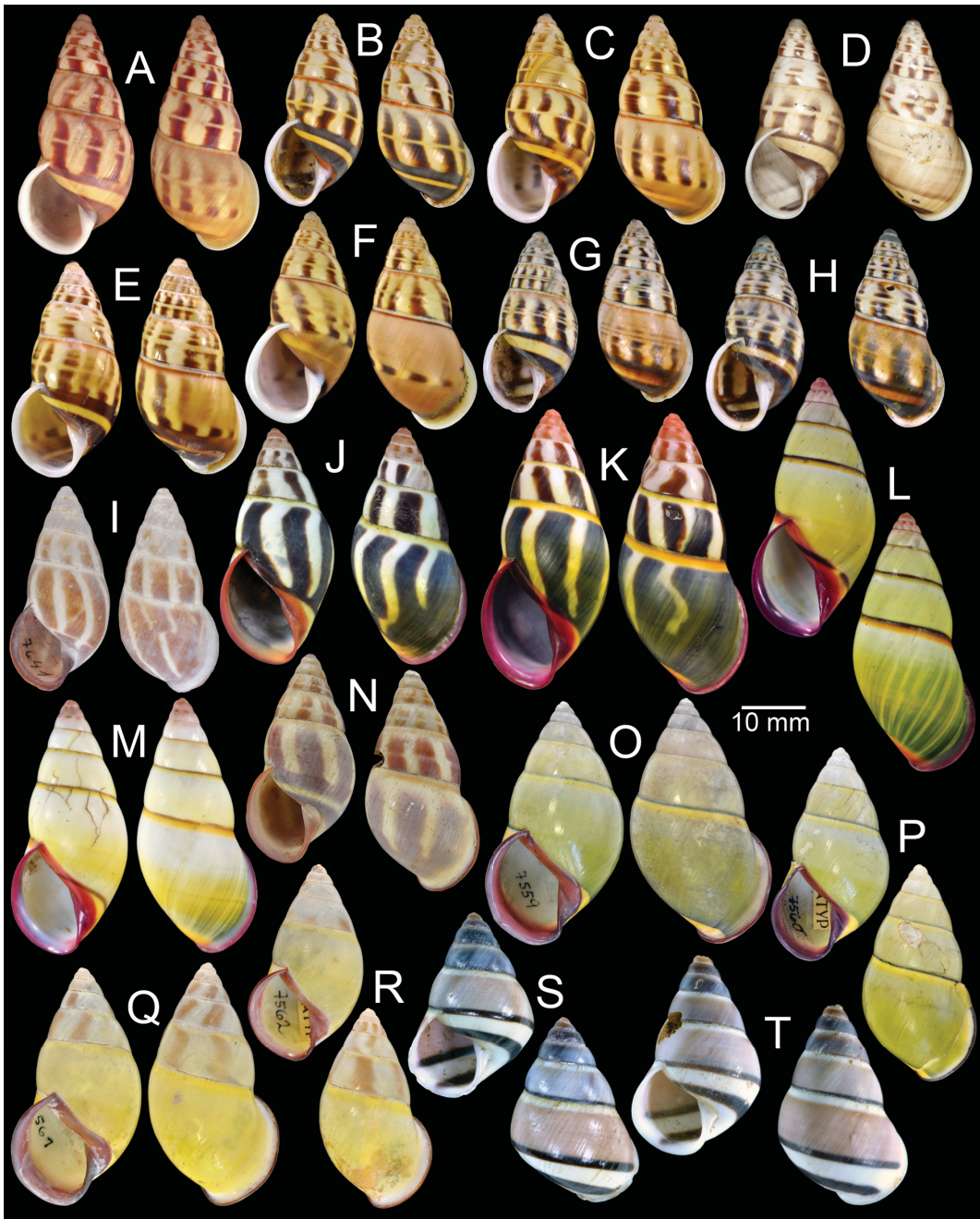


Fig. 13. Shells of *Amphidromus* (*Syndromus*) spp. **A–C.** *Amphidromus xiengensis* Morlet, 1891. **A.** Lectotype (MNHN-IM-2000-5249). **B.** Specimen from Thailand (CUMZ 7050). **C.** Specimen from Tam Chiang Dao, Chiangmai, Thailand (CUMZ 7034). **D–F.** *Amphidromus xiengensis* var. “*clausus*” Pilsbry, 1900. **D.** Lectotype (ANSP 31496). **E.** Specimen from Ban Na Deauy, Luang Phrabang, Laos (CUMZ 7036). **F.** Specimen from Pha Tang, Prayao, Thailand (CUMZ 7052). **G–H.** *Amphidromus xiengensis* var. “*multifasciata*” Fulton, 1896 from Phu Nang National Park, Phayao, Thailand (CUMZ 7038). **I–M.** *Amphidromus fuscolabris* Möllendorff, 1898. **I.** Holotype (SMF 7641). **J–M.** Specimens from Ban Phon, Sekong, Laos (CUMZ 7041–7042). **N.** *Amphidromus eudeli* Ancy, 1897, syntype from Binh Dinh, Annam (RBINS 617427). **O–P.** *Amphidromus haematostoma* Möllendorff, 1898. **O.** Lectotype (SMF 7559). **P.** Paralectotype (SMF 7560). **Q–R.** *Amphidromus haematostoma* var. “*varians*” Möllendorff, 1898. **Q.** Lectotype (SMF 7561). **R.** Paralectotype (SMF 7562). **S–T.** *Amphidromus xiengkhaungensis* sp. nov. **S.** Holotype (CUMZ 7045). **T.** Paratype (CUMZ 7046).

