

CHAPTER IV

TAXONOMIC REVIEW OF THE TREE SNAIL *AMPHIDROMUS* ALBERS, 1850 (PULMONATA: CAMAENIDAE) IN THAILAND: I. SUBGENUS *AMPHIDROMUS*

4.1 Introduction

Amphidromus Albers, 1850, is one of the largest groups of colourful tree dwelling snails which have radiated in the Southeast Asian region. It has a distribution demarcated in the north by the Himalayas and in the east by Weber's Line (Solem, 1959; Laidlaw and Solem, 1961), with a single species occurring in Northern Australia (Solem, 1983). Within the overall limits of its total geographical range *Amphidromus* occupies discrete, more restricted areas, as do other camaenids such as the papuinids of New Guinea, helicostylids of the Philippines and the camaenid genus *Beddomea* in southern peninsular India and Sri Lanka (Pilsbry, 1901; Gude, 1914; Solem, 1959; Laidlaw and Solem, 1961). The majority of species are known only from shell characters. Features of the internal anatomy have been described for a few species, and have been used in some instances for developing hypotheses on systematic relationships (Semper, 1874; Jacobi, 1895; Collinge, 1901; 1902; Bishop, 1977; Solem, 1983).

Amphidromus has been placed in the family Camaenidae on the basis that it lacks vaginal accessory organs, possesses a penis that is continuous with the epiphallus and epiphallic caecum (flagellum and appendix), and exhibits an unbranched gametolytic duct (Pilsbry, 1900; Thiele, 1931; Benthem Jutting, 1950; Richardson, 1985). Currently 86 species (Laidlaw and Solem, 1961; Richardson, 1985; Dhrama, 1993; Panha, 1996) in two distinct subgenera (sections in Pilsbry, 1900) and one dubious subgenus are recognized. The nominate *Amphidromus* (*Amphidromus*) has a rather large shell, exhibits dimorphic shell coiling, and has a long epiphallic caecum. *Amphidromus* (*Syndromus*) Pilsbry, 1900, possesses a smaller, more slender shell, and has a shorter epiphallic caecum. The two species of *Amphidromus* (*Goniodromus*) Bülow, 1905 are poorly known and *Goniodromus* has doubtful subgeneric status (Haas, 1934; Laidlaw and Solem, 1961). Sutcharit *et al.* (2004) provided a molecular phylogeny of some *Amphidromus* species from Thailand and nearby countries which supports subgeneric status for *Amphidromus* (*Amphidromus*) and *Amphidromus* (*Syndromus*).

Most species of *Amphidromus* were described in the nineteenth century (Gould, 1844; Pfeiffer, 1860, 1862; Crosse and Fischer, 1863, 1864; Möllendorff, 1894) and descriptions were based mainly on shell characters

such as shape and colour pattern. After the peak of descriptive taxonomy in the nineteenth century, descriptions of new taxa and systematic reviews based on shell morphology accumulated at a much lower rate (Fulton, 1901; Geret, 1912; Bartsch, 1917; 1918; 1919; Benthem Jutting, 1950; Dharma, 1993). Fulton (1896), Pilsbry (1900) and Laidlaw and Solem (1961) provided detailed taxonomic revisions, but outstanding problems with morphological variation remained. Pilsbry (1900) reported 34 species of *Amphidromus* (*Amphidromus*), whereas the later analysis of Laidlaw and Solem (1961) recognized only 19 distinct species and placed several nominal species in an unresolved species complex. With few exceptions (Semper, 1874; Jacobi, 1895), prior to 1900 *Amphidromus* descriptions provided no more than measurements of height, breadth and whorl number for an individual shell. A few papers such as those of Collinge (1901, 1902) provided basic descriptions and figures of reproductive anatomy. Bishop (1977) and Solem (1983) provided evidence that features of the reproductive system supply valuable information for recognizing *Amphidromus* species.

In the present paper we revise Thai *Amphidromus* species from recent collections deposited in Chulalongkorn University's Museum of Zoology. We have concentrated on the morphology of the genitalia and radula of the poorly known species *A. (A.) perversus natunensis*, *A. (A.) inversus*, *A. (A.) atricallosus*, *A. (A.) schomburgki* and *A. (A.) givenchy*, which were previously known only from their shells, and we provide the description of two new subspecies.

4.2 Systematic Accounts

Camaenidae Albers, 1850

Genus *Amphidromus* Albers, 1850

Diagnosis: Shell moderately large (25 to 70 mm height), smooth, conic or elongate conic; dextral or sinistral, glossy and generally yellow. Usually from 6 to 8 moderately convex whorls with or without varix. Aperture oblique or ovate. Peristome thickened, expanded and/or reflected. Columella simple straight or twisted. Radula spatulate, usually with moncuspid central tooth and bicuspid or tricuspid lateral teeth. Genitalia typical of camaenids with a short or long epiphallic caecum (flagellum and appendix). Cross-section of spermatophore pentagonal. Genus entirely arboreal.

Key to Subgenera of *Amphidromus*

- 1a. Shell large, height usually greater than 35 mm and h/d ratio less than 1.85. Shell smooth, with a variable colour pattern, usually yellow or greenish; epiphallus and flagellum long; appendix usually present..... *Amphidromus*
- 1b. Shell small, height usually less than 35 mm and h/d ratio greater than 1.85; epiphallus and flagellum short; appendix absent..... *Syndromus*

Amphidromus (Amphidromus) Albers, 1850

Type species: By subsequent designation of *Helix perversus* Linnaeus, 1758.

Diagnosis: Shell height 35 to 70 mm, dimorphic coiling and one or more varices usually present. Genitalia of characteristic camaenid type with long epiphallic caecum.

Remarks: von Martens (1860) recognized two groups within *Amphidromus* the second being formally recognized by Pilsbry (1900) as *Amphidromus (Syndromus)*. *Amphidromus (Amphidromus)* was used by Pilsbry (1900) to indicate shells that possess a varix and dimorphic shell and *Amphidromus (Syndromus)* was applied to the smaller, thinner sinistral shells, without varix. Zilch (1960) subsequently defined the type species of both subgenera.

Fulton (1896) and Pilsbry (1900) arranged *Amphidromus* into 19 informal species groups according to their supposed affinities. Laidlaw and Solem (1961) developed this arrangement into 20 informal groups based on apparent morphological similarity and on geographic distribution. A formal nomenclature was not adopted for all these provisional groupings and they referred to Groups I through VI as "*Amphidromus*, base stock"; Groups VII to XIII as "*Amphidromus s. str.*"; Groups XIV to XIX as "*Syndromus*"; and Group XX as "*Goniodromus*".

To date, 19 species are included in *Amphidromus (Amphidromus)* (Laidlaw and Solem, 1961). The distribution of *Amphidromus (Amphidromus)* extends from mainland Southeast Asia to Sulawesi, the Lesser Sunda Islands and the southern Philippines. The genital morphology included in the papers of Jacobi (1895), Collinge (1901; 1902), Bishop (1977), and Solem (1983) indicated, but failed to clearly demonstrate that the epiphallic caecum of *Amphidromus (Amphidromus)* tended to be longer than *Amphidromus (Syndromus)*.

Amphidromus has been considered to be closely related to *Beddomea* Nevill, 1878 and *Pseudopartula* Pfeiffer, 1855, two camaenid genera with a similar shell shape, some shared genital structures, radula and tree-dwelling habit (Pilsbry, 1901; Rensch, 1930; Laidlaw and Solem, 1961). Gude (1903b,

1914), Thiele (1931) and Butot (1955) placed both *Beddomea* and *Pseudopartula* as subgenera within *Amphidromus* but this has not been followed widely by subsequent workers. *Beddomea* differs from *Amphidromus* in the right ocular retractor muscle passing to the right of the genitalia (not between both branches) and the radula tooth being greater in length than its breadth (Pilsbry, 1901). *Pseudopartula* differs from *Amphidromus* in possessing a smaller shell and lacking both an epiphallic caecum and distinct epiphallus; the penis is slender; the gametolytic sac extremely long (Butot, 1955).

Key to Species and Subspecies of *Amphidromus* (*Amphidromus*)

- 1a. Shell yellowish, whitish, greenish or purplish colour..... 2
- 1b. Shell brown or radially streaked..... 5
- 2a. Shell yellow or white, usually chirally dimorphic, occasional brown streak at lower periphery; peristome white..... 3
- 2b. Shell green or yellowish green, peristome white or purple..... 9
- 3a. Parietal callus white; whorls convex; straight or twisted columella..... 4
- 3b. Parietal callus black or brownish; whorls relatively flat; columella straight. Shell conic or elongate-conic..... 7
- 4a. Columella straight, monochrome yellowish, sometimes with brown streak at lower periphery. Lip reflected and adnate to last whorl.....
..... *A. (A.) perversus natunensis*
- 4b. Columella straight or twisted, monochrome yellow or white. Lip reflected and free..... 8
- 5a. Shell with irregular radial streaks, distinct brown spiral band present at lower periphery of last whorl. Penial appendix (ap) absent..... 6
- 5b. Shell with parallel radial streaks, brown spiral band absent. Long penial appendix (ap) present..... *A. (A.) atricallosus leucoxanthus* var. *laidlawi*
- 6a. Shell height 50 to 55 mm, usually chirally dimorphic. Spire slightly convex, pale brown or whitish..... *A. (A.) inversus inversus*
- 6b. Shell height 40 to 50 mm, usually dextral. Spire pink to brownish.....
..... *A. (A.) inversus annamiticus*
- 7a. Parietal callus black. Shell height 40 to 50 mm, conic and usually chirally dimorphic, yellow or white, penis long..... *A. (A.) atricallosus atricallosus*
- 7b. Parietal callus blackish. Shell height 35 to 40 mm, elongate-conic, always sinistral invariably yellow, and penis slightly short.
..... *A. (A.) atricallosus* ssp.
- 8a. Columella straight or twisted, monochrome yellow or white and one or more varices usually present..... *A. (A.) atricallosus leucoxanthus*

- 8b. Columella always twisted, monochrome yellow and varix absent.
 *A. (A.) atricallosus perakensis*
- 9a. Periostracum with irregular green streaks. Lip, columella, parietal callus
 and apex purple or white. 10
- 9b. Periostracum a uniform yellowish-green. Lip, columella, parietal callus and
 apex white. Last whorl with a dark green subsutural band.
 *A. (A.) givenchyi*
- 10a. Shell tinted pink or creamy, apex deep purple, peristome, columella and
 parietal callus purplish or brownish whitish.
 *A. (A.) schomburgki schomburgki*
- 10b. Shell, peristome, apex, columella and parietal callus whitish.
 *A. (A.) schomburgki* ssp.

Amphidromus (Amphidromus) perversus (Linnaeus, 1758)

Diagnosis: Shell oblong-ovate, relatively large, dextral or sinistral. Whorls flattened, umbilicus sealed or perforate, spire conic with wide and shallow suture. Apex white, brownish or dark purplish. Colour pattern slightly matted brownish with irregular brown to dark-brown radial streaks and a light brown subsutural band. Radial streaks are abruptly fused with a wide dark-brown spiral band below the periphery of the last whorl. One or more black to dark-brown varices present. Aperture oblique or lunate, with white internal lip; peristome thickened, expanded, reflected, folded and adnate to last whorl. Parietal callus whitish, thick to thin. Columella white, vertical and straight.

***Amphidromus (Amphidromus) perversus natunensis* Fulton, 1896**
 (Figures 4.1, 4.3A-B, 4.5, 4.6)

Amphidromus perversus var. *natunensis* Fulton, 1896: 69.

Amphidromus aureus var. *natunensis*—Pilsbry, 1900: 162-163, pl. 55, figs 87-90.

Amphidromus perversus natunensis—Laidlaw and Solem, 1961: 536-537, 643, fig. 19. Richardson, 1985: 36.

Material examined: Great Natuna Island, Indonesia: 2177 (4D).

Shell (Fig. 4.3A, B; Table 4.1): Shell large, solid, dimorphically coiled, umbilicus minute. Whorls slightly flattened, suture slightly depressed; spire short and conic, last whorl large. Colour variable, wide white subsutural band usually present. Apex acute, whitish. Aperture broad and ovate; peristome white, slightly thickened, folded, expanded, reflected and adnate to last whorl.

Parietal callus white or transparent; columella white, vertical and straight; one or more varices present.

Four examined specimens dextral; colour pattern variable with crowded irregular or ragged chestnut streaks that terminate before the suture. Some specimens yellowish with several oblique brown stripes and pale radial streaks in lower half of last whorl.

Radula (Fig. 4.5A-C): Teeth arranged in anteriorly pointed V-shaped rows, each row containing about 204 (101-(66-68)-1-(67-69)-102) teeth. Central tooth monocuspid and spatulate (Fig. 4.5A). Lateral teeth bicuspid, endocone small with truncated cusp, and ectocone large with curved cusp (Fig. 4.5A). From tooth 66 to 69 outwards (Fig. 4.5B) lateral teeth gradually transformed to tricuspid marginals. Marginal teeth asymmetric, endocone medium sized, mesocone large with curved margins and ectocone small (Fig. 4.5C).

Genital system (Fig. 4.6A-F): Atrium (at) relatively long (n=3). Penis (p) slender, short, distally enlarged and folded at penial verge base. Epiphallus (e) long, nearly straight and smaller in diameter. Flagellum (fl) almost the same length as epiphallus and distal portion forms a single coil. Appendix (ap), located beyond coiled portion of flagellum, half the length of flagellum. Vas deferens (vd) a narrow tube, extending from free oviduct (fo) to end of epiphallus. Penial retractor muscle (pr) relatively long, and inserts near distal end of penis (Fig. 4.6A).

Internal wall of penis corrugated, exhibiting a series of thickened and swollen longitudinal penial pilasters (pp), which form a fringe around fleshy penial verge. Penial verge (pv) short, conic, smooth with long penial verge orifice (pvo) (Fig. 4.6B). Internally flagellum possesses strong, folded epiphallic pilasters (ep) that taper to low protuberances near entrance of vas deferens (evd). Longitudinal pilasters overhang and obscure aperture of vas deferens where it enters flagellum (Fig. 4.6C).

The slender and cylindrical vagina (v) about twice the length of penis. A series of muscles originating from the base of foot insert on external wall of vagina. Gametolytic duct (gd) extends from vagina, long, proximally enlarged cylindrical tube, abruptly tapering to small tube distally, and terminally connected to gametolytic sac (gs). Free oviduct (fo) relatively short, oviduct (ov) compact and enlarged to form lobule alveoli. Prostate gland ventrally fused with oviduct. Albumen gland (ag) large, curved and lingulate (Fig. 4.6A). Hermaphroditic gland (hg) contracts from numerous small lobules to narrow and convoluted hermaphroditic duct (hd), which connects to middle of talon (ta) (Fig. 4.6D).

Internally vagina possesses longitudinal vaginal pilasters (vp). Proximal to genital orifice, pilasters smooth and continuous ridges; proximal to free oviduct and gametolytic duct (gd) they interrupted by transverse divisions (Fig. 4.6B).

Two spermatophores observed and examined. Each approximately 80 mm long, pentagonal in cross-section and with thin prominent keels, running the length of sperm sac at each angle (Fig. 4.6E). Each keel composed of a series of 33 to 35 oblong knobs (Fig. 4.6F). Anterior (sperm sac) straight and long, pentagonal in cross-section with distally coiled expanded section (ces). The end of coiled expanded section tapered, rounded and smooth (Fig. 4.6E). Sperm sac (ss) formed in epiphallus and flagellum, and coiled expanded section (ces) forms in coiled portion of flagellum and appendix.

Distribution (Fig. 4.1): This species is known only from Bunguran, Great Natuna Islands, Indonesia (Fulton, 1896; Pilsbry, 1900; Laidlaw and Solem, 1961). The specimens examined were collected from the Great Natuna Islands, Indonesia.

Remarks: The two spermatophores described for this species were from copulating pairs in which the coiled expanded section was retained in the donating male duct. The four preserved individuals remain pigmented with a black mantle cavity, white vessels, and brownish body.

Radula morphology and reproductive anatomy, including internal sculpture of penis and epiphallic caecum, are similar to that given for *A. (A.) perversus* var. *interruptus* (Müller, 1774) (Solem, 1983). Both show the long epiphallus, the flagellum consisting of a coiled portion as long as the blind appendix. However, in *A. (A.) perversus natunensis*, the hermaphroditic duct enters close to the middle of the talon, whereas in *A. (A.) perversus* var. *interruptus* it connects very near the head of the talon.

***Amphidromus (Amphidromus) inversus* (Müller, 1774)**

Diagnosis: Shell relatively large, oblong-ovate, with dextral or sinistral coiling. Whorls flattened, umbilicus imperforate or perforate, spire long and conic with wide, shallow suture. Apex white, brownish or dark purplish. Colour pattern slightly matted brown with irregular brown to dark brown radial streaks and a light brown subsutural band. The radial streaks run to a wide dark brown spiral band below the periphery of the last whorl. One or more black to dark brown varices present. Aperture oblique or lunate; lip white; peristome thickened, expanded and reflected. Parietal callus whitish, thick to thin. Columella white, straight and vertical.

Table 4.1. Shell size variation in *A. (A.) perversus natunensis* and *A. (A.) atricallosus*. Catalogue numbers of specimens are indicated in parentheses.