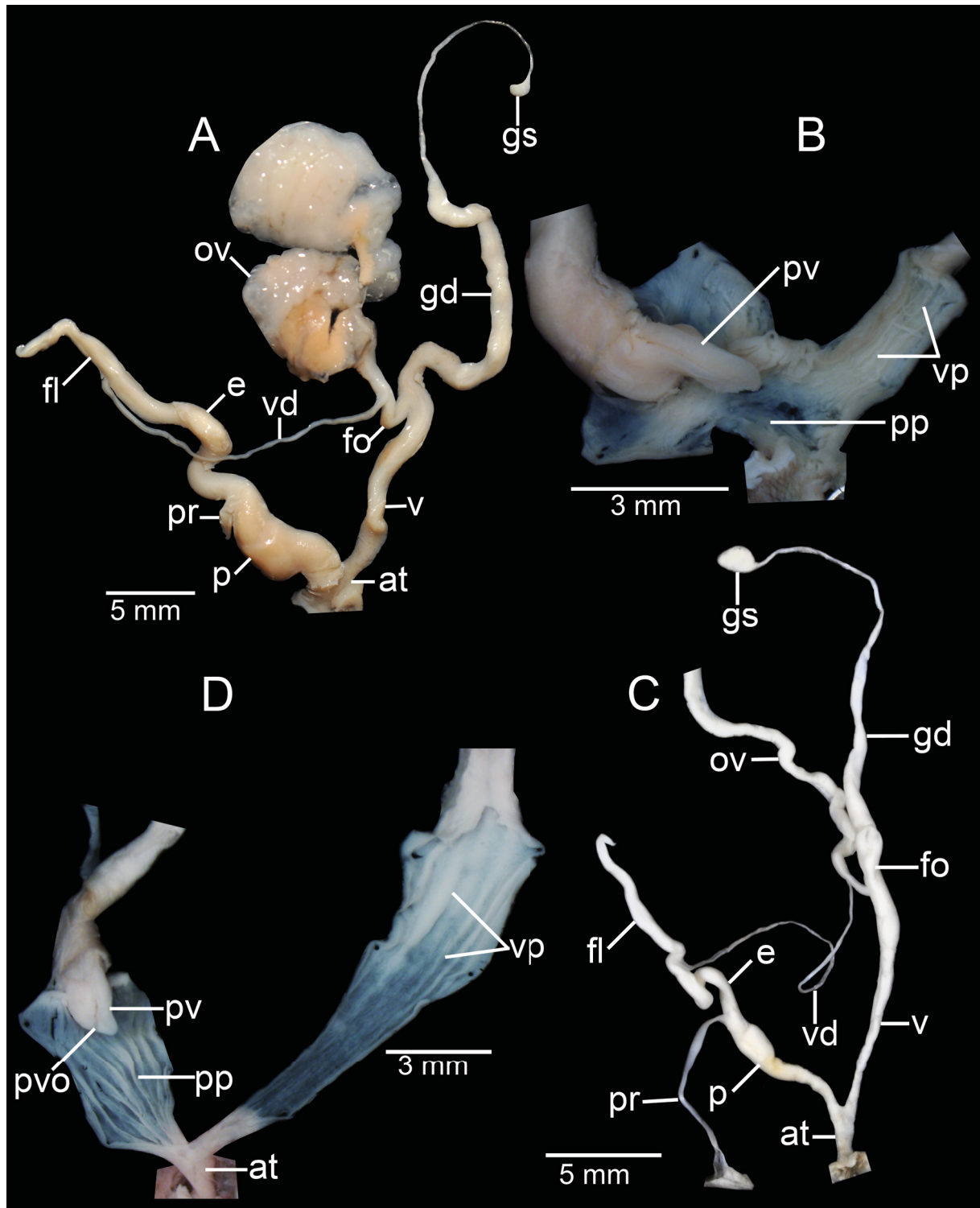


Fig. 14. Genitalia of *Amphidromus (Syndromus)* spp. **A–B.** *Amphidromus xiengensis* Morlet, 1891 from Luang Phrabang showing the reproductive system and interior structures of the penis and vaginal chamber (CUMZ 7035). **C–D.** *Amphidromus fuscolabris* Möllendorff, 1898 from Ban Phone, Sekong, Laos showing the general characteristics of the genital system and the interior structures of the penis, atrium and vaginal chamber (CUMZ 7041).

single specimen. There is a single specimen of *L. Morlet* in the MNHN collection with an original label stating “Type”. Fischer-Piette (1950: 159) wrote the “holotype, 38 mm”, which we consider to be an inadvertent lectotype designation (ICZN 1999: Art. 74.5). Therefore, lectotype MNHN-IM-130306224 (Fig. 8A) was designated by Fischer-Piette (1950: 153) to stabilise the name.

Type material

CAMBODIA: lectotype of var. “*multifasciata*” Fulton, 1896, NHMUK 19601458 (Sutcharit *et al.* 2015: fig. 11f); paralectotypes, NHMUK 19601459 (2 shells).

CAMBODIA: lectotype of var. “*clausus*” Pilsbry, 1900, ANSP 31496 (Fig. 11D); paralectotypes, ANSP 252752 (2 shells).

Other material

LAOS: 1 shell, Xieng-Moi (W Laos) (NHMUK 1893.12.8.40, ex. Dautzenberg collection); 32 shells, Ban Phon Pai, Bachieng District, Champasak (CUMZ 7030); 9 shells, Thad Phasoam, Boloven Plateau, Paksong District, Champasak (CUMZ 7031); 6 shells, Ban Oudom, Pakbeng District, Oudomxay (CUMZ 7032); 7 shells, Mouhot’s Tomb, E bank of Kan River, Luang Phrabang District, Luang Phrabang (CUMZ 7033); 2 specimens, in ethanol (Figs 9C–D, 14A–B), Thad Kacham Waterfall, Luang Phrabang District, Luang Phrabang (CUMZ 7035); 4 shells (Fig. 13E, CUMZ 7036), 2 specimens, in ethanol (Fig. 12D–F, CUMZ 7037), Ban Na Deauy, Luang Phrabang District, Luang Phrabang; 1 specimen, in ethanol, Thad Khaungsy Waterfall, Luang Phrabang District, Luang Phrabang (CUMZ 7039).

CAMBODIA: 1 shell, Dautzenberg collection (RBINS); 3 shells, Lao Moutains (NHMUK 19601539, ex. Cuming Collection).