Species, Locality and CUMZ nos.	Number of adult shell examined	Ranges, Mean \pm SD in mm of:			Whorl Ranges
		Shell Height	Shell Width	h/d Ratio	
<i>A. (A.) perversus natunensis</i> Fulton, 1896					
Natuna Island, Indonesia (2177)	4	41.19-49.60 46.12 \pm 3.89	24.46-27.77 26.08 \pm 1.77	1.68-1.82 1.77 \pm 0.06	6 ³ / ₈ - 6 ⁵ / ₈
<i>A. (A.) atricallosus atricallosus</i> (Gould, 1843)					
Ban Takun, Suratthani (2061, 2093, 2094, 2114, 2124, 2129, 2153)	199	32.01-46.98 40.11 \pm 2.92	20.11-26.48 23.69 \pm 1.28	1.41-1.91 1.69 \pm 0.08	6 ¹ / ₈ - 7 ³ / ₈
Khao Sok, Suratthani (2025, 2026)	101	39.82-51.78 45.34 \pm 2.44	21.97-27.86 25.31 \pm 1.22	1.66-1.97 1.81 \pm 0.07	6 ⁴ / ₈ - 7 ⁵ / ₈
<i>A. (A.) atricallosus leucoxanthus</i> (von Martens, 1864)					
Khao Kiew, Chonburi (2041, 2043)	244	34.34-54.41 43.03 \pm 2.49	22.95-29.49 25.75 \pm 1.23	1.48-2.02 1.67 \pm 0.07	6 ¹ / ₈ - 7 ² / ₈
Khao Soidao, Chantaburi (2096, 2116, 2227)	30	45.65-53.94 49.33 \pm 2.05	24.45-28.55 27.00 \pm 1.07	1.69-2.03 1.83 \pm 0.08	6 ⁴ / ₈ - 7 ⁴ / ₈
Plieu waterfall, Chantaburi (2039, 2042, 2090, 2100, 2101, 2103, 2104, 2154, 2155, 2157)	562	34.20-53.50 45.52 \pm 2.56	20.87-29.41 25.91 \pm 1.21	1.35-2.00 1.76 \pm 0.08	6 - 7 ⁵ / ₈
Makhm District, Chantaburi (2231)	88	35.83-50.44 44.18 \pm 2.90	22.80-27.98 25.35 \pm 1.10	1.49-1.98 1.74 \pm 0.09	6 ² / ₈ - 7 ⁵ / ₈
Makok waterfall, Chantaburi (2059, 2145)	122	40.82-51.60 46.09 \pm 2.16	23.39-28.98 26.14 \pm 1.17	1.54-1.99 1.77 \pm 0.08	6 ⁵ / ₈ - 7 ⁶ / ₈
<i>A. (A.) atricallosus perakensis</i> Fulton, 1901					
Nee Soon, Singapore (2067, 2133, 2198)	5	43.32-48.02 46.33 \pm 1.84	25.84-28.06 26.74 \pm 0.81	1.68-1.79 1.73 \pm 0.04	6 ⁴ / ₈ - 7
<i>A. (A.) atricallosus</i> ssp.					
Koh Tachai, Pangnga (2011, 2013, 2014, 2232, 2233)	23	35.24-43.93 38.33 \pm 2.04	19.82-22.59 21.28 \pm 0.72	1.68-1.99 1.80 \pm 0.07	6 ² / ₈ - 7 ¹ / ₈

External features: Living animals brown to brownish and usually covered with light brown to creamy reticulated skin. Unlike in *A. (A.) perversus natunensis* and *A. (A.) atricallosus*, mantle edge brownish to dark brown, and mantle cavity creamy or unpigmented. Foot broad and greyish with a brownish margin. Eye tentacles drumstick shaped, dark brown at base, becoming lighter with black eye spots on the tips. Head, mouth and lower tentacles dark brown to blackish.

Distribution: *Amphidromus (A.) inversus* was recorded from several localities in Vietnam, Thailand, Peninsular Malaysia, Borneo, Sumatra and the Celebes (Pilsbry, 1900; Laidlaw and Solem, 1961; Solem, 1965). There are no records for Java or the Philippine Islands. The closely related *A. (A.) javanicus* (Sowerby, 1841) and *A. (A.) heerianus* (Pfeiffer, 1871) occur in Java (Laidlaw and Solem, 1961). In the present study, specimens were collected from several islands in both eastern and southern Thailand and from Singapore and Sumatra.

Remarks: Populations in which all individuals were dextral, were found in many islands in the Gulf of Thailand *i.e.* Koh Samet, Koh Samaesan and Koh Samui. *Amphidromus (A.) inversus* is the most widely distributed and one of the most morphologically variable species of *Amphidromus* and the status of all of the different forms has not been established. Based on limited information Laidlaw and Solem (1961) recognised three subspecies. *Amphidromus (A.) inversus inversus* ranging from Sumatra and the islands in the Java Sea to the southern tip of the Malaysian peninsula. *Amphidromus (A.) inversus annamiticus* (Crosse and Fischer 1863), from Annam in Vietnam, the Lower Mekong Valley of Cambodia and east to southern Thailand. There are apparently no *Amphidromus* in the Andaman Island. *Amphidromus (A.) inversus andamensis* (Pfeiffer, 1871) has been found in Sarawak, North Borneo and Natuna Island (Pilsbry, 1900). *Amphidromus (A.) inversus andamensis* has a smaller shell and darker colour than the nominotypical subspecies.

Our findings indicate that *A. (A.) inversus roseotincta* Möllendorff, 1894 may be restricted to eastern peninsular Thailand and that Zilch (1953) was correct in attributing subspecific status to what other workers have considered to be only a colour variety. However, current information is insufficient to confirm this.

In the present study, we have collected numerous samples of *A. (A.) inversus inversus* and *A. (A.) inversus annamiticus* from many localities in Thailand, Singapore and Sumatra. Shell morphology, anatomy of genitalia, spermatophore and radula morphology were investigated. There is sufficient material and evidence to delineate the two following subspecies.

***Amphidromus (Amphidromus) inversus inversus* (Müller, 1774)**
(Figures 4.1, 4.3C-D, 4.7A-C, 4.8)

Helix inversus Müller, 1774: 93-94.

Bulimus jayanus Lea, 1841: 31. Fulton, 1896: 70. Pilsbry, 1900: 168. Laidlaw and Solem, 1961: 630, 632.

Bulimus contusus Reeve, 1848: pl. 37, fig. 220. Fulton, 1896: 70. Pilsbry, 1900: 168. Laidlaw and Solem, 1961: 612, 630.

Bulimus elongatus Hombron and Jacquinot, 1854: pl. 8, figs 3, 4. Fulton, 1896: 70. Pilsbry, 1900: 168. Laidlaw and Solem, 1961: 616, 630.

Amphidromus inversus—Pilsbry, 1900: 167-168, pl. 56, figs 91, 92. Benthem Jutting, 1959: 163. Richardson, 1985: 21-22. Smith and Djajasasmita, 1988: 392.

Amphidromus inversus inversus—Laidlaw and Solem, 1961: 560.

Material examined: Botanic Garden, Singapore: 2063 (3D), 2171 (3D), 2183 (6D), 2234 (1D). South Sumatra, Indonesia: 2235 (1D+2S), 2236 (3S).

Shell (Fig. 4.3C, D; Table 4.2): Shell characters are those given for the species description. The prominent shell characteristics are large shell, dimorphic coiling, whitish to creamy spire, and several black to dark brown varices.

Radula (Fig. 4.7A-C): Each row containing about 162 (80-(20-22)-1-(20-22)-81) teeth. Central tooth tricuspid with a gouge shaped depression, mesocone truncate with small ectocones on both sides (Fig. 4.7A). Lateral teeth bicuspid, endocone cylindrical, slightly oblique with wide notch, and ectocone large with truncated to rounded cusp (Fig. 4.7A). Marginal teeth start at tooth number 20 to 22 (Fig. 4.7B), endocone medium sized, mesocone large with curved margins, and ectocone small with sharp cusp (Fig. 4.7C).

Genital system (Fig. 4.8A-D): Atrium (at) short (n=4). Penis (p) cylindrical, half vaginal length, and distally folded at penial verge base. Epiphallus (e) longer than with other examined species, with variable coiling. Flagellum (fl) smaller than epiphallus and terminates with folded coiled portion. Appendix (ap) very short or absent. Vas deferens (vd) long narrow tube, entering from free oviduct (fo) passing into spiral structure of epiphallus and terminating in distal epiphallus. Penial retractor muscle (pr) long, thickened and inserts near proximal end of epiphallus (Fig. 4.8A).

Internal wall of penis corrugated, forming series of swollen longitudinal pilasters (pp), which form fringe around penial verge tip. Penial verge (pv) relatively long, cylindrical, nearly smooth with longitudinal ridges, and orifice (pvo) located at the tip (Fig. 4.8B). Internally flagellum possesses strong epiphallic pilasters (ep), with some parts forming distinct fissures proximal to the entrance of vas deferens (evd) where they form discrete knobs. Large central epiphallic pilaster (ep) runs from flagellum and extends over entrance to vas deferens (evd) as flap (Fig. 4.8C).

Vagina (v) cylindrical and long about twice the length of penis. Gametolytic duct (gd) long, folded and convoluted proximal to vagina, and terminates distally in swollen gametolytic sac (gs). Free oviduct (fo) short,

oviduct (ov) enlarged and compressed, and fused prostate gland located below oviduct. Albumen gland (ag) curved lingulate (Fig. 4.8A). Hermaphroditic gland (hg) contracts to form numerous small lobuli. It connect to middle of talon (ta) by convoluted hermaphroditic duct (hd) (Fig. 4.8D)

Internal walls of vagina possess several longitudinal vaginal pilasters (vp) (Fig. 4.8B). Proximal to genital orifice, pilasters compressed and smooth crenulated ridges, and around free oviduct become irregular in form with deep crenellations.

Distribution (Fig. 4.1): Previous records are from Singapore; Buguran and Natuna islands off the northwest coast of Borneo; Sarawak, North Borneo; Ranau in Sabah, North Borneo; Sambas and Sintang, Kalimantan, West Borneo; Klapa island, off the northeast coast of Borneo; Karimata island, off the west coast of Borneo; Billiton Island and its satellite islands in the Java Sea; Krakatau and Rakata islands between Sumatra and Java; the North Celebes; and Banda Island in the Banda Sea (Pilsbry, 1900; Laidlaw and Solem, 1961). The specimens examined were collected from the Botanic Gardens of Singapore and from Lampung in the south of Sumatra.

Remarks: The genital morphology of Singapore and Sumatran specimens appears identical. Specimens from both areas exhibit a relatively long and coiled epiphallus, long cylindrical penial verge, a flagellum with a coiled terminal portion and lack an appendix. Specimens from Singapore exhibit a more convex last whorl with an intense suprasutural band (Fig. 4.3D), the subperipheral band is slightly distinctive; the parietal callus is relatively thinner than that of Sumatran specimens (Fig. 4.3C).

Amphidromus (A.) inversus inversus possesses a tricuspid central tooth, and extremely long epiphallus; the vas deferens enters at the spiral epiphallus. In *A. (A.) inversus annamiticus* there is a monocuspid central tooth and a straight and shorter epiphallus (Figs 4.7A, D; 4.8A; 4.9A).

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Table 4.2. Shell size variation in *A. (A.) inversus*. Catalogue numbers of specimens are indicated in parentheses.

Species, Locality and CUMZ nos.	Number of adults shell examined	Ranges, Mean \pm SD in mm of:			Whorl Ranges
		Shell Height	Shell Width	h/d Ratio	
<i>A. (A.) inversus inversus</i> (Müller, 1774)					
South of Sumatra, Indonesia (2235, 2236)	6	44.30-54.58 49.49 \pm 4.08	24.70-31.24 28.25 \pm 2.81	1.68-1.85 1.76 \pm 0.07	6 ⁴ / ₈ - 7 ⁴ / ₈
Botanic Garden, Singapore (2063, 2183, 2234)	8	41.69-50.47 46.08 \pm 3.21	24.87-28.98 26.32 \pm 1.23	1.68-1.91 1.75 \pm 0.08	6 ⁷ / ₈ - 7 ⁴ / ₈
<i>A. (A.) inversus annamiticus</i> (Crosse and Fischer, 1863)					
Koh E-lar, Chonburi (2085, 2088, 2229)	305	32.70-47.97 39.27 \pm 2.79	20.33-27.08 23.46 \pm 1.19	1.42-1.98 1.67 \pm 0.07	6 ³ / ₈ - 7 ⁴ / ₈
Koh Jarn, Chonburi (2035, 2150)	101	34.55-47.77 43.08 \pm 2.74	20.60-26.77 23.93 \pm 1.26	1.58-1.94 1.76 \pm 0.07	6 - 7 ³ / ₈
Koh Juang, Chonburi (2044)	47	34.46-52.74 42.13 \pm 3.86	20.29-27.21 23.70 \pm 1.45	1.65-1.94 1.78 \pm 0.71	6 ⁴ / ₈ - 7 ⁶ / ₈
Koh Kharm, Chonburi (2033, 2089)	116	33.38-46.92 39.95 \pm 2.77	19.78-25.97 22.79 \pm 1.05	1.54-1.95 1.75 \pm 0.08	6 ⁴ / ₈ - 7 ⁵ / ₈
Koh Lueam, Chonburi (2084)	288	34.38-48.51 42.16 \pm 2.43	21.48-27.27 24.32 \pm 0.99	1.53-1.94 1.73 \pm 0.07	6 ³ / ₈ - 7 ⁴ / ₈
Koh Marn Vichai, Chonburi (2038, 2149)	215	37.64-54.79 44.54 \pm 2.50	21.21-27.77 25.18 \pm 1.00	1.59-1.99 1.77 \pm 0.07	6 ⁷ / ₈ - 7 ⁶ / ₈
Koh Pai, Chonburi (2037, 2034)	82	39.16-51.4 46.64 \pm 2.86	22.61-27.53 25.17 \pm 1.16	1.65-2.10 1.85 \pm 0.08	6 ⁶ / ₈ - 7 ⁷ / ₈
Kon Rin, Chonburi (2206, 2087)	174	37.48-50.87 43.75 \pm 2.68	22.79-26.92 24.82 \pm 0.86	1.56-1.97 1.76 \pm 0.08	6 ⁴ / ₈ - 7 ⁷ / ₈
Koh Samaesan, Chonburi (2083, 2138, 2143)	39	34.21-49.43 42.20 \pm 3.72	20.80-26.69 23.64 \pm 1.29	1.40-1.99 1.79 \pm 0.12	6 ⁴ / ₈ - 7 ⁵ / ₈
Koh Samet, Rayong (2086)	7	39.84-46.36 42.49 \pm 2.11	24.05-26.18 24.79 \pm 0.81	1.65-1.78 1.71 \pm 0.05	6 ⁶ / ₈ - 7 ¹ / ₈
Hin Lad waterfall, Samui (2139, 2196)	7	36.92-47.55 42.60 \pm 4.06	21.90-25.31 23.71 \pm 1.39	1.65-1.91 1.79 \pm 0.09	7 ¹ / ₈ - 8
Na Muang waterfall, Samui (2137, 2141, 2156, 2186)	14	40.59-45.53 43.55 \pm 1.61	22.18-25.21 23.89 \pm 0.89	1.71-1.99 1.83 \pm 0.08	7 ³ / ₈ - 8
Koh Tan, Suratthani (2140, 2184)	23	38.00-47.10 43.48 \pm 2.63	21.37-28.16 24.96 \pm 1.69	1.62-1.88 1.74 \pm 0.06	7 - 8

Amphidromus (Amphidromus) inversus annamiticus
(Crosse and Fischer, 1863)
 (Figures 4.1, 4.3E-H, 4.7D-F, 4.9)

Bulimus annamiticus Crosse and Fischer, 1863: 357-359. Crosse and Fischer, 1864: 329, pl. 12, fig. 8. Mabilille and Mesle, 1866: 128.

Amphidromus annamiticus—Morlet, 1889: 126.

Amphidromus annamiticus var. *roseotincta* Möllendorff, 1894: 150.

Amphidromus inversus annamiticus—Pilsbry, 1900: 169-170, pl. 56, figs 98-100. Laidlaw and Solem, 1961: 561, 600. Solem, 1965: 624.

Amphidromus inversus annamiticus var. *roseotincta*—Pilsbry, 1900: 170. Laidlaw and Solem, 1961: 561, 655-656. Solem, 1965: 624.

Amphidromus inversus var. *annamiticus*—Gude, 1903b: 50, 51. Abbott, 1989: 160.

Amphidromus inversus roseotincta—Zilch, 1953: 135, pl. 23, fig. 26.

Material examined: Koh Srichang, Chonburi: 2147 (4D). Koh Pai, Chonburi: 2034 (39D), 2037 (49D), 2152 (6D), 2167 (12D), 2176 (5D), 2178 (19D), 2185 (29D), 2226 (2D). Koh Lueam, Chonburi: 2084 (316D), 2170 (3D), 2190 (28D), 2221 (13D). Koh Khram, Chonburi: 2033 (43D), 2089 (34D), 2173 (1D), 2200 (2D). Koh Khram Noi, Chonburi: 2223 (15D). Koh E-lar, Chonburi: 2085 (193D), 2088 (40D), 2181 (15D), 2187 (10D), 2229 (150D). Koh Rin, Chonburi: 2064 (8D), 2087 (84D), 2163 (4D), 2172 (7D), 2206 (107D), 2224 (15D). Koh Samaesan, Chonburi: 2065 (7D), 2083 (27D), 2138 (3D), 2143 (9D), 2144 (183D), 2166 (1D), 2175 (3D). Koh Marnvichai, Chonburi: 2038 (193D), 2149 (31D). Koh Juang, Chonburi: 2044 (44D), 2062 (32D), 2151 (17D), 2168 (22D), 2179 (8D), 2188 (17D), 2189 (28D), 2225 (9D). Koh Jarn, Chonburi: 2035 (59D), 2066 (8D), 2150 (31D), 2180 (31D), 2182 (29D), 2222 (1D). Koh Samet, Rayong: 2086 (12D). Na Muang waterfall, Koh Samui District, Suratthani: 2137 (2D), 2141 (3D), 2156 (48D), 2186 (11D). Hin Lad waterfall, Koh Samui District, Suratthani: 2139 (4D), 2169 (7D). Koh Tan, Suratthani: 2140 (4D), 2184 (46D). Chaiya District, Suratthani: 2216 (28D).

Shell (Fig. 4.3E-H; Table 4.2): The prominent shell characters are dextral coiling and the presence of dark brown varices. Spire rosaceous, with lighter or dark purplish suprasutural band, and dianthus or dark purplish apex.

Radula (Fig. 4.7D-F): Each row containing about 185 (91-(63-67)-1-(66-68)-93) teeth. Central tooth monocuspid (Fig. 4.7D). Laterals and marginals closely resemble those described for *A. (A.) inversus*

inversus (Fig. 4.7D). Marginal teeth start from tooth 63 to 68 (Fig. 4.7E, F) outwards.

Genital system (Fig. 4.9A-F): Atrium (at) rather short (n=10). Penis (p) cylindrical, long and slender, and epiphallus (e) relatively large. Flagellum (fl) long, straight, almost the same size as epiphallus and may possess short distally hooked, and appendix-like structure formed by coiled constriction of flagellum (Fig. 4.9A).

The external form of the female genital system and the internal walls of the penis, vagina and epiphallus (Fig. 4.9A-D) are similar to those described for the nominotypical form.

The spermatophore (n=1) is long and pentagonal in cross-section (Fig. 4.9E). Generally, the morphology of the sperm sac (sc) is similar to that of *A. (A.) perversus natunensis*. However, the coiled expanded section (ces) has several spiral ridges instead of a series of oblong knobs (Fig. 4.9F).

Distribution (Fig. 4.1): Records available to Pilsbry (1900) led him to conclude that *A. (A.) inversus annamiticus* was confined to the lower reaches of the Mekong drainage system in Cambodia and Vietnam. Laidlaw and Solem (1961) and Solem (1965) reported additional sites at Tschaya and Bandon in southern Thailand; Koh Srichang, Koh Samet and other islands around Sriracha in eastern Thailand.

Current records are from several islands in the Gulf of Thailand: Koh Srichang, Koh Lueam, Koh Pai, Koh Marnvichai, Koh Rin, Koh Khram, Koh Khram Noi, Koh E-lar, Koh Samaesan, Koh Juang, Koh Jarn and Koh Samet, all in eastern Thailand, and Koh Samui and Koh Tan in the southern gulf of Thailand. In Thailand *A. (A.) inversus annamiticus* seems to be largely confined to islands along the coast although a single population was recently found on the mainland at Chaiya District, Suratthani.

Remarks: *Amphidromus (A.) inversus annamiticus* is reliably distinguished from *A. (A.) inversus inversus*, by a dianthus spire, nearly flat whorls and a purple suprasutural band near the apex. The pink or dark purplish apex, monocuspid central tooth, and relatively straight epiphallus.

All specimens collected in Thailand were dextral with just one Cambodian sinistral specimen being recorded by Pilsbry (1900). Both the eastern and southern Thailand populations have slightly smaller shells than the typical subspecies from Indonesia and Singapore (Table 4.2). The eastern populations show the lighter pinkish to creamy spire and pale purple suprasutural band on the upper spire as in *A. (A.) inversus annamiticus* (Crosse and Fischer, 1863, 1864; Pilsbry, 1900). Specimens from Koh Samui (type locality), Koh Tan and Chaiya District of Suratthani are the 'variety'

roseotincta Möellendorff, 1894. The rosaceous spire and purple apex are very distinct characters, which easily allow recognition of '*roseotincta*' from typical *A. (A.) inversus annamiticus* and snails from Singapore and Sumatra. Observed genital and radula and shell morphology (Table 4.2) between the two Thailand populations are almost the same. '*roseotincta*' from Koh Samui and its satellites, and Chaiya District is apparently a distinct geographical form in southern Thailand that with additional supporting evidence could be treated as a subspecies.

Four specimens from Koh Samui (Fig. 4.3H) and Koh Tan show a whitish-cream pattern and lack a brown radial streak and dark brown spiral band below the periphery of the last whorl. Although they still possess the pinkish to rosaceous spire there are no significant differences in genital anatomy between the two different shell colour forms.

Specimens from Koh Lueam (Fig. 4.3E) and Koh Samet exhibit a nearly smooth radial streak with a concentrated dark brown band at the lower periphery. Koh Samaesan and Koh Juang specimens (Fig. 4.3F) have an intense dark brown lower peripheral band with a light radial streak on the white spire. Specimens from Koh Khram and Koh E-lar are relatively smaller than other eastern populations (Table 4.2). Specimens from Koh Rin, Koh Pai, Koh Jarn and Koh Srichang show irregular brown radial streaks on a pinkish spire as described above.

In September 2002, five snails were collected from Koh E-lar, 3 of which produced eggs in captivity. The eggs were clumped together with sticky mucus into a long elliptical cluster. The eggs were whitish and approximately 0.3 mm in diameter. The numbers of eggs per clutch were 100, 110 and 116 respectively.

***Amphidromus (Amphidromus) atricallosus* (Gould, 1843)**

Diagnosis: Shell relatively large, conic or ovate and exhibiting dimorphic chirality. Whorls smooth, slightly flattened to moderately convex. Shell glossy greenish-yellow to yellowish or whitish to brown, with white subsutural band. Apex white; aperture ovate-lunate or somewhat angulated at base. Peristome whitish; lip expanded, folded and reflected, not attach to last whorl. Umbilicus imperforate; columella whitish, generally straight but sometimes folded and twisted. Parietal callus blackish to dark brown or whitish; varix present or absent.

External features: Foot broad and long, soft body almost white to pale yellow. Body pigmentation varies from nearly colourless in juveniles to strongly pigmented in old adults. Body normally covered with creamy or whitish reticulated skin. Mantle edge dark-orange to pale brown. Basal

longitudinal orange stripes run the length of lateral foot. Upper tentacles long and drumstick shaped, yellowish to brownish with dark eye spot on the tips. Lower tentacles yellowish to orange, as on the head and around the mouth. Mantle cavity possesses pattern of black-pigmentation, which pale over blood vessels. This pigmentation retained in preserved specimens.

Distribution: *Amphidromus (A.) atricallosus* ranges from Tavoy in Myanmar to eastern Thailand near its frontier with Cambodia and the Malaysian peninsula. Early records were from Tavoy, and Mergui and King Islands of Myanmar; Chantaburi, Sakeo and Salanga Island (Phuket) of Thailand; Penang island off the coast of Malaysian peninsula and probably in Cochinchina (south Vietnam) (Pilsbry, 1900; Gude, 1903b, 1914). Laidlaw and Solem (1961) and Solem (1965) reported additional localities, specifically Petchaburi, Prachuapkirikhan, Chumporn, Ranong, Suratthani, Nakornsrihammarat, Trang in peninsular Thailand and Chonburi, Sakeo and Trat in eastern Thailand; and Perak, Johore, and Pahang in Peninsular Malaysia.

Remarks: The shell can be distinguished from other *Amphidromus* by being long, smooth, convex, monochrome yellowish or whitish, with a white subsutural band. After critical investigation of 3,862 specimens from 30 localities deposited in CUMZ, we propose a new subspecies.

Four subspecies can be recognized, the nominate subspecies, *A. (A.) atricallosus leucoxanthus* von Martens, 1864, *A. (A.) atricallosus perakensis* Fulton, 1901 and *A. (A.) atricallosus* ssp. The shell characters and geographical distribution of these subspecies are distinctive. *Amphidromus (A.) atricallosus atricallosus* (Gould, 1843) is distinguished by a dark parietal callus, a relatively smooth spire and straight columella. While *A. (A.) leucoxanthus* (von Martens, 1864) was considered to be a distinct species (Morlet, 1889), it was subsequently placed as a subspecies of *A. (A.) perversus* by Pilsbry (1900), who noted that some specimens of *A. (A.) aureus* (Martyn, 1784) have a similar columellar fold. Based on similarity of shell form and colour pattern Laidlaw and Solem (1961) synonymized *A. (A.) aureus* as simply a colour variant of *A. (A.) perversus*, and *A. (A.) leucoxanthus* as a variety of *A. (A.) atricallosus*. Fulton (1901) described *A. (A.) perakensis* as a distinct species from Malaysia. *A. (A.) perakensis* is similar to *A. (A.) perversus*, but significantly, *A. (A.) perakensis* possesses an interiorly thickened columella plait. Based on an inadequate sample size, Laidlaw and Solem (1961) synonymized *A. (A.) perakensis* as a colour variant of *A. (A.) atricallosus*. Solem (1965) suggested that the distributions of *A. (A.) atricallosus atricallosus* and *A. (A.) atricallosus leucoxanthus* were likely to be allopatric and this is confirmed by current distributional data. *Amphidromus (A.) atricallosus atricallosus* ranges from

western Thailand across the southern border of Myanmar (Tenasserim) to Malaysia. *Amphidromus (A.) atricallosus leucoxanthus* is restricted to eastern Thailand and possibly also occurs in Cambodia, while *A. (A.) atricallosus perakensis* is currently known only from Malaysia and Singapore.

Amphidromus (A.) atricallosus exhibits interesting evolutionary characteristics worthy of in-depth study. Panha *et al.* (2001) reported various analyses on the proportion of colour forms, and chirality of some *Amphidromus* species from various localities in Thailand and provided a phylogenetic tree based on morphological characters. Here we provide additional morphological data based on genital anatomy, radula morphology and geographic distribution. The impetus for identifying and naming these *Amphidromus* species and subspecies at this time is that they are included in a current molecular study of various *Amphidromus* species in Thailand.

Amphidromus (Amphidromus) atricallosus atricallosus (Gould, 1843)

(Figures 4.2, 4.3I-N, 4.10A-C, 4.12A, 4.13A-C, 4.14A, B, 4.15A, B)

Bulimus atricallosus Gould, 1843: 140. Gould, 1844: 457, pl. 24, fig. 3.

Bulimus eques Pfeiffer, 1857: 158. Crosse and Fischer, 1863: 359. Fulton, 1896: 69. Pilsbry, 1900: 165-166. Laidlaw and Solem, 1961: 617.

Amphidromus perversus var. *atricallosus*—Fulton, 1896: 69.

Amphidromus atricallosus—Pilsbry, 1900: 165-166, pl. 58, figs 19-21. Gude, 1914: 179-180. Laidlaw and Solem, 1961: 530. Solem, 1966: 102. Richardson, 1985: 8

Amphidromus atricallosus var. *atricallosus*—Solem, 1965: 620, pl. 1, figs 1, 2. Abbott, 1989: 160.

Material examined: Myanmar (near Kanchanaburi): 2293 (1S). Kaeng Kracharn, Petchaburi: 2108 (1D+1S), 2294 (1S). Prachuapkirikhan: 2142 (2D+1S). Sawi District, Chumporn: 2071 (6D+2S), 2126 (4D+1S). Khao Krieb, Lamae District, Chumporn: 2070 (24d+9S). Nam Pu Ron, Ranong: 2080 (18D+1S), 2164 (7D). Wat Suan Moka, Suratthani: 2131 (2D+1S), 2278 (7D+4S). Ban Takun, Suratthani: 2015 (4D+4S), 2019 (13D+20S), 2020 (12D+4S), 2024 (26D+27S), 2027 (21D+53S), 2028 (11D+47S), 2029 (33D+66S), 2030 (29D+66S), 2057 (35D+52S), 2058 (13S), 2061 (88D+207S), 2069 (8D+9S), 2093 (4D+7S), 2094 (3D+10S), 2095 (10D+11S), 2124 (3D+3S), 2129 (1D+4S), 2132 (2D+2S), 2153 (32D+55S), 2159 (3D+2S), 2160 (7D+7S), 2161 (9D+14S), 2191 (13D+33S), 2197 (12D+16S), 2280 (10D+2S), 2284 (1D), 2285 (4S), 2291 (7S). KhlongSang Wildlife Sanctuary, Suratthani: 2082 (6D+6S), 2114 (1D+2S), 2134 (2D+4S). Wat Tham Wararam, Suratthani: 2022 (14D+24S). Wat Tham Sok Panthurat, Suratthani: 2023 (19D+2S), 2068 (7D+1S), 2106 (60D+9S). Khao Sok,

Suratthani: 2021 (1D+4S), 2025 (29D+24S), 2026 (57D+102S), 2112 (2S).
 Khao Luang, Nakhonsrithammarat: 2078 (16D+10S), 2079 (3D+1S), 2097 (3D+1S).

Shell (Fig. 4.3I-N; Table 4.1): The nominotypical subspecies is characterized by slightly flattened whorls, wide and shallow suture, black or dark brown parietal callus, and straight columella.

Radula (Fig. 4.10A-C): Each row containing about 170 (88-(49-51)-1-(50-51)-81) teeth. Central tooth monocuspid and gouge shaped (Fig. 4.10A). Lateral teeth bicuspid, endocone small curved cusp with wide notch, and ectocone large with truncate cusp margin (Fig. 4.10A). Marginal teeth tricuspid with tricuspid structure expressed from tooth number 49 to 51 outwards (Fig. 4.10B). Endocone medium size with rounded cusps, mesocone large with curved cusp margin, and ectocone small and with sharp cusp. Outermost marginal teeth exhibit wide space between each row (Fig. 4.10C).

Genital system (Figs 4.12A, 4.13A-C, 4.14A, B): Atrium (at) relatively long (n=10). Penis (p) conical, tapering proximally, as long as vagina and distally ending with folded ring at its widest point. Epiphallus (e) large and convoluted. Flagellum (fl) long and folded into single coil at distally near the appendix. Appendix (ap) long, and narrow. Vas deferens (vd) a narrow tube, passing forward from free oviduct (fo) to the end of epiphallus. Penial retractor muscle (pr) short, flattened, and inserts distally on penis (Fig. 4.12A).

Internal wall of penis corrugated, forming series of smooth longitudinal pilasters (pp) with fringe around penial verge. Penial verge (pv) relatively short and conic with apical orifice (pvo) (Fig. 4.13A). Internally flagellum possesses long and crenulated epiphallic pilasters (ep). The regular arrangement of these pilasters interrupted by entrance of vas deferens (evd), which marked by pilaster forming overhanging flap (Fig. 4.13B).

Vagina (v) relatively short, slender and cylindrical. Gametolytic sac (gs) swollen and connected to long gametolytic duct (gd). Free oviduct (fo) short; oviduct (ov) compact and enlarged; prostate gland fused and located under oviduct. Albumen gland (ag) large and curved ligulate (Fig. 4.12A). Hermaphroditic gland (hg) compact mass of numerous small lobuli, and connected to middle of talon (ta) by convoluted hermaphroditic duct (hd) (Fig. 4.13C).

Internal wall of vagina possesses longitudinal vaginal pilasters (vp). Proximal to genital orifice, pilasters smooth and curved; proximal to gametolytic duct (gd) they rugged in form. (Fig. 4.13A).

Spermatophores (n=5) are about 90 μ m long, and pentagonal in cross-section (Fig. 4.14A). They are very similar in general shape and structure

to those of *A. (A.) perversus natunensis*. A distinctive feature is the similarly sized sharp keels, which run along the sperm sac. One major keel transforms to oblong knobs, of which there are 30 to 37 on the coiled expanded section (ces) (Fig. 4.14B).

Distribution (Fig. 4.2): The earliest distribution records are from Myanmar and Malaysia (Pilsbry, 1900); the range of this subspecies was extended by Laidlaw and Solem (1961) and Solem (1965) to include western and southern Thailand. In the present study, we recorded this snail from a number of previously unknown localities ranging from Petchaburi and Prachuapkirikhan in northern peninsular Thailand to Chumporn, Ranong, Suratthani, Nakornsrihammarat, Trang, Phuket and Narativat further southwards. This is a mainland subspecies occurring widely in synanthropic habitats.

Remarks: The shell is slender with nearly flattened spire and distinct black to dark brown parietal calluses, which differ from the white parietal callus of *A. (A.) atricallosus leucoxanthus* and *A. (A.) atricallosus perakensis*. Shells vary from yellowish to whitish. Specimens from Kaeng Krachan (2108) exhibit the size range of this subspecies (57.10 to 59.06 mm height; 30.96 to 31.58 mm width; $7\frac{3}{8}$ to $7\frac{4}{8}$ whorls) while specimens from Chumporn, Ranong and Suratthani look very similar in shell shape and colour pattern, but are smaller in size (Table 4.1).

Juveniles are readily distinguished by the sharp apertural lip, without folding or reflection. Several juvenile specimens (10 to 20 mm height) from Suratthani show slight angulations and a reddish brown spiral band at the periphery that are not discernable in adults (Fig. 4.3M, N).

The specimens collected from Pangnga: 2074 (1S), 2081 (41D+49S), 2128 (2S), 2220 (2D+18S), 2279 (25D+17S), 2283 (2S); Trang: 2118 (3D), 2130 (1D), 2281 (7D); Phuket: 2113 (1D); Narativat: 2292 (2D+1S) exhibit a unique colour pattern and their status is currently uncertain (Fig. 4.3O). The general colour pattern and shell shape are as for the nominotypical subspecies, but they possess a whitish parietal callus similar to that of *A. (A.) atricallosus perakensis*, and usually lack dark varices. This could be due to homoplasy or possibly gene flow between nominotypical *A. (A.) atricallosus* and southern *A. (A.) atricallosus perakensis*.

Some individuals were observed laying eggs on leaves of trees including pomelo (*Citrus maximus* (Burm.f.) Merr.), banyan (*Ficus* spp.) and rambutan (*Nephelium lappaceum* L.). The foot is used to secrete sticky mucus that traps the lower surface of leaves to form a nest (Fig. 4.15A). Two leaves are glued giving a cavity, opened at both ends, in which the snail gradually lays between 100 to 150 eggs (Fig. 4.15B). The eggs exposed to air at each end were

shrunk and are possibly sacrificed as a strategy to safeguard the remaining eggs. Eggs are globular, whitish, with a soft and flexible membrane, 2 to 3 mm diameter, and held together in sticky mucus. Newly emerged individuals were transparent, 1 to 2 whorls, 2 to 3 mm in height and helicoid. Newly hatched individuals initially remain in the nest and eat the eggshell before dispersing into the trees. Such egg laying behavior has been reported from Java in *A. (A.) palaceus*. This larger species was reported to build nests using bamboo, Jack fruit (*Artocarpus integrifolia* L.f.) and mango (*Mangifera indica* L.) leaves (Paravicini, 1921). Although the 234 eggs recorded from an individual *A. (A.) palaceus* were more than those observed in the current study, such egg numbers are possibly proportionate to body size.