THAILAND: 1 shell (Fig. 13B, CUMZ 7050); 1 shell (Fig. 13C), Tam Chiang Dao, Chiang Dao District, Chiang Mai (CUMZ 7034); 1 shell (Fig. 13F), Pha Tang, Pong District, Prayao (CUMZ 7052); 3 shells (Fig. 13G–H), Doi Phou Nang National Park, Chiangmouan District, Phayao (CUMZ 7038).

Description

Shell sinistral, conical to elongate conical, rather thick and glossy. Spire conical; apex acute with brown or black spot on tip. Whorls 6 to 7 slightly convex; suture depressed; last whorl rounded. Periostracum thin and corneous. Last whorl with reddish to brown Band 1; Bands 2 and 3 as concurrent slanted brownish blotches continuous to expanded lip; Bands 4 and 5 with brownish spiral bands; Band 6 absent or yellowish to reddish. Parietal callus transparent or weakly thickened and white. Aperture sub-ovate; peristome rather thick and expanded; lip whitish. Columella thickened, perpendicular and white. Umbilicus narrowly opened to perforated.

Radula

Each row contains about 157 (79-(21-17)-1-(17-21)-77) teeth. Central tooth monocuspid, with spatulate shape. Lateral teeth bicuspid; endocone with elongate shape, curved cusp and separated from truncated or curved cusps of ectocone by wide notch, teeth gradually transformed to tricuspid marginal teeth. Marginal teeth tricuspid starting around teeth number 17 to 21 outwards; endocone curved and pointed cusps; mesocone large, with truncate or obtuse cusps; ectocone small, of triangular shape, with pointed cusp. Outermost teeth with pointed cusps on endocone; mesocone large, with curved cusps; ectocone sometimes with serrated shape (Fig. 12D–F).

Genital organs

Atrium (at) somewhat short (n = 5). Penis (p) long, cylindrical and enlarged at middle. Epiphallus (e) cylindrical, two times as long as penis; flagellum (fl) short, one third as long as epiphallus; appendix

absent. Penial retractor muscle (pr) thickened and relatively short. Vas deferens (vd) small tube, connecting epiphallus and free oviduct (Fig. 14A).

Internal penial wall corrugated into weak penial pilasters, which form fringe around penial verge. Penial verge conical, rough surface and orifice open near tip (Fig. 14B).

Vagina cylindrical, long, slender, about 1.5 times as long as penis. Gametolytic duct long, proximal to genital orifice of same diameter as vagina and distally tapering; distal to genital orifice very small tube of about same length as proximal part and connected to gametolytic sac. Oviduct and albumin gland very large (Fig. 14A).

Internal wall of vagina shows longitudinal vaginal pilasters (vp); pilasters vary narrow and thin throughout vaginal length (Fig. 14B).

Distribution

The species is widely distributed and can be found in several habitats such as forests, fruit orchards and limestone areas between latitudes 14° and 16° N.

Remarks

Amphidromus xiengensis differs from *A. areolatus* and *A. zebrinus* in having a larger shell, reddish Band 1, concurrent slanted and brownish blotched Bands 2 and 3, and brownish spiral Bands 4 and 5. In contrast, the other two species have a smaller shell, Band 1 absent and Bands 2 and 3 merged and becoming brownish slanted blotches in *A. zebrinus* or brownish slanted blotches with a flame shape in *A. areolatus*. It differs from *A. eudeli* Ancey, 1897 (Fig. 13N, syntype RBINS 617427) and *A. fuscolabris* Möllendorff, 1898 (Fig. 13I, holotype SMF 7641) in having a white peristome, reddish Band 1, and Bands 2 and 3 usually separated. In comparison, *A. fuscolabris* shows a purplish-pink peristome, yellowish Band 1, Bands 2 to 5 merged and roseated Band 6, while *A. eudeli* exhibits a brownish lip, yellow color Band 1 and Bands 2 and 3 usually merged.

Two subspecific entities have been proposed; we, however, recognize them as a single biological species, *A. xiengensis*.

1. Typical form: Band 1 reddish to brownish; Bands 2 and 3 concurrent slanted brownish blotches continuous to expanded lip; Bands 4 and 5 brownish spiral band; Band 6 absent (Fig. 13A–C).

2. var. “*multifasciata*” Fulton, 1896: similar to the typical form, but Band 1 yellowish; Bands 2 and 3 usually divided into several smaller bands; Band 6 reddish (Fig. 13G–H; Sutcharit *et al.* 2015: fig. 11f–g).

3. var. “*clausus*” Pilsbry, 1900: similar to the typical form and var. “*multifasciata*”, but Bands 2 and 3 have disappeared and turned to a pinkish stain on the second half of the last whorl (Fig. 13D–F).

Amphidromus (Syndromus) fuscolabris Möllendorff, 1898

Figs 1, 9E–F, 12G–I, 13J–M, 14C–D; Table 1

Amphidromus zebrinus fuscolabris Möllendorff, 1898: 75. Type locality: Boloven (Boloven Plateau, Paksong District, Champasak, Laos).

Amphidromus zebrinus fuscolabris – Pilsbry 1900: 199–200. — Zilch 1953: 134, pl. 23, fig. 22. — Laidlaw & Solem 1961: 564, 621. — Richardson 1985: 49.

Material examined

Type material

LAOS: holotype SMF 7641 (Fig. 13I).

Other material

LAOS: 34 shells, typical form (Fig. 13J–K, CUMZ 7040); 2 specimens, in ethanol (Figs 9E, 12G–I, 14C–D, CUMZ 7041); 73 + 10 juveniles, yellowish form (Fig. 13L–M, CUMZ 7042); 2 specimens, in ethanol (Fig. 9F, CUMZ 7043), Ban Phone, La-Marm District, Sekong; 2 shells, Ban Xai Na Pho, Phatumphone, Champasak (CUMZ 7044).

Description

Shell sinistral, elongate conical, rather solid and glossy. Spire elongate conical; apex acute, with pinkish tint to brownish without black spot on tip. Whorls 6 to 7 nearly smooth; suture wide and shallow; last whorl rounded. Periostracum transparent to thin corneous, with greenish streaks on lower half of last whorl. Last whorl shows yellow to orange Band 1; Bands 2 to 5 merged and become six or seven black or brown slanted blotches; Band 6 yellow; varix absent. Parietal callus thickened, bright purplish-pink. Aperture elongated auriform; peristome thickened, expanded and not reflected; lip purplish-pink. Columella rather thick, straight, dilated and purplish-pink. Umbilicus imperforated.

Radula

Each row contains about 161 (80-(35-31)-1-(31-35)-80) teeth. Central tooth unicuspid, with curved cusp. Lateral and marginal teeth similar to that described in *A. areolatus*. Marginal teeth start from lateral tooth 17 to 21 outwards (Fig. 12G–I).

Genital organs

Atrium (at) rather long ($n = 10$). Penis (p) long, cylindrical and slightly swollen at distal end. Epiphallus (e) short, half of penis length; flagellum (fl) of about same length as epiphallus and terminated with pointed tip. Appendix absent. Penial retractor muscle (pr) thin and long. Vas deferens (vd) very narrow tube connecting epiphallus and free oviduct (Fig. 14C).

Internal penial wall corrugated into strong penial pilasters, which form fringe around penial verge. Penial verge conical, with smooth surface and orifice open near tip (Fig. 14D).

Vagina cylindrical, long, slender, about two times as long as penis. Gametolytic duct long, proximal to genital orifice of a relatively larger diameter than vagina and distally tapering; distal to genital orifice small tube of about same length as proximal part and connected to gametolytic sac. Oviduct and albumin gland very small (Fig. 14C).

Internally, vaginal wall shows longitudinal vaginal pilasters (vp); proximal to genital orifice with thin wall and smooth surface, distally pilasters show continuous ridges (Fig. 14D).