Amphidromus (Amphidromus) atricallosus leucoxanthus
(von Martens, 1864)

(Figures 4.2, 4.3P, 4.4A-E, 4.10D-F, 4.12B, 4.14C, D, 4.15C)

Bulimus leucoxanthus von Martens, 1864: 526. von Martens, 1867: 348-349, pl. 20, figs 11, 12.

Bulimus leucoxanthus var. *oculata* von Martens, 1867: 348, pl. 20, fig. 12.

Amphidromus leucoxanthus—Morlet, 1889: 127. Laidlaw and Solem, 1961: 530.

Amphidromus perversus var. *leucoxanthus*—Fulton, 1896: 69.

Amphidromus aureus leucoxanthus—Pilsbry, 1900: 163-164, pl. 54, figs 73-79.

Amphidromus aureus leucoxanthus var. *oculata*—Pilsbry, 1900: 163-164, pl. 54, fig. 73.

Amphidromus aureus var. *leucoxanthus*—Gude, 1903a: 8.

Amphidromus atricallosus var. *leucoxanthus*—Laidlaw and Solem, 1961: 635-636. Solem, 1965: 620, pl. 1, fig. 8. Abbott, 1989: 160.

Amphidromus atricallosus var. *laidlawi* Solem, 1965: 620-624, pl. 1, fig. 3 (Holotype). Abbott, 1989: 160.

Amphidromus atricallosus var. *perakensis*—Solem, 1965: 620-624, pl. 1, fig. 9. (not Fulton, 1901)

Amphidromus atricallosus laidlawi—Abbott, 1989: 160 (Holotype).

Material examined: Khao Ang Rue Nai Wildlife Sanctuary, Chachoengsao : 2006 (1S), 2091 (6D+4S), 2111 (1D+2S), 2120 (1D+2S), 2121 (1D), 2122 (1D+3S), 2125 (1S), 2135 (3D+3S), 2193 (3D+4S), 2195 (20D+9S), 2287 (2D), 2289 (1D). Khao Takrub, Chachoengsao : 2165 (18D+1S), 2228 (12D). Khao Cha Ang, Chonburi: 2146 (1D+1S). Khao Kiew, Chonburi: 2041 (121D+62S), 2043 (40D+25S), 2148 (2D+2S). Khao Soidao Wildlife Sanctuary, Chantaburi: 2075 (2D), 2076 (2D), 2096 (18D+6S), 2116

(2D+1S), 2227 (2D+5S). Makham District, Chantaburi: 2214 (5D+1S), 2231 (147D+23S). Makok waterfall, Chantaburi: 2008 (1D+1S), 2059 (201D+172S), 2060 (68D+43S), 2145 (38D+20S), 2162 (38D+25S), 2194 (12D+5S), 2230 (22D+18S). Trog Nong waterfall, Chantaburi: 2099 (3D+4S). Kong Sri Rai, Chantaburi: 2192 (16D+2S). Pliue waterfall, Chantaburi: 2007 (2D+2S), 2010 (5D+4S), 2018 (16D+5S), 2039 (67D+28S), 2042 (51D+39S), 2073 (7D+3S), 2090 (19D+8S), 2092 (3D+4S), 2100 (36D+8S), 2101 (24D+13S), 2102 (17D+7S), 2103 (5D+8S), 2104 (22D+16S), 2105 (26D+12S), 2109 (2D), 2110 (1D+2S), 2115 (5D+1S), 2117 (6D+2S), 2119 (4D+2S), 2123 (3D+2S), 2127 (2D+1S), 2154 (55D+33S), 2155 (78D+39S), 2157 (32D+20S), 2196 (36D+9S), 2201 (2D), 2202 (9D+7S), 2203 (50D+32S), 2286 (3D), 2290 (4D+2S), 2295 (10D+5S).

Shell (Figs 4.3P, 4.4A-E; Table 4.1): Shell characters similar to those of the typical subspecies, but the shell differs in possessing a white parietal callus. The colour varies from yellowish to white with brown radial streaks. Whorls convex, suture wider and deeper than the typical subspecies. The columella plait may vary from being strongly pronounced to completely absent.

Radula (Fig. 4.10D-F): Each rows containing about 171 (85-(16-18)-1-(16-18)-85) teeth. Central and lateral teeth similar to those of typical subspecies (Fig. 4.10D). Marginal teeth start from tooth number 16 to 18 (Fig. 4.10E), mesocone largest with curved margins, both endocone and ectocone with sharp cusp (Fig. 4.10F).

Genital system (Figs 4.12B, 4.14C, D): Atrium (at) relatively long (n=10). Penis (p) conical, approximately one-third the length of vagina, and distally folded at the base of penial verge. Epiphallus (e) large and long. Flagellum (fl) small and coiled distally. Appendix (ap) small and as long as flagellum. Vas deferens (vd) runs from free oviduct (fo) to the end of epiphallus. Penial retractor muscle (pr) inserts at penial/epiphallus junction (Fig. 4.12B). The external morphology of the female genitalia and the internal sculpture of the penis, vagina and epiphallus closely resemble those of the nominotypical subspecies.

Two spermatophores were examined. They were about 85 mm long, and pentagonal in cross-section (Fig. 4.14C). They are similar to those of *A. (A.) atricallosus atricallosus*, but the oblong knobs on one keel vary from 25 to 27 (Fig. 4.14D).

Distribution (Fig. 4.2): *Amphidromus (A.) atricallosus leucoxanthus* exhibits a narrow distribution in eastern Thailand and may occur in Cambodia. Previous records were from several localities in Eastern Thailand, namely Trat,

Srakeo, Chantaburi and Chonburi (Pilsbry, 1900; Laidlaw and Solem, 1961; Solem, 1965). In the present study, we recorded this subspecies from the following localities in Eastern Thailand: Plieu waterfall, Makok waterfall, Trog Nong waterfall, Khao Soidao Wildlife Sanctuary, Makham District in Chantaburi; Khao Takrub, Khao Ang Rue Nai Wildlife Sanctuary in Chachoengsao ; Khao Kiew and Khao Cha Ang in Chonburi.

Remarks: The 2,183 specimens from 10 localities examined by us clearly demonstrate the existence of polymorphism with three shell-color morphs of *A. (A.) atricallosus leucoxanthus* being recorded: yellowish-green (Figs 4.3P, 4.4A), white (Fig. 4.4B, C) and brown (Fig. 4.4D, E). Detailed examination of the general anatomy, genitalia and radula show no anatomical differences between the three morphs.

The brown shelled form with crowded brown radial streaks on a white background was described from Nong Khor, Southeast Thailand and nominated as the variety *laidlawi* of *A. (A.) atricallosus leucoxanthus* by Solem (1965) (Fig. 4.4D, E). It was subsequently recognized as a subspecies (Abbott, 1989). In most of our collecting sites, the three forms are sympatric. From our data the yellow shelled is the most abundant form followed by white and brown with approximate ratios being 25:9:1 respectively.

Topotypic specimens from Khao Sabab (Plieu Waterfall National Park), Chantaburi and specimens from Chonburi and Chachoengsao are clearly *A. (A.) atricallosus leucoxanthus* with the characteristic white apex and parietal callus, convex whorls, depressed suture and wide white subsutural band.

The thickness of the columellar plait has been used to distinguish *A. (A.) atricallosus perakensis* from *A. (A.) perversus* and *A. (A.) atricallosus* subspecies (Fulton, 1901; Solem, 1965). However, on the basis of our data, this character is of little value. Specimens collected from Plieu waterfall, Khao Soidao and Khao Kiew show a wide range of variation in the degree of thickness of the columella plait. All the specimens from eastern Thailand of *A. (A.) atricallosus leucoxanthus* exhibit the typical colouration of the subspecies and one or two varices while the columellar plait varies from simple and straight to highly folded within populations. Furthermore, the Malaysian specimens examined (*A. (A.) atricallosus perakensis*) exhibit various columella plait shapes from simple and straight to strong and folded. Thus *A. (A.) atricallosus leucoxanthus* and *A. (A.) atricallosus perakensis* cannot be distinguished on the basis of columella form.

Amphidromus (Amphidromus) atricallosus leucoxanthus was observed laying eggs on rambutan leaves (*Nephelium lappaceum* L.) (Fig. 4.15C) and constructing a nest as described above for the typical subspecies.

***Amphidromus (Amphidromus) atricallosus perakensis* Fulton, 1901**

(Figures 4.1, 4.4F-G, 4.11A-C, 4.12C)

Amphidromus perakensis Fulton, 1901: 104, pl. 9, figs 8-10. Zilch, 1953: 137.
Laidlaw and Solem, 1961: 530.

Amphidromus perversus—Collinge, 1902: 81-83 (not Linnaeus, 1758).

Amphidromus atricallosus var. *perakensis*—Laidlaw and Solem, 1961: 647-648. Abbott, 1989: 160

Amphidromus aureus Martyn (part)—Pilsbry, 1900: 163-164, pl. 54, figs 76, 77.

Amphidromus atricallosus perakensis—Ng and Wee, 1994: 82.

Material examined: Nee Soon Nature Reserve, Singapore: 2067 (2D), 2133 (1D), 2198 (10D). Tulai Island near Tioman Island, Malaysia: 2009 (1D), 2237(1D+2S), 2288 (1D).

Shell (Fig. 4.4F, G; Table 4.1): *A. (A.) atricallosus perakensis* is characterized by a white parietal callus, narrow white subsutural band, and yellowish inside the aperture; columella white; columella plait ranging from distinctly folded to simple and straight; parietal callus white or transparent; varices always absent.

Radula (Fig. 4.11A-C): Each row containing about 193 (95-(53-56)-1-(53-56)-97) teeth. Central tooth monocuspid and lateral teeth bicuspid (Fig. 4.11A). Marginal teeth start from tooth number 53 to 56 outward (Fig. 11B, C).

Genital system (Fig. 4.12C): As described by Collinge (1902), atrium (at) long (n=5). Penis (p) conical and half the length of vagina. Flagellum (fl) short with prominent and swollen distal coil. Appendix (ap) small and almost the same length as epiphallus (Fig. 4.12C). The internal penial wall, and the vagina and epiphallus are similar to the two subspecies described above.

Distribution (Fig. 4.1): This subspecies has been recorded in the southern part of peninsular Malaysia including Singapore. Previous records of this species were from Johore, Pahang, Penang and Perak in Peninsular Malaysia (Fulton, 1901; Collinge, 1902; Laidlaw and Solem, 1961). In the present study, we have collected specimens from Nee Soon Nature Reserve in Singapore and from Tulai Island off the east coast of Peninsular Malaysia.

Remark: *Amphidromus (A.) atricallosus perakensis* differs from *A. (A.) atricallosus leucoxanthus* in possessing a narrowly whitish subsutural area, usually absence of any dark varices, slightly broad aperture, large last whorl,

short conic spire and slightly enlarged coiled portion of the epiphallic caecum (Fig. 4.12C). On current evidence it is confined to the southern Malaysian Peninsula (southern Thailand, Malaysia and Singapore) (Laidlaw and Solem, 1961; this study).

***Amphidromus (Amphidromus) atricallosus* subspecies**
(Figures 4.2, 4.4H-I, 4.11D-F, 4.12D, 4.13D, 4.14E-F)

Material examined: Koh Tachai, Pangnga, southern Thailand in the Andaman Sea: 2215 (Fig. 4.4H), 2011 (10S) (Fig. 4.4I), 2232 (5S), 2013 (19S), 2014 (45S), 2233 (12S), 2277 (5S).

Shell (Fig. 4.4H, I; Table 4.1): Shell relatively small, elongate conic, solid, and always sinistral. Whorls slightly convex, spire conic and suture depressed. Last whorl rounded, elongate with sealed umbilicus. Shell glossy yellow with narrow to wide white subsutural band. Apex acute; one or more black to brown varices present. Aperture ovate; peristome whitish with thickened, expanded and reflected lip. Parietal callus thick, white to brown or black. Columella straight, vertical, without columella plait.

Radula (Fig. 4.11D-F): Radula teeth similar to those of typical subspecies. Each rows containing about 171 (85-(37-39)-1-(37-39)-85) teeth. Central tooth monocuspid with wide spatulate cusp (Fig. 4.11D). Lateral teeth bicuspid. Marginal teeth tricuspid started from tooth number 37 to 39 outwards (Fig. 4.11E, F).

Genital system (Figs 4.12D, 4.13D, 4.14E-F): Atrium (at) long (n=7). Penis (p) somewhat short and cylindrical and approximately half the length of vagina. Epiphallus (e) long. Flagellum (fl) small and distally folded with appendix (ap) located beyond coiled portion (Fig. 4.12D). Penial pilasters (pp) smooth longitudinal ridges. Penial verge (pv) short and conic (Fig. 4.13D).

The spermatophore (n=1) is long and pentagonal in cross-section (Fig. 4.14E). It is very similar in general shape and structure to that described above for *A. (A.) atricallosus atricallosus*. One examined spermatophore possessed 37 oblong knobs along one keel of the coiled expanded section (ces) (Fig. 4.14F).

The reproductive system is similar to that of the other subspecies. However, the smaller size of the genitalia in relation to shell size (Table 4.1) combined with differences in the spermatophore, particularly in the coiled expanded section, allow this subspecies to be recognised.

Distribution (Fig. 4.2): *Amphidromus (A.) atricallosus* ssp.1 is known only from the type locality of Koh Tachai, an island in the Andaman Sea off Pangnga Province, southern Thailand. Specimens were found on the trunks and leaves of trees in dry evergreen forest on a low sandstone hill, near a sandy beach on the eastern side of the island.

Remarks: *Amphidromus (A.) atricallosus* ssp. is distinct from the other three nominate subspecies in exhibiting smaller shell size (Table 4.1), shorter penis (Fig. 4.12D), in being invariably sinistral with a yellowish colour. It differs from the nominotypical subspecies in being elongate conic with convex whorl and depressed suture. From *A. (A.) atricallosus leucoxanthus* it differs in possessing a brown to black parietal callus, elongated conic shells and slightly shorter vagina. It can be distinguished from *A. (A.) atricallosus perakensis* by the brown or black parietal callus, varices always present, straight columella and slightly shorter vagina.

Living animals exhibit a colour pattern similar to that described above. The distinctive features of this subspecies indicate that it may have been isolated for a considerable time and one explanation could be that it became separated from mainland populations when the island of Koh Tachai was formed by rising sea levels during the Quaternary. The founder effect could also account for lack of shell variability with all examples being sinistral, yellow and small shell.

***Amphidromus (Amphidromus) schomburgki* (Pfeiffer, 1860)**

Diagnosis: Shell relatively large, ovate, solid, umbilicus imperforate, dimorphic. Last whorl expanded and rounded, spire short conic, whorls convex and suture depressed. Periostracum deciduous or oblique greenish radial streaks on tinted-pink to whitish ground colour. Apex deep purplish or white; later whorls possess purplish suprasutural band, which fades by second and third whorls. Spire becomes purplish-pink as periostracum lost. Aperture broad and truncate-ovate. Peristome purple or brown, thickened, lip folded and reflected. Columella purple and straight. Parietal callus thickened, dark purple or brown. Varix absent.

External features: Living animals greenish-gray. Body and foot bright reticulated creamy-white. Foot margin and underside pale yellowish to brown. Tentacles drumstick shaped, proximally greenish-gray and pale yellowish distally with black eye spots on the tips. Lower tentacles pale gray with yellowish tips, being same colour as around mouth. Mantle collar dark brown to deep purple; mantle cavity light brown to whitish or without pigment except in whitish specimens.

Remarks: Early records indicated that *A. (A.) schomburgki* may be restricted to eastern Thailand (Pilsbry, 1900). However, Solem (1965) reported the species from Pranburi District in Prachuap Khirikhan in southern Thailand. In the present study we extend the current known range to include Ban Khok Klang, Tao Ngoi District in Sakonnakhon, northeastern Thailand and Phung Chang cave in Pangnga, southern Thailand. More extensive surveys are needed to determine the full range of *A. (A.) schomburgki*, particularly in northeastern and southern Thailand.

Our surveys have demonstrated that *Amphidromus (A.) schomburgki* is endemic to Thailand and is not a common species as reported by Laidlaw and Solem (1961) and Solem (1965). Populations appear to be rapidly declining through human pressure and are restricted to vulnerable, generally isolated and small fragments of forest. It is an uncommon snail and is possibly threatened.

Laidlaw and Solem (1961) could not place *A. (A.) schomburgki* with confidence in a recognized subgeneric category. They associated *A. (A.) schomburgki* loosely with *Amphidromus (Syndromus)*, but included it with their group III 'basal' species group. The large and thick chirally dimorphic green radially streaked shell and long epiphallic caecum (flagellum and appendix), support placing *A. (A.) schomburgki* in *Amphidromus (Amphidromus)* s. str. as done by Pilsbry (1900) and Zilch (1953).

Materials of the remaining five species that Laidlaw and Solem (1961) included in their group III was not available for examination and their affinities are unknown.

***Amphidromus (Amphidromus) schomburgki schomburgki* (Pfeiffer, 1860)**
(Figures 4.2, 4.4J-L, 4.16A-C, 4.17A-E)

Bulimus schomburgki Pfeiffer, 1860: 137, pl. 51, fig. 9.

Bulimus crossei Pfeiffer, 1862: 43-44, pl. 5, fig. I.

Amphidromus schomburgki—Morlet, 1889: 127. Fulton, 1896: 90-91. Pilsbry, 1900: 182, pl. 59, fig. 30. Gude, 1903a: 8. Laidlaw and Solem, 1961: 526, 657. Solem, 1965: 618-619. Richardson, 1985: 42. Abbott, 1989: 161.