Distribution

The original description of this species was given by Möllendorff (1898) and the type locality was Boloven, Laos. Unfortunately, we couldn't obtain any specimen from the type locality in our recent survey. The specimens were collected from a mountain at Ban Phone (Phone village), Sekong Province, and Ban Xai Na Pho (Xai Na Pho village) Phatumphone, Champasak, Laos, which are both located at a lower altitude than the Boloven Plateau. It seems that this species is only found in low altitude habitats.

Remarks

Amphidromus fuscolabris differs from *A. zebrinus* and *A. eudeli* in having a large and elongate shell, apex tinted pink, purplish-pink parietal callus, Band 1 yellowish and Bands 2 to 5 merged and becoming 6 to 7 slanted blotches (on last whorl). In comparison, *A. zebrinus* (see Sutcharit *et al.* 2015: fig. 15k) has a smaller shell, Band 1 absent, Bands 2 and 5 merged and becoming fifteen narrow slanted stripes on last whorl, and reddish band in between Bands 5 and 6. On the other hand, *A. eudeli* (Fig. 13N, holotype RBINS 617427) has a smaller shell, thin parietal callus, Bands 2 and 3 merged and Bands 4 and 5 well developed.

Two color forms were observed from Sekong, Laos. These are the typical form (Fig. 13I–K) and the yellowish form that is monochrome yellowish, with Bands 2 to 5 absent and stained with pale yellowish color, and Band 6 sometimes present as a brownish color (Fig. 13L–M). However, these two color forms show a pinkish to purplish-pink parietal callus and columella, and have identical genital structures and sculptures inside the penis and vagina. In addition, they occur sympatrically and so we recognize them as conspecific.

Amphidromus (Syndromus) haematostoma Möllendorff, 1898

Figs 1, 13O–R

Amphidromus haematostoma Möllendorff, 1898: 74–75. Type locality: Boloven (Boloven Plateau, Champasak, Laos).

Amphidromus haematostoma var. *viridis* Möllendorff, 1898: 75. Type locality: Boloven (Boloven Plateau, Champasak, Laos).

Amphidromus haematostoma var. *varians* Möllendorff, 1898: 75. Type locality: Boloven (Boloven Plateau, Champasak, Laos).

Amphidromus haematostoma – Pilsbry 1900: 182–183. — Zilch 1953: 132. — Laidlaw & Solem 1961: 527, 625. — Richardson 1985: 19.

Amphidromus haematostoma var. *viridis* – Pilsbry 1900: 183. — Zilch 1953: 132, pl. 22, fig. 4. — Laidlaw & Solem 1961: 527, 670. — Richardson 1985: 19.

Amphidromus haematostoma var. *varians* – Pilsbry 1900: 183. — Zilch 1953: 132, pl. 22, fig. 5. — Laidlaw & Solem 1961: 527, 668. — Richardson 1985: 19.

Amphidromus (Syndromus) haematostomus – Lehmann & Maassen 2004: 20.

Material examined

Type material

The species description included two varieties, “var. *A. viridis*” and “var. *B. varians*”, but only one set of shell measurements was given in the original description, of the nominotypical variety. The specimen SMF 7559, labelled as “var. *A. viridis*”, exactly matches the dimensions given in the original description. Therefore, we believe this implied that the specimens of “var. *A. viridis*” pertain to the type series of *A. haematostomus* s.s. The specimen SMF 7559 (Fig. 13O) was designated as the lectotype in Zilch (1953: 132, pl. 22, fig. 4), which is considered to be a valid lectotype designation of the species, and the other specimen from the same lot becomes the paralectotype SMF 5760 (1 shell; Fig. 13P).

The other specimens labeled as “var. *B. varians*” are distinct variants and are, therefore, excluded from the type series of this nominal species (ICZN 1999: Art. 72.4.1). The specimen SMF 7561 (Fig. 13Q) was designated as the lectotype in Zilch (1953: 132, pl. 22, fig. 5), which is considered to be a valid lectotype designation of “var. *B. varians*”. Another specimen from the same lot became the paralectotype, SMF 5762 (1 shell; Fig. 13R).