Amphidromus schomburgki var. *crossei*—Pilsbry, 1900: 182, pl. 59, fig. 31. Laidlaw and Solem, 1961: 526, 613.

Amphidromus kobelti Möllendorff, 1902: 157 (not Rolle, 1893). Laidlaw and Solem, 1961: 633.

Amphidromus moellendorffi Haas, 1934: 96, fig. 13 (new name for *A. kobelti* Möllendorff, 1902). Zilch, 1953: 137, pl. 25, fig. 43. Laidlaw and Solem, 1961: 526, 641.

Amphidromus schomburgki var. *moellendorffi*—Solem, 1965: 526, 618.

Material examined: Khao Lookchang, Nakhonratchasima: 2040 (7D), 2051 (20D), 2052 (9D). Khonburi District, Nakhonratchasima: 2054 (1D). Koh Kud, Trat: 2002 (8D), 2004 (13D), 2005 (17D), 2036 (43D). Khao Kiew, Chonburi: 2001 (3D), 2031 (65D+21S), 2032 (31D+10S). Sriracha District, Chonburi: 2217 (1D). Phung Chang cave, Pangnga: 2053 (1S).

Shell: (Fig. 4.4J-L; Table 4.3): Chirally dimorphic; periostracum with irregular pink-tinted radial streaks on cream background; apex purplish; suprasutural band present or absent; peristome, columella and parietal callus purple or brownish.

Radula (Fig. 4.16A-C): Each row containing about 220 (107-(72-73)-1-(72-73)-112) teeth. Central tooth monocuspid with gouge shaped depression (Fig. 4.16A). Lateral teeth bicuspid, endocone more convex with curved cusp, and ectocone large, broad with truncate posterior cusp (Fig. 4.16A). Lateral teeth gradually transform to tricuspid marginal teeth from 72-73 outwards (Fig. 4.16B). Outermost marginal teeth asymmetric, endocone of medium size with rounded cusp, mesocone large with curved posterior margin, and ectocone small with sharp cusp (Fig. 4.16C).

Genital system (Fig. 4.17A-E): Atrium (at) relatively long (n=5). Penis (p) slender, conic and short; with weak folded keel around the base of penial verge. Epiphallus (e) long, coiled and twisted upon itself. Long slender flagellum (fl) extends from epiphallic coil and terminates in folded coil. Appendix (ap) longer than flagellum. Vas deferens (vd) small tube passing from free oviduct (fo) and terminating distally on epiphallus. Penial retractor muscle (pr) long and inserts distally on penis (Fig. 4.17A).

Internal penial wall corrugated with thick vertical pilasters (pp), which form series of protuberances around penial verge. Penial verge (pv) small, conic and smooth with basal and folded spiral ridge and orifice (pvo) located at the tip (Fig. 4.17B). Internally flagellum possesses strong and smooth longitudinal epiphallic pilasters (ep). Ridges smooth around entrance of vas deferens (evd) (Fig. 4.17C).

An individual specimen of *A. (A.) schomburgki* observed with everted male genitalia (Fig. 4.17D), atrium and penis being fully extended. Atrium showed distinct vertical ridges, swollen at conical base. Introverted penis formed elongate, proboscis-like structure with well-defined penial pilasters (as shown in Fig. 4.17B), ridges being absent proximal to penial verge. Penial verge base enlarged and forms spiral ridge with penial verge located at the tip.

Table 4.3. Shell size variation in *A. (A.) schomburgki schomburgki*, *A. (A.) schomburgki* ssp.1 and *A. (A.) givenchyi*. Catalogue numbers of specimens are indicated in parentheses.

Species, Locality and CUMZ nos.	Number of adult shell examined	Ranges, Mean \pm SD in mm of:			Whorl Ranges
		Shell Height	Shell Width	h/d Ratio	
<i>A. (A.) schomburgki schomburgki</i> (Pfeiffer, 1860)					
Khao Kiew, Chonburi (2031, 2032)	101	32.83-51.39 44.48 \pm 3.40	20.11-29.07 25.89 \pm 1.77	1.55-1.87 1.72 \pm 0.07	6 ⁵ / ₈ - 7 ⁵ / ₈
Khao Lookchang, Nakhonratchasima (2040, 2051, 2052)	11	42.79-49.38 46.97 \pm 2.02	25.43-28.05 26.47 \pm 0.84	1.68-1.88 1.78 \pm 0.06	7 ¹ / ₈ - 7 ⁶ / ₈
Koh Kud, Trat (2004, 2005, 2036)	27	36.07-50.29 42.11 \pm 3.49	20.59-26.79 23.27 \pm 1.34	1.67-1.85 1.81 \pm 0.08	6 ⁴ / ₈ - 7 ² / ₈
<i>A. (A.) schomburgki</i> ssp.					
Tao Ngoi District, Sakonnakhon (2017, 2040, 2055, 2077, 2219)	15	45.39-57.98 50.79 \pm 3.09	32.96-27.33 30.11 \pm 1.53	1.54-1.79 1.69 \pm 0.07	7 ¹ / ₈ - 7 ⁷ / ₈
<i>A. (A.) givenchyi</i> Geret, 1912					
Phataem, Ubonratchathani (2003, 2056)	22	31.60-39.62 36.02 \pm 2.19	19.94-22.74 21.41 \pm 0.84	1.54-1.84 1.68 \pm 0.08	6 ⁴ / ₈ - 7 ⁴ / ₈
Naku District, Kalasin (2158, 2218)	7	45.13-50.01 47.12 \pm 1.53	25.35-28.20 26.90 \pm 0.97	1.70-1.81 1.75 \pm 0.04	7 ³ / ₈ - 7 ⁷ / ₈

Female organs and associated features closely resemble to those shown in Figures 4.17A-B and 4.17E. Internally vagina possesses longitudinal pilasters (vp). These smooth and crenulated proximal to genital orifice and extend to middle of vagina; proximal to free oviduct pilasters become uneven and discontinuous (Fig. 4.17B).

Distribution: Early records of *Amphidromus (A.) schomburgki schomburgki* indicate a distribution west of the Cambodian Elephant chain of mountains to Sakeo in eastern Thailand (Pilsbry, 1900; Laidlaw and Solem, 1961). Solem (1965) added records from other localities in Eastern Thailand, namely Hinlab, Khao Sabap, Pak Chong, Sriracha, Aranya Predesha in eastern Thailand and Pran (?) in northern peninsular Thailand. Here we add records from Koh Kud off Trat, Khao Kiew and Sriracha of Chonburi, Khonburi District and Khao Lookchang of Nakhonratchasima in eastern Thailand; Phung Chang in Pangnga, southern peninsular Thailand.

Remark: The colour variation found in dextral examples that we collected from Koh Kud (Fig. 4.4L) and specimens from Khao Kiew, Khao

Look Chang and Phung Chang include the range described for *A. crossei* (Pfeiffer, 1862) and *A. moellendorffi* Haas, 1934. These nominal taxa are clearly junior synonyms of *A. (A.) schomburgki schomburgki*.

***Amphidromus (Amphidromus) schomburgki* ssp.**

(Figures 4.2, 4.4M, 4.16D-F, 4.17F)

Material examined: Ban Khok Klang, Tao Ngoi District, Sakonnakhon: 2296 (Fig. 4.4M); 2017 (19D), 2055 (1D), 2077 (9D), 2199 (3D), 2219 (20D).

Shell: (Fig 4.4M; Table 4.3): Relatively large; periostracum deciduous with oblique greenish radial streaks on whitish background; apex white; later whorls with or without purplish suprasutural band; peristome, columella and parietal callus whitish.

Radula (Fig. 4.16D-F): Each row containing about 194 (96-(63-67)-1-(63-68)-97) teeth. Central tooth monocuspid (Fig. 4.16D). Lateral teeth bicuspid and transformed to tricuspid marginal teeth from 63-67 outwards (Fig. 4.16E). Marginal teeth asymmetric tricuspid (Fig. 4.16F).

Genital system (Fig. 4.17F): Atrium (at) short (n=5); penis (p) slender and about half length of vagina (v); epiphallus (e), flagellum (fl) and appendix (ap) the same length as in nominotypical subspecies. The external form of the female genitalia and the internal wall of the penis, vagina and epiphallus are the same as for the nominotypical subspecies.

Distribution (Fig. 4.2): Known only from the type locality of Ban Khok Klang, Tao Ngoi District, Sakonnakhon in northeastern Thailand, which is remote from the nominotypical type locality.

Remarks: *Amphidromus (A.) schomburgki* ssp.1 differs from the nominotypical subspecies in having a dextral shell, lacking pink or bright purple on shell, peristome and parietal callus. The differences from *A. (A.) givenchy* are the greenish periostracum, convex whorls, lack of the dark green subsutural band, and presence of a purplish to brownish suprasutural band.

Twenty one specimens (total n=130) of our collection from Khao Kiew, and previous examples from Pak Chong and Chuntut populations (Solem, 1965) exhibited a white shell, with no indication of purple or brownish colour on the parietal callus, lip and apex. However, the living animals possess a greenish gray body with yellowish foot and tentacles, mouth parts and black eye spots and are identical with the nominotypical subspecies. Thus we

conclude that these white-shelled populations probably represent a morphotype of *A. (A.) schomburgki*.

Amphidromus (Amphidromus) givenchy Geret, 1912

(Figures 4.2, 4.4N-Q, 4.18, 4.19)

Amphidromus givenchy Geret, 1912: 55-56, pl. 2, figs 21-22. Laidlaw and Solem, 1961: 526, 621. Richardson, 1985: 43.

Material examined: Phataem, Ubonratchathani: 2003 (3D), 2050 (1D), 2056 (43D), 2271 (9D), 2273 (4D). Phu Lom Khao, Na Ku District, Kalasin: 2158 (1D), 2218 (4D), 2271 (9D), 2273 (4D). Luang Prabang, Laos: 2049 (1D). Dong Phu Wiang, Sawanakhet, Laos: 2016 (2D).

Shell (Fig. 4.4N-Q; Table 4.3): Shell relatively large, ovate-conic, solid, usually dextral; umbilicus imperforate or rimate; spire conic, suture wide and slightly flattened. Last whorl relatively large, rounded-ovate. Shell surface glossy, with smooth or minute and continuous greenish radial streaks, most distinct on last whorl. A narrow dark green subsutural band present and fades to yellowish or disappears in upper whorls. Apex acute; tiny black apex present in some specimens. Aperture truncated and oblique; peristome thickened, expanded and reflected. Parietal callus white or yellowish when transparent. Columella white, straight and perpendicular. Dark-green or brown varix rarely present.

Radula (Fig. 4.18A-C): Radula teeth tightly packed, each row containing about 153 (75-(39-42)-1-(39-42)-77). Central tooth monocuspid, broadly gouge or spatulate shaped (Fig. 4.18A). Lateral teeth bicuspid, endocone relatively small with sharp cusp, ectocone large, broad and rounded with posterior cusp (Fig. 4.18A). Marginal teeth start from 39 to 42 outwards (Fig. 4.18B). Endocone medium size with wide notch, mesocone large with curved posterior margin, and ectocone minute with sharp cusp. Outermost marginal teeth tricuspid with wide and deep endocone-ectocone notch (Fig. 4.18C).

Genital system (Fig. 4.19A-D): Atrium (at) relatively long (n=4). Penis (p) long and slender. Epiphallus (e) relatively short and curved. Flagellum (fl) small and equal in length to epiphallus; proximal to appendix it enlarged and coiled. Appendix (ap) slender and short. Vas deferens (vd) thin and enters from free oviduct (fo) to distal epiphallus. Penial retractor muscle (pr) long and inserts proximally near penis (Fig. 4.19A).

Internal penial wall corrugated with series of longitudinal pilasters (pp) as in above species. Penial verge (pv) smooth and cylindrical with long orifice

(pvo) at the tip (Fig. 4.19B). Internally flagellum possesses strong epiphallic pilasters (ep). Central pilaster runs from flagellum and extends over the entrance to vas deferens (evd) as a flap (Fig. 4.19C).

Vagina (v) slender and cylindrical. Gametolytic duct (gd) long; proximal to vagina it wide and distally it tapers abruptly to small tube that connects to enlarged gametolytic sac (gs). Free oviduct (fo) short and oviduct (ov) smaller than in other species. This may be due to seasonal changes outside of reproductive season. Albumen gland (ag) curved (Fig. 4.19A). Hermaphroditic gland (hg) possesses numerous small lobules; hermaphroditic duct (hd) small, convoluted and connected to head of talon (ta) (Fig. 4.19D).

Internally vagina possesses longitudinal vaginal pilasters (vp), which corrugated proximal to genital orifice and then smooth and corrugated again for about one third of the length of vagina. This corrugated area followed by smooth section and further corrugations, which extend up to gametolytic duct (Fig. 4.19B).

External features: Living animals exhibit pale gray body with creamy-white reticulated pattern; underside of foot pale yellowish. Mantle cavity pale creamy-brown covered with fine black spots. Mantle edge and mantle collar creamy to grayish. Eye tentacles drumstick shaped proximally gray fading distally to black eye spots on the tips. Lower tentacles and mouth pale yellowish.

Distribution (Fig. 4.2): The type locality of *A. (A.) givenchy* was not given in the original description, which was based on a single unlocalised shell. Laidlaw and Solem (1961) suggested that the type locality would be in Cambodia. We obtained *A. (A.) givenchy* in northeastern Thailand and Laos and from the known distribution, it probably does occur in Cambodia. The specimens examined were collected from Phataem National Park, Ubonratchathani and Phu Lom Khao, Naku District of Kalasin in the northern Thailand; Luang Prabang and Sawanaket in Laos. All records are from dry dipterocarp forest on sandstone hills at elevations of 300 to 500 m above sea level.

Remarks: Examples of *A. (A.) givenchy* collected from Phataem National Park (Fig. 4.4N, O) and Luang Prabang show an equal shell size (Table 4.3) and most closely resemble the holotype. They possess a dark green subsutural band, brown embryonic shell and the periostracum of the body whorl is yellow-green. Small juvenile specimens collected from Phataem possessed a narrow brown spiral band at the angulation of the last whorl (Fig. 4O), which is not present in adult shells. In some individuals, the brown spiral band was present as a suprasutural band on earlier whorls. Specimens from Phu

Lom Khao, Kalasin (Fig. 4.4P) exhibit a similar colour pattern. However, shells reached a larger size than in other populations (Table 4.3). Specimens from Sawanakhet, Laos possessed a relatively long and slender shell shape with a yellow-brown periostracum, rather than green, and pale brown subsutural band (Fig. 4.4Q).

Laidlaw and Solem (1961) considered that *A. (A.) givenchyi* differed in minor characters from, and was probably synonymous with, *A. (A.) schomburgki*, which was followed by Richardson (1985). Other than the holotype, our collections represent the only recorded material of this species and we provide the first detailed description, based on extensive material.

Amphidromus (A.) givenchyi differs from *A. (A.) schomburgki*, in the shell being relatively small (Table 4.3) and slender, in possessing a continuous yellowish green periostracum and in exhibiting a distinctive dark green subsutural band. The reproductive anatomy of *A. (A.) givenchyi* consists of a longer and slender penis, shorter epiphallus and a shorter appendix than *A. (A.) schomburgki* (Figs 4.17A, 4.19A).

A number of taxa bear a superficial resemblance to *A. (A.) givenchyi*. *Amphidromus roseolabiatus* Fulton, 1896, *A. haematostomus* var. *viridis* Möllendorff, 1898, and *A. haematostomus* var. *varians* Möllendorff, 1898 are dextral and lack a pink or bright purple peristome and parietal callus. They possess a straight columella, a shell without spirally green subsutural band, and have the upper three whorls pale brown or white. *Amphidromus mouhoti* (Pfeiffer, 1861) possesses a larger and wider shell and the parietal callus is transparent or whitish. The distinct dark green subsutural band of the last whorl is gradually transformed to yellow or white or may be completely absent in the upper whorls. In addition, a narrow white band is present beneath the green subsutural band, the peristome is white and the columella and apex pale brown. *Amphidromus laosianus* var. *albocaerulescens* Bavay, 1898 possesses a wider shell, with very fine yellow-greenish radial striations on the last whorl. The internal surface of the aperture is white or a creamy whitish, the columella is straight, the parietal callus transparent and the lip white. *Amphidromus smithii* Fulton, 1896 and *A. ventrosulus* Möllendorff, 1900 possess larger shells, which are dextral, lack oblique banding on the upper spire and have the apex and aperture white.

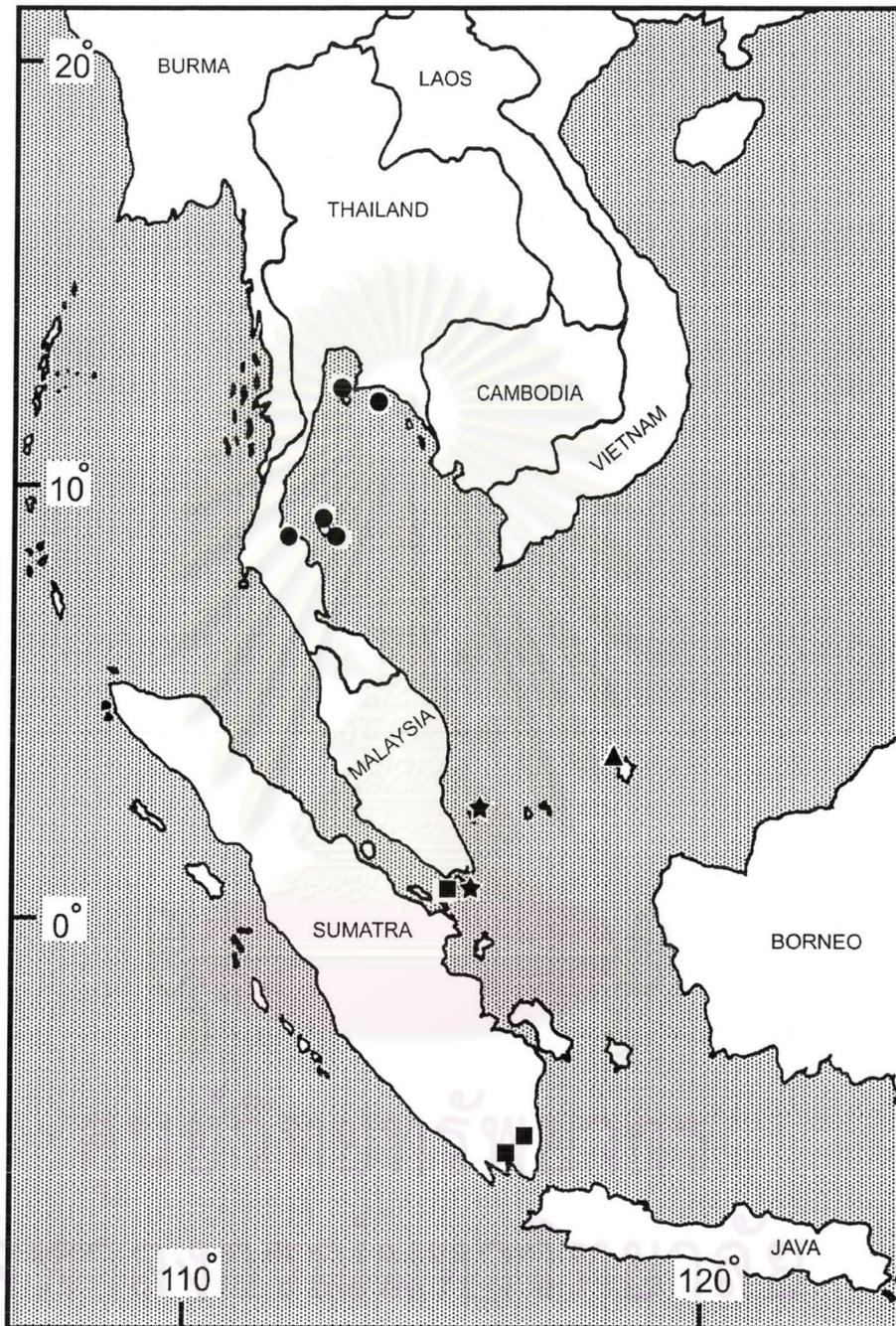


Figure 4.1 Distributions of some *Amphidromus* (*Amphidromus*) species; *A. (A.) perversus natunensis* (▲), *A. (A.) inversus inversus* (■), *A. (A.) inversus annamiticus* (●) and *A. (A.) atricallosus perakensis* (★).

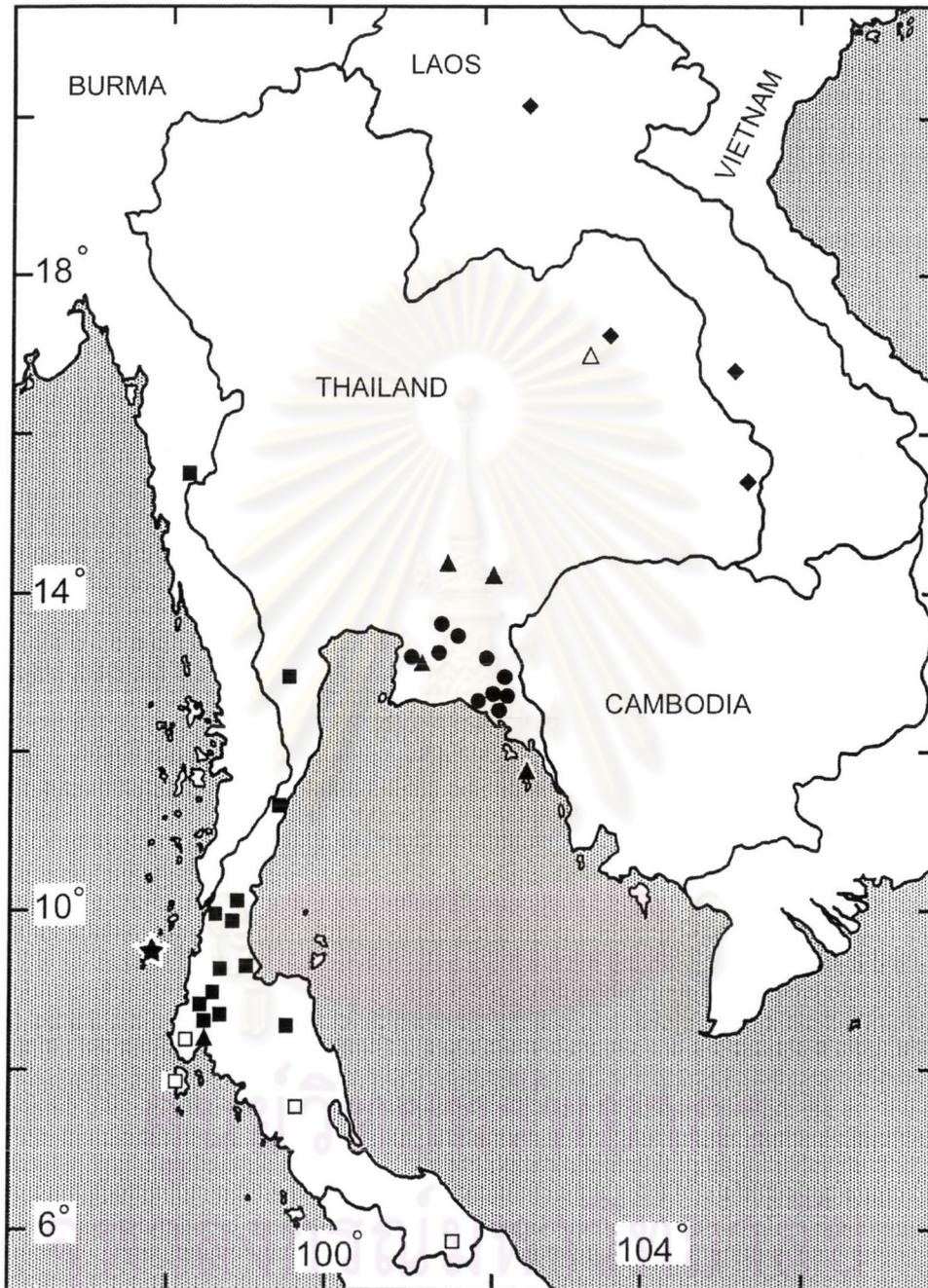
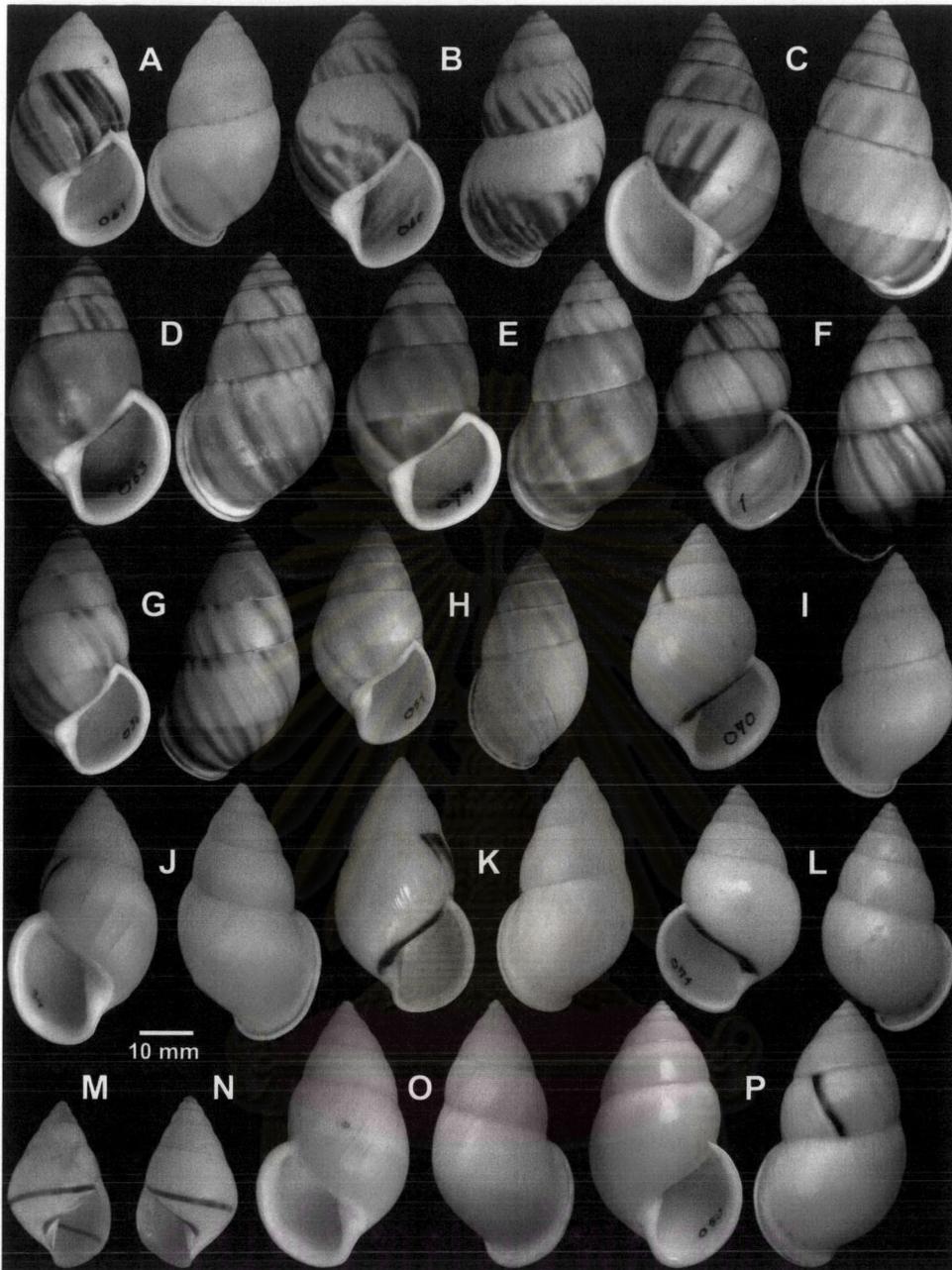
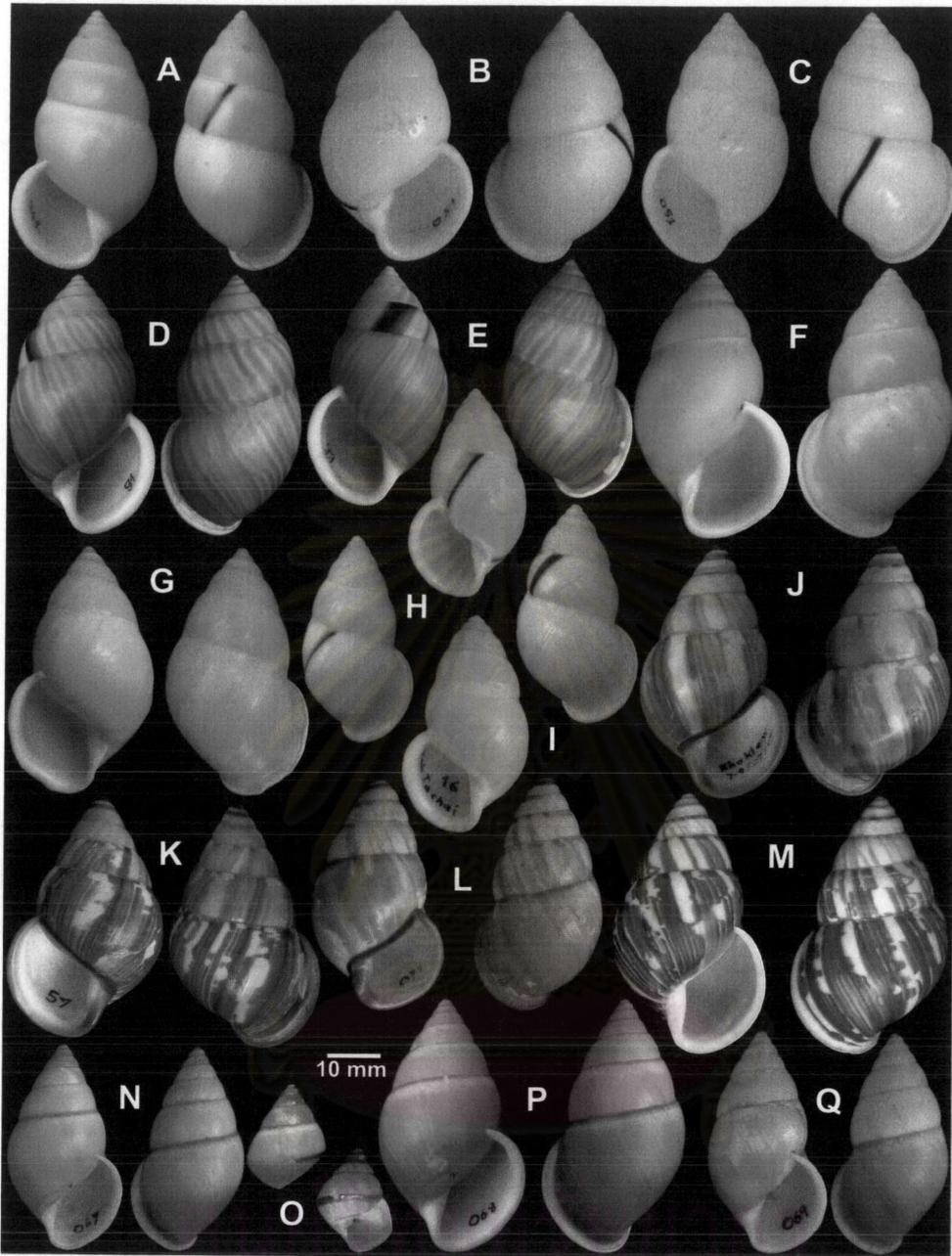


Figure 4.2 Distributions of some *Amphidromus* (*Amphidromus*) species; *A.* (*A.*) *atricallosus atricallosus* (■) and an uncertain status subspecies (□), *A.* (*A.*) *atricallosus leucoxanthus* (●), *A.* (*A.*) *atricallosus* ssp. (★), *A.* (*A.*) *schomburgki schomburgki* (▲), *A.* (*A.*) *schomburgki* ssp. (△), and *A.* (*A.*) *givenchy* (◆).



Figures 4.3 Shell characteristics of some *Amphidromus* (*Amphidromus*) species. **A, B.** *A. (A.) perversus natunensis* from Great Natuna Island, Indonesia (2177). **C, D.** *A. (A.) inversus inversus*, (**C**) from Indonesia (2235), and (**D**) from Botanic Garden, Singapore (2183). **E-H.** *A. (A.) inversus annamiticus*, (**E**) from Koh Lueam, Chonburi (2190), (**F**) from Koh Juang, Chonburi (2062), and (**G, H**) from Koh Samui, Suratthani (2186). **I-N.** *A. (A.) atricallosus atricallosus*, (**I, K, L**) from Ban Takhun, Suratthani (2019), (**J**) from Khao Sok, Suratthani (2021), and (**M, N**) from Ban Takhun, Suratthani, showing the juveniles specimens with reddish brown spiral band (2191). **O.** *A. (A.) atricallosus*, an uncertain status subspecies from Wat Suwannakhuha, Pangnga (2220). **P.** *A. (A.) atricallosus leucoxanthus* Makok waterfall, Chantaburi (2162).



Figures 4.4 Shell characteristics of some *Amphidromus* (*Amphidromus*) species. **A-E.** *A. (A.) atricallosus leucoxanthus*, (**A-C**) from Makok waterfall, Chantaburi (2162), and (**D, E**) from Makham District, Chantaburi (2214). **F, G.** *A. (A.) atricallosus perakensis* from Nee Soon, Singapore (2282). **H, I.** *A. (A.) atricallosus* ssp., Koh Tachai, Pangnga (2215, 2011). **J-L.** *A. (A.) schomburgki schomburgki*, (**J, K**) from Khao Kiew, Chonburi (2031) and (**L**) from Koh Kud, Trat (2005). **M.** *A. (A.) schomburgki* ssp. from Ban Khok Klang, Tao Ngoi District, Sakonnakhon (2296). **N-Q.** *A. (A.) givenchyi*, (**N**) from Phataem, Ubonratchathani (2003), (**O**) from Phataem, Ubonratchathani, showing the juveniles specimens with reddish brown spiral band (2273), (**P**) from Phu Lom Khao, Nakhu District, Kalasin (2218), and (**Q**) from Sawanakheth, Laos (2016).