Other material

LAOS: 6 + 2 juveniles, Boloven Plateau, Pakxong District, Champasak (RMNH 101050); two lots in W.J.M. Maassen Collection (8S) and (12+2 juveniles); 1 shell, Boloven, Annam (NHMUK 1899.4.22.74); 15 shells (ZMB, ex. Lehmann Collection), 5 + 1 juvenile (ZMB, ex. Lehmann Collection), in coffee plantation, near Pakxong, Boloven Plateau, Champasak.

Remarks

This species is currently known from the type locality only. The shell characters are clearly distinct from all other recognized species. The shell is sinistral and ovate conical. Then apex is acute, with a black spot on the tip. The last whorl is rounded; the color of the shell is a monochrome greenish (faded in old specimen), and there are a yellowish subsutural band and an umbilical area. Then aperture is ovate; the peristome expanded and weakly reflected; the lip is reddish-purple. The parietal callus is reddish-purple and thickened; the columella is also reddish-purple and dilated; the umbilicus imperforated.

Laidlaw & Solem (1961) suggested that this species was probably a junior synonym of *A. roseolabiatus*. However, after comparing the type specimens of both species and recently collected specimens of *A. roseolabiatus*, *A. haematostoma* clearly differs from it in having an ovate conical shape, uniform greenish to yellowish shell, yellowish subsutural and umbilical area, thickened parietal callus, lip widely expanded, and reddish-purple lip and parietal callus. Moreover, *A. roseolabiatus* exhibits an elongate conical shell, greenish radial streaks, white subsutural band, transparent parietal callus, and lip pinkish or white and expanded.

Lehmann & Maassen (2004: 20) recorded the genital characters (without illustration) of the topotypic population and mentioned that it had a “very short flagellum and a short conical verge”. These are the distinguishing characters of this subgenus. However, further investigation of the genitalia is necessary to confirm the subgeneric status.

Amphidromus (Syndromus) xiengkhaungensis Inkhavilay & Panha sp. nov.
[urn:lsid:zoobank.org:act:7BA4B989-3003-4F09-94E5-F21B392BEA28](https://zoobank.org/act:7BA4B989-3003-4F09-94E5-F21B392BEA28)

Figs 1, 13S–T; Table 1

Diagnosis

The new species is superficially similar to *A. roemeri*, but the distinguishing characters are a relatively large and thick shell, dark to brownish spire, Bands 2 and 3 merged and become tinted pink stained, with a pale tinted pink lip. In contrast, *A. roemeri* shows a relatively small and thin shell, whitish ground color, Bands 2 and 3 absent, and has a white lip. *Amphidromus xiengkhaungensis* sp. nov. differs from *A. sinensis* and *A. flavus* by having an ovated conic shell, Bands 2 and 3 stained with tinted pink, ovate aperture and slightly angular last whorl. In comparison, *A. sinensis* and *A. flavus* have an elongate conical, relatively small and thin shell, with a yellowish color and rounded last whorl. In addition, *A. globonevilli* differs from this new species by having a small and thin shell, with a yellowish color, last whorl rounded and Bands 2 and 3 absent.

Etymology

The specific epithet ‘*xiengkhaungensis*’ refers to the type locality of the new species.

Type material

Holotype

LAOS: shell height 25.6 mm, shell width 15.6 mm, with 6 whorls (CUMZ 7045, Fig. 13S).

Paratypes

LAOS: 10S shells (CUMZ 7046, Fig. 13T); 2S shells (NHMUK).

Type locality

LAOS: limestone outcrop at Ban Nong Tang, Phou Kood District, Xieng Khaung, 19°30'59.2" N, 102°53'37.6" E, 1140 m amsl.