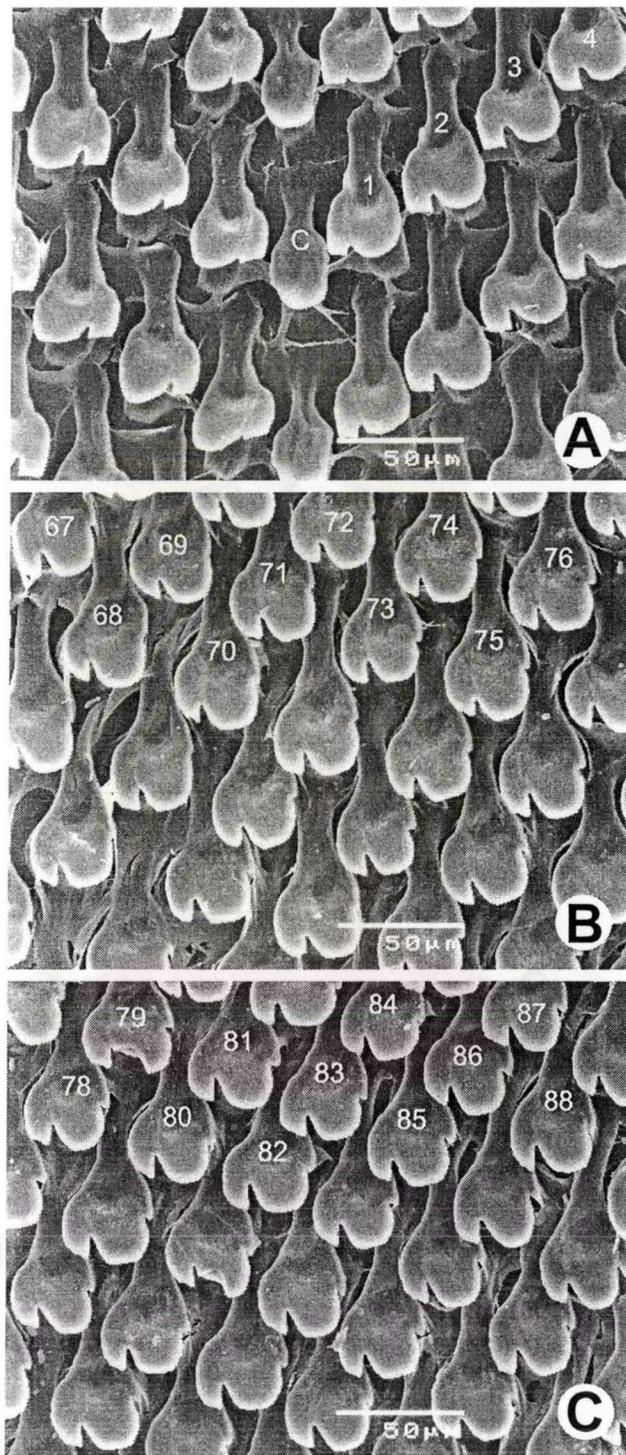


Figure 4.5 SEM images of the radula of *A. (A.) perversus natunensis* (2177). **A.** Central tooth with the first to the fourth lateral teeth. **B.** Lateral teeth with the tricuspid marginal teeth transition. **C.** Outermost marginal teeth. Numbers indicated order of lateral and marginal teeth. Central tooth indicated by 'C'.

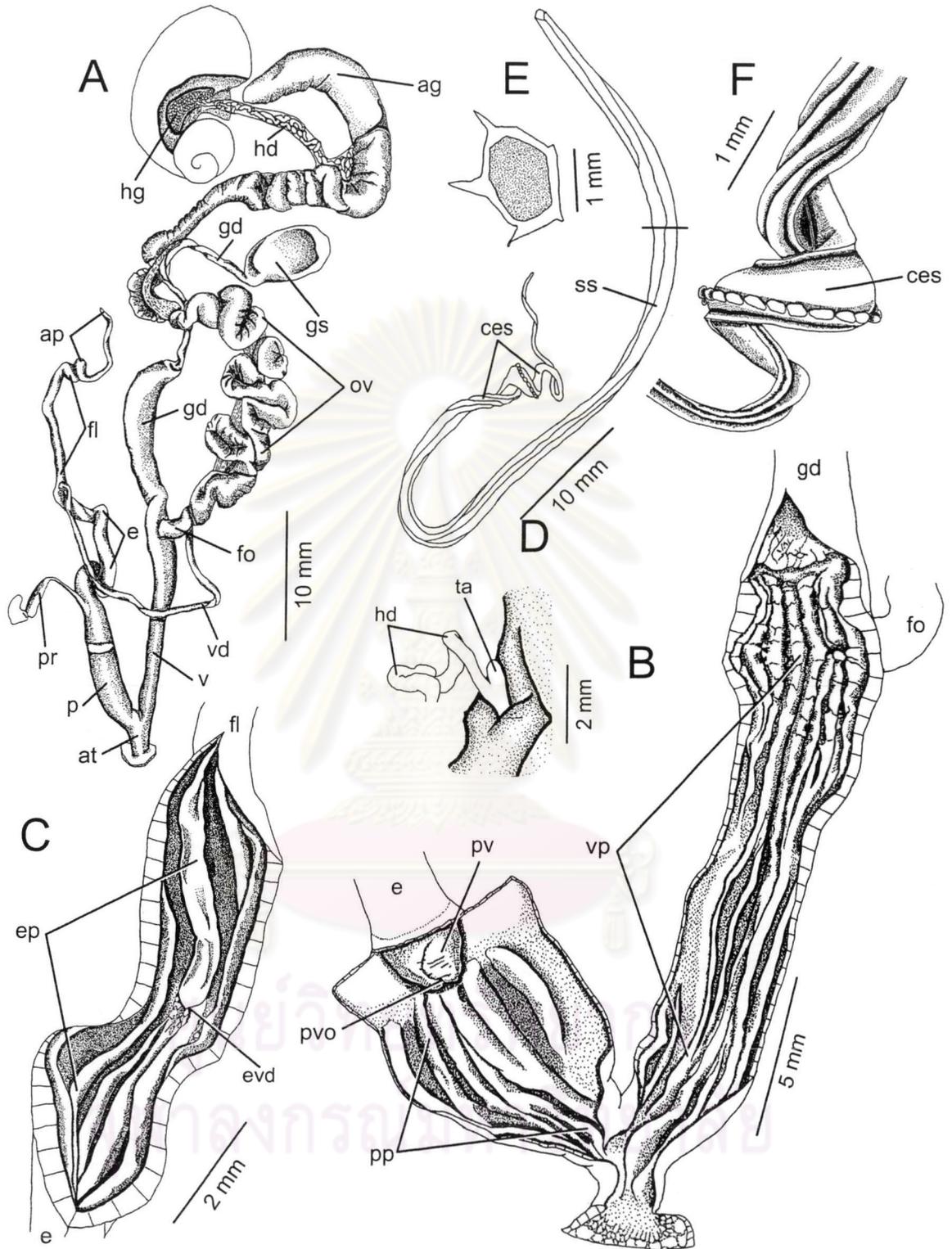


Figure 4.6 *Amphidromus (A.) perversus natunensis* (2177, October 2002)—Anatomy. **A.** The whole genital system. **B.** Interior structure of penis, atrium and vagina chamber. **C.** Interior structure of epiphallus. **D.** Details of hermaphroditic duct and talon junction. **E.** Entire a spermatophore including cross-section at the middle of sperm sac. **F.** Posterior coiled expanded section of spermatophore.

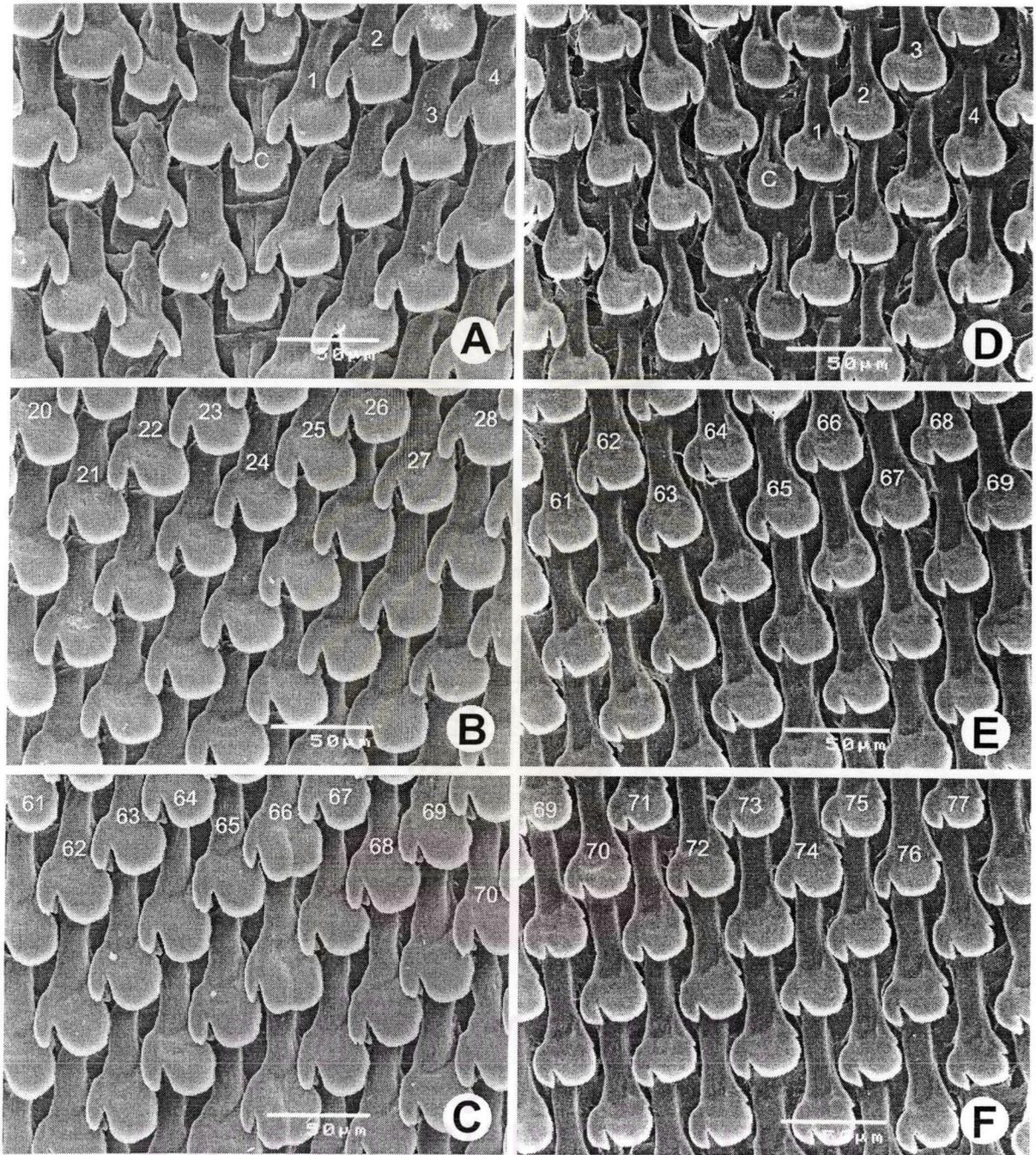


Figure 4.7 SEM images of the radula. **A-C.** *A. (A.) inversus inversus* (2183), **(A)** central tooth with the first to the fourth lateral teeth, **(B)** lateral teeth with the tricuspid marginal teeth transition, and **(C)** outermost marginal teeth. **D-F.** *A. (A.) inversus annamiticus* (2186), **(D)** central tooth with the first to the fourth lateral teeth, **(E)** lateral teeth with the tricuspid marginal teeth transition, and **(F)** outermost marginal teeth. Numbers indicated order of lateral and marginal teeth. Central tooth indicated by 'C'.

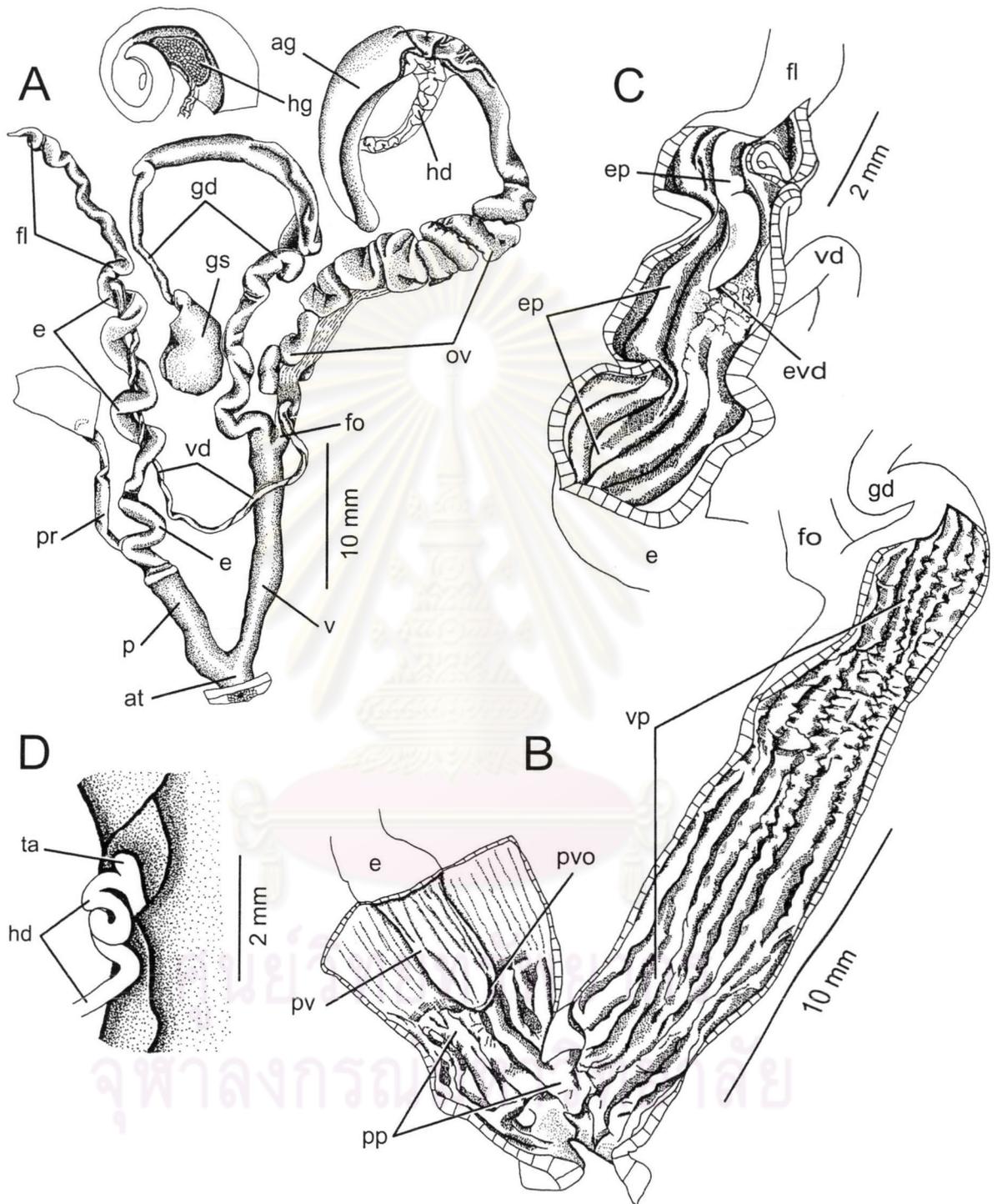


Figure 4.8 *Amphidromus (A.) inversus inversus* (2183, 3 December 2001)—Anatomy. **A.** The whole genital system. **B.** Interior structure of penis, atrium and vagina chamber. **C.** Interior structure of epiphallus. **D.** Details of hermaphroditic duct and talon junction.

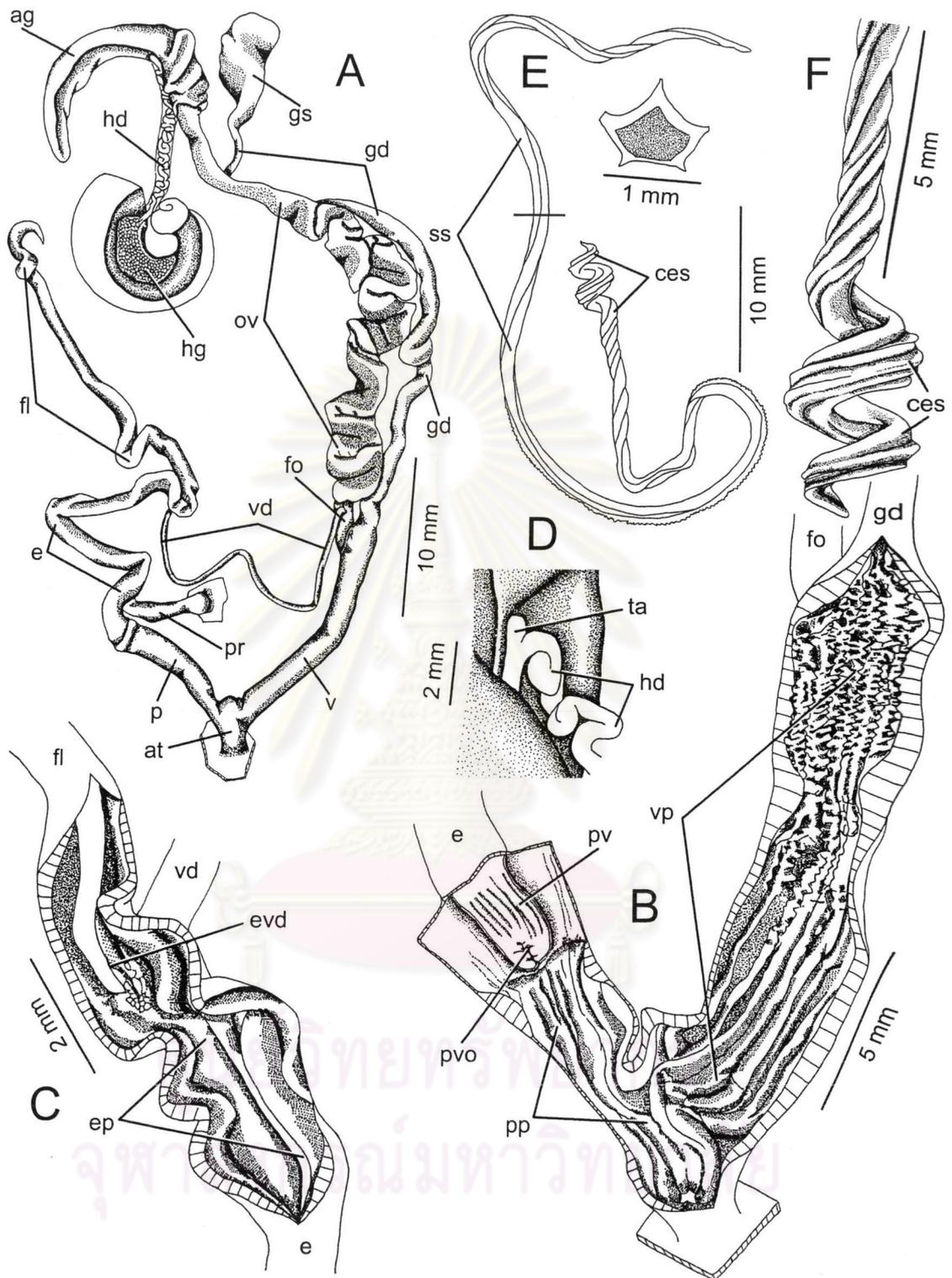


Figure 4.9 *Amphidromus (A.) inversus annamiticus* (2186, 10-11 February 2000)—Anatomy. **A.** The whole genital system. **B.** Interior structure of penis, atrium and vagina chamber. **C.** Interior structure of epiphallus. **D.** Details of hermaphroditic duct and talon junction. **E.** Entire body of spermatophore including cross-section at the middle of sperm sac. **F.** Posterior coiled expanded section of spermatophore.