Description

Shell sinistral, ovate conical, rather thick and glossy. Apex acute, color tinted pink; spire conical with dark color; suture wide and depressed. Whorls 5 and 6 nearly smooth; last whorl slightly angular. Periostracum thin, corneous and transparent. Earlier whorls with darker color; varix absent. Shell banding without Band 1; Bands 2 and 3 merged and becoming tinted pink stained; Bands 4 and 5 dark brown; Band 6 absent. Parietal callus thin and transparent to slightly thick and white. Aperture ovate; peristome expanded and weakly thickened; lip pale tinted pink to white. Columella straight, thickend and white. Umbilicus narrowly opened.

Remarks

Amphidromus xiengkhaungensis sp. nov. is currently known from the type locality only, a dry green forest and isolated limestone forest surrounded by a reservoir and agricultural areas. The empty shells were found on the floor among the leaf litter. Unfortunately, no living specimens have been collected.

Discussion

The first species of *Amphidromus* from Laos, *A. roemeri*, was described by Pfeiffer (1863a). Subsequently, *A. xiengensis*, *A. laosianus* and *A. haematostoma* were reported by Morlet (1891), Bavay (1898) and Möllendorff (1898), and the latest described species was *A. protania* by Lehmann & Maassen (2004), collected from Ban Donxé, Salavan Province. However, there are many species for which basic information is still unclear, such as the type locality for, e.g., *A. roemeri*, where the author stated only “Laos Mountains” as the locality. Almost all records were from southern areas or lowlands, except for *A. xiengensis*, which was recorded in the north (Fig. 1).

In this paper we describe two new species, both known from their type localities only. *Amphidromus syndromoideus* sp. nov. has a small shell size, dextral and sinistral, green color with long epiphallus and flagellum, and very long appendix. *Amphidromus xiengkhaungensis* sp. nov. is described based on shells only. The shell is superficially similar to that of *A. roemeri*, but it is larger and thicker, with a dark to brown spire. Moreover, the two recorded species *Amphidromus xiengensis* and *A. flavus* were described here using shells and genital anatomy.

In the southern part of Laos we collected the four species *A. givenchyi*, *A. fuscolabris*, *A. areolatus* and *A. xiengensis*. The most dominant species were *A. givenchyi*, *A. fuscolabris* and *A. areolatus*, which could be found between the altitudes of 140 and 190 m amsl. Only two species were collected in the central region of Laos, *A. roseolabiatus* and *A. syndromoideus* sp. nov., with the most dominant species being *A. roseolabiatus*. In the northern part of Laos we collected five species of *Amphidromus*; surprisingly *A. roseolabiatus* and *A. xiengensis* were found in both southern and northern Laos, but *A. flavus*, *A. pervariabilis* and *A. xiengkhaungensis* sp. nov. were only found in northern Laos, from Vang Viang to Phongsaly.

Amphidromus roseolabiatus and *A. xiengensis* were the most dominant and widely distributed species throughout Laos. They can be found in several habitats, even in limestone areas from the south to the north. However, *A. givenchyi*, *A. syndromoideus* sp. nov. and *A. xiengkhaungensis* sp. nov. were specific to their unique habitats, whereas *A. givenchyi* was restricted to the Salavan Province (southern Laos). *Amphidromus syndromoideus* sp. nov. is found at the type locality, Khammouan Province (central Laos),

only and *A. xiengkhaungensis* sp. nov. is rare and only found in an isolated limestone area at Nong Tang Village, Xieng Khaung Province, which is between the northern and central border at 800 m amsl.

The occurrence of *A. roseolabiatius* and *A. xiengensis* in the southern, central and northern parts of Laos may suggest (i) they originally had a widespread origin, (ii) one or both have been translocated by humans or (iii) they have been subjected to long range dispersal. These hypotheses await to be resolved.

The results show that the diversity of the species of *Amphidromus* in Laos is low compared to that in Thailand (Panha 1996; Sutcharit *et al.* 2015) and Vietnam (Schileyko 2011), where 19 and 23 species are known, respectively. However, this may simply reflect a collecting bias, having been spent less survey time and a smaller number of sites in Laos having been sampled compared to the other two countries, rather than demonstrating the actual species diversity. Thus, more extensive (intensity and coverage) sampling is required.

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