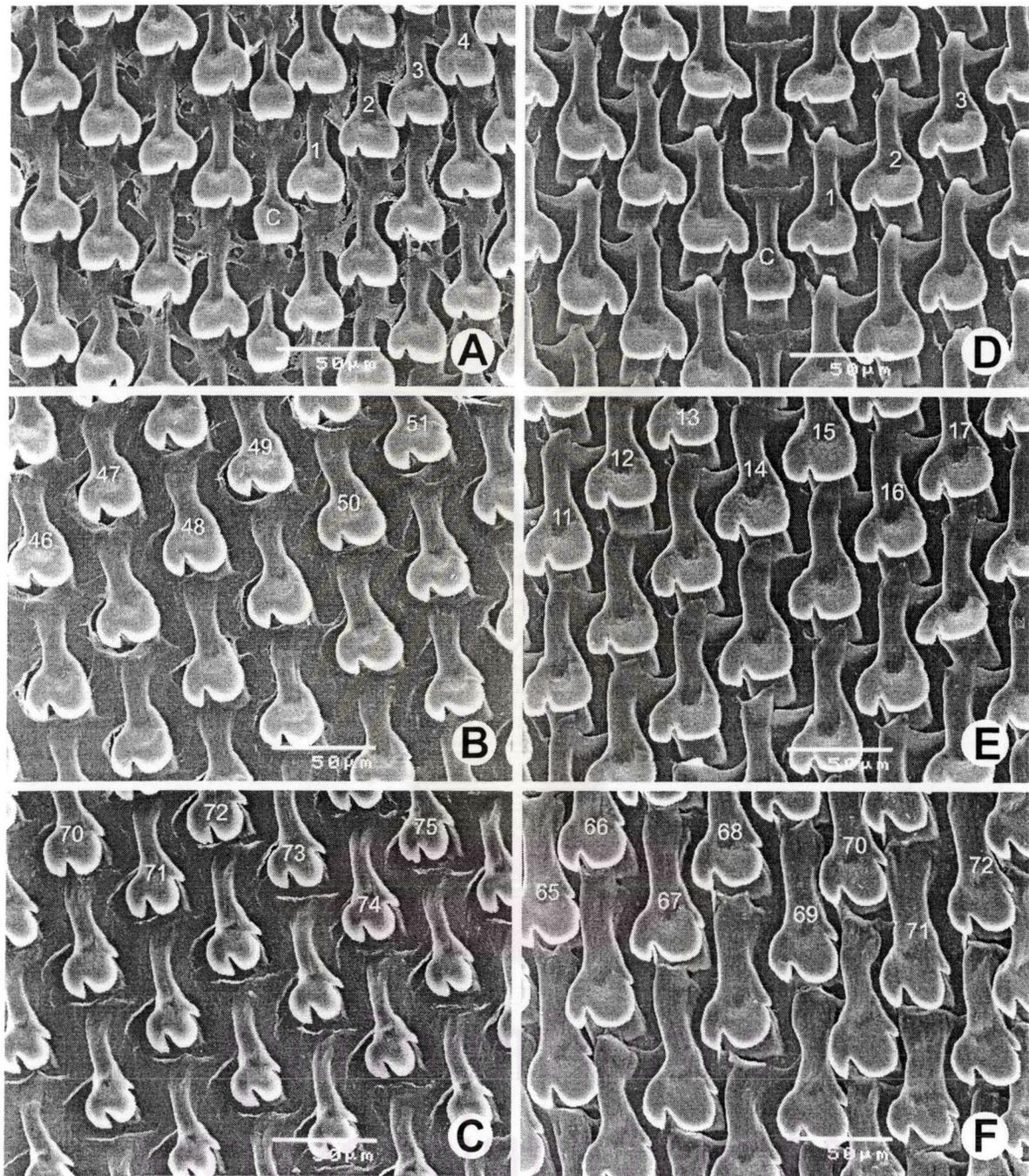


Figure 4.10 SEM images of the radula. **A-C.** *A. atricallosus atricallosus* (2019), **(A)** central tooth with the first to the fourth lateral teeth, **(B)** lateral teeth with the tricuspid marginal teeth transition, and **(C)** outermost marginal teeth. **D-F.** *A. atricallosus leucoxanthus* (2162), **(D)** central tooth with the first to the third lateral teeth, **(E)** lateral teeth with the tricuspid marginal teeth transition, and **(F)** outermost marginal teeth. Numbers indicated order of lateral and marginal teeth. Central tooth indicated by 'C'.

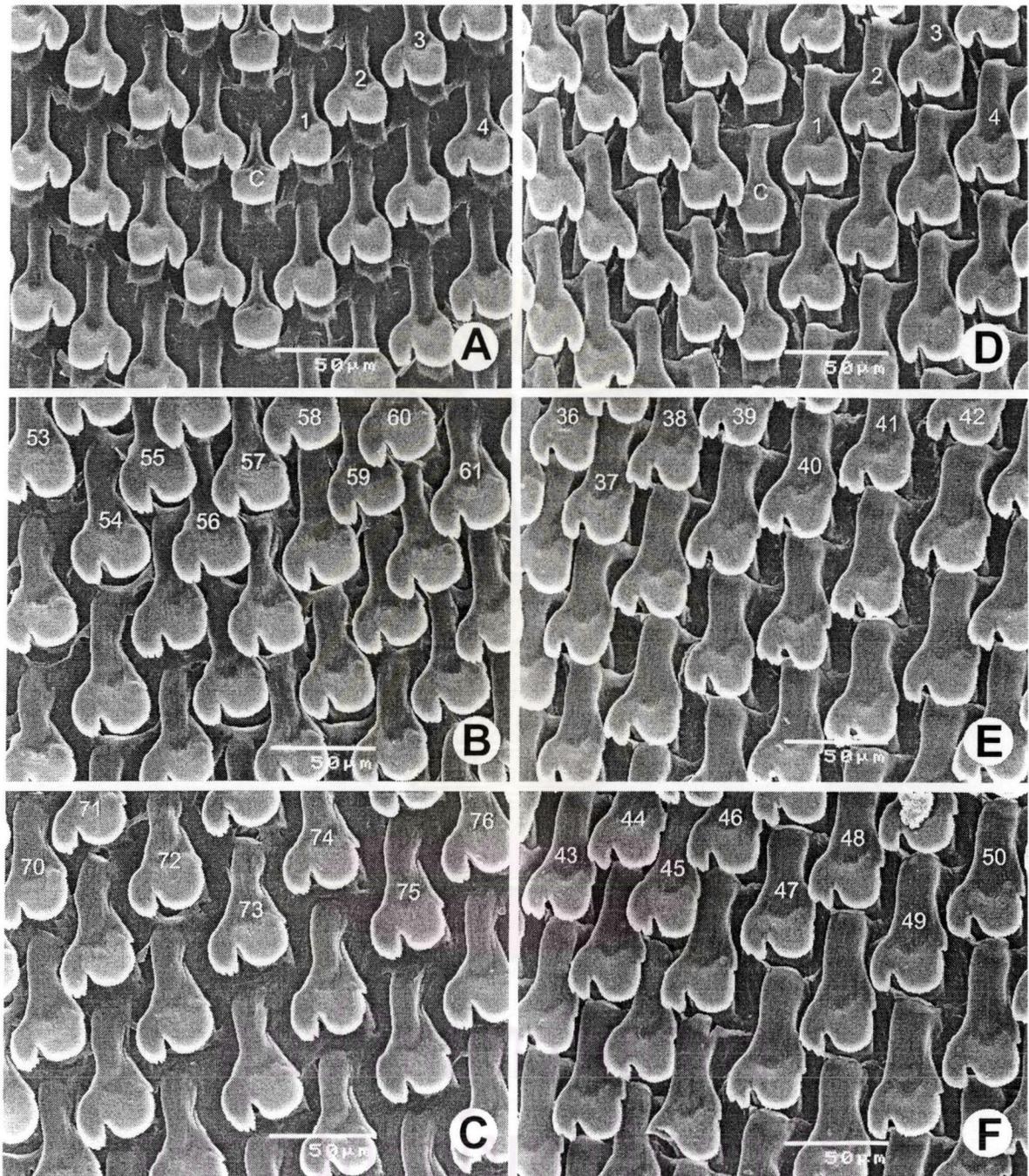


Figure 4.11 SEM images of the radula. **A-C.** *A.* (*A.*) *atricallosus perakensis* (2198), (**A**) central tooth with the first to the fourth lateral teeth, (**B**) lateral teeth with the tricuspid marginal teeth transition, and (**C**) outermost marginal teeth. **D-F.** *A.* (*A.*) *atricallosus* ssp. (2011), (**D**) central tooth with the first to the fourth lateral teeth, (**E**) lateral teeth with the tricuspid marginal teeth transition, and (**F**) outermost marginal teeth. Numbers indicated order of lateral and marginal teeth. Central tooth indicated by 'C'.

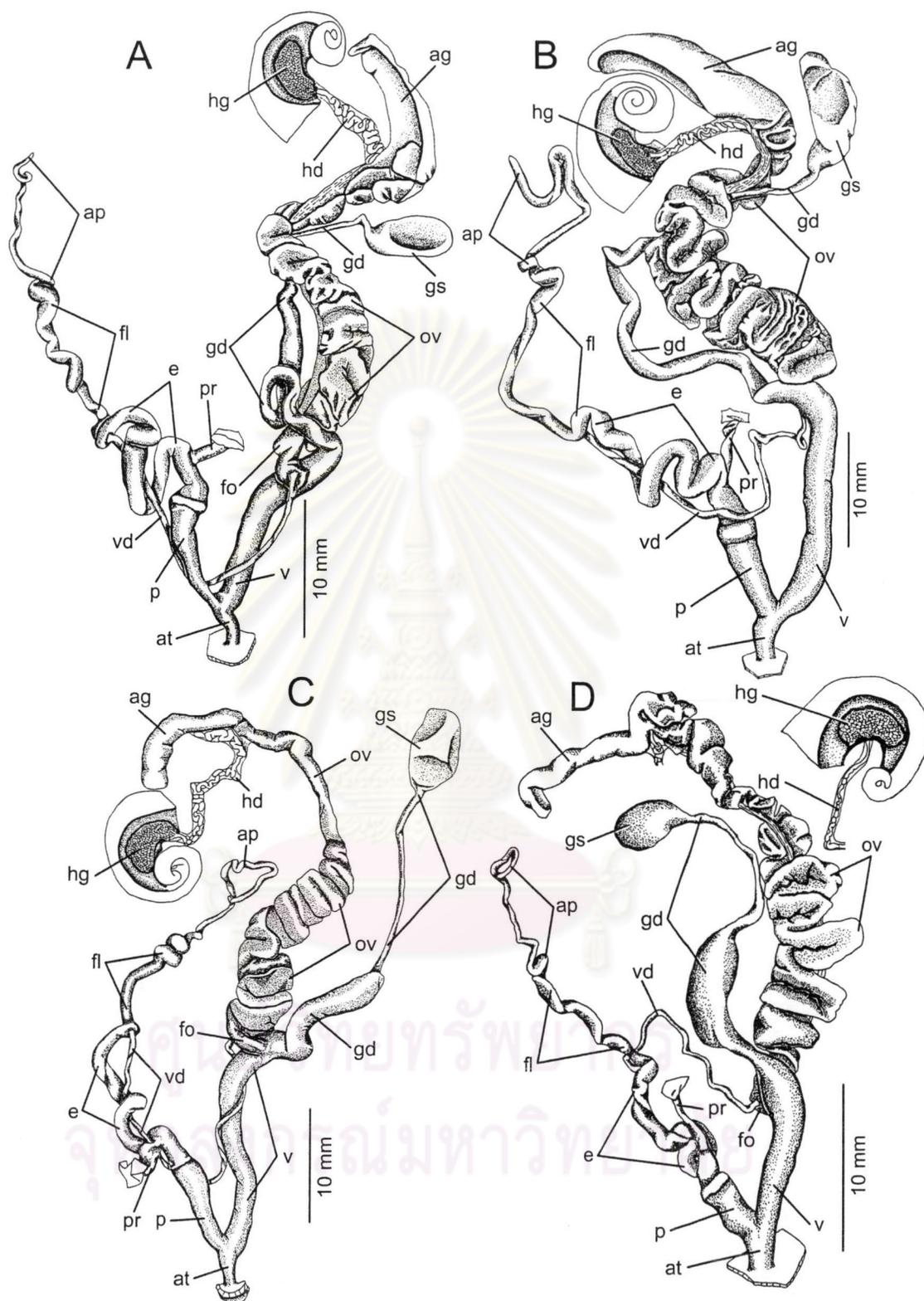


Figure 4.12 The whole genital system of *A. (A.) atricallosus* ssp. **A.** Nominotypical subspecies (2019, 5 May 2000). **B.** *A. (A.) atricallosus leucoxanthus* (2162, 31 August 2002). **C.** *A. (A.) atricallosus perakensis* (2198, 19 February 2001). **D.** *A. (A.) atricallosus* ssp. (2011, 4 April 1999).

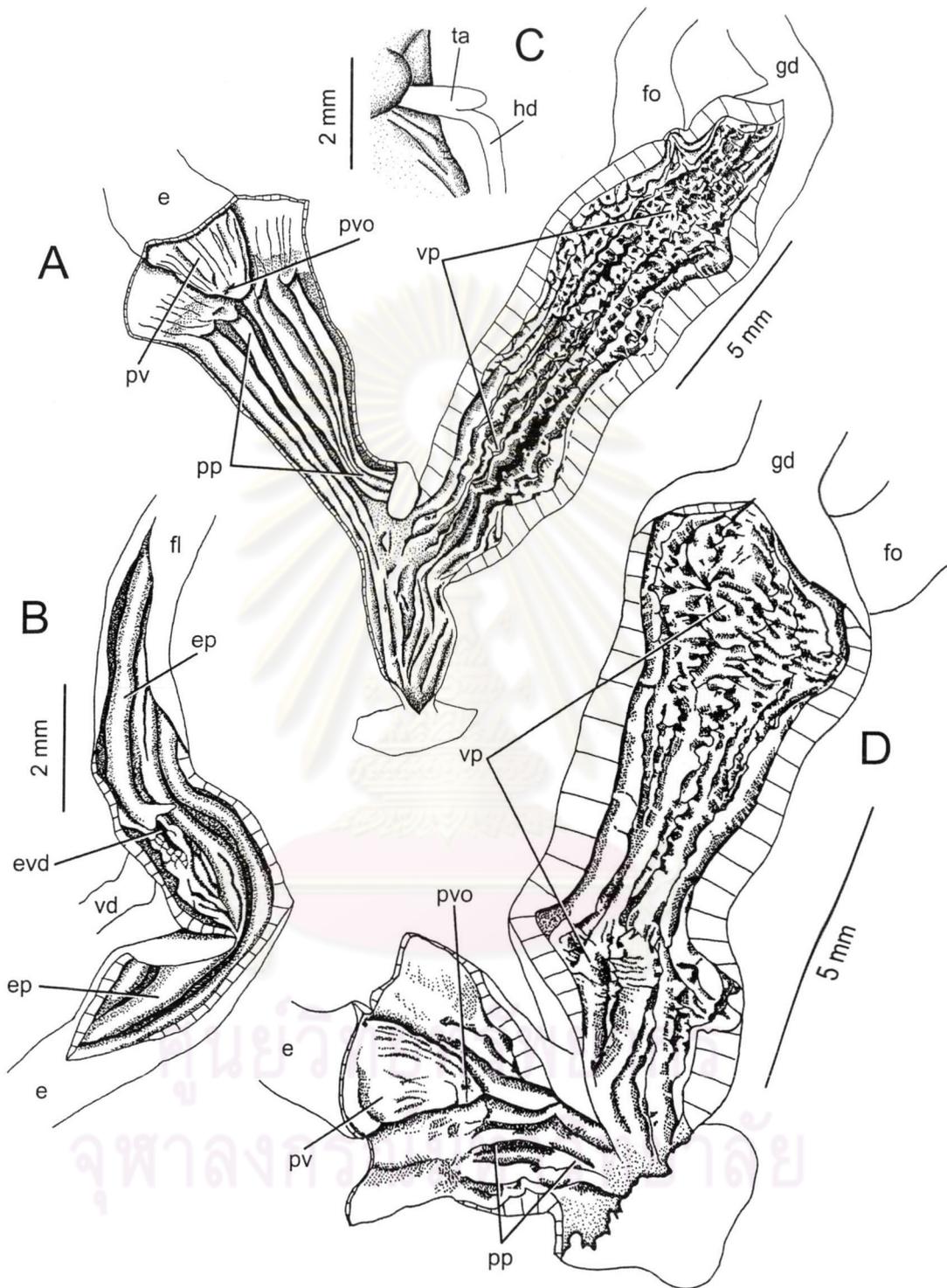


Figure 4.13 *Amphidromus (A.) atricallosus atricallosus* (2019). **A.** Interior structure of penis and vagina. **B.** Interior structure of epiphallus. **C.** Details of hermaphroditic duct and talon junction. **D.** Interior structure of penis and vagina of *A. (A.) atricallosus ssp.* (2011).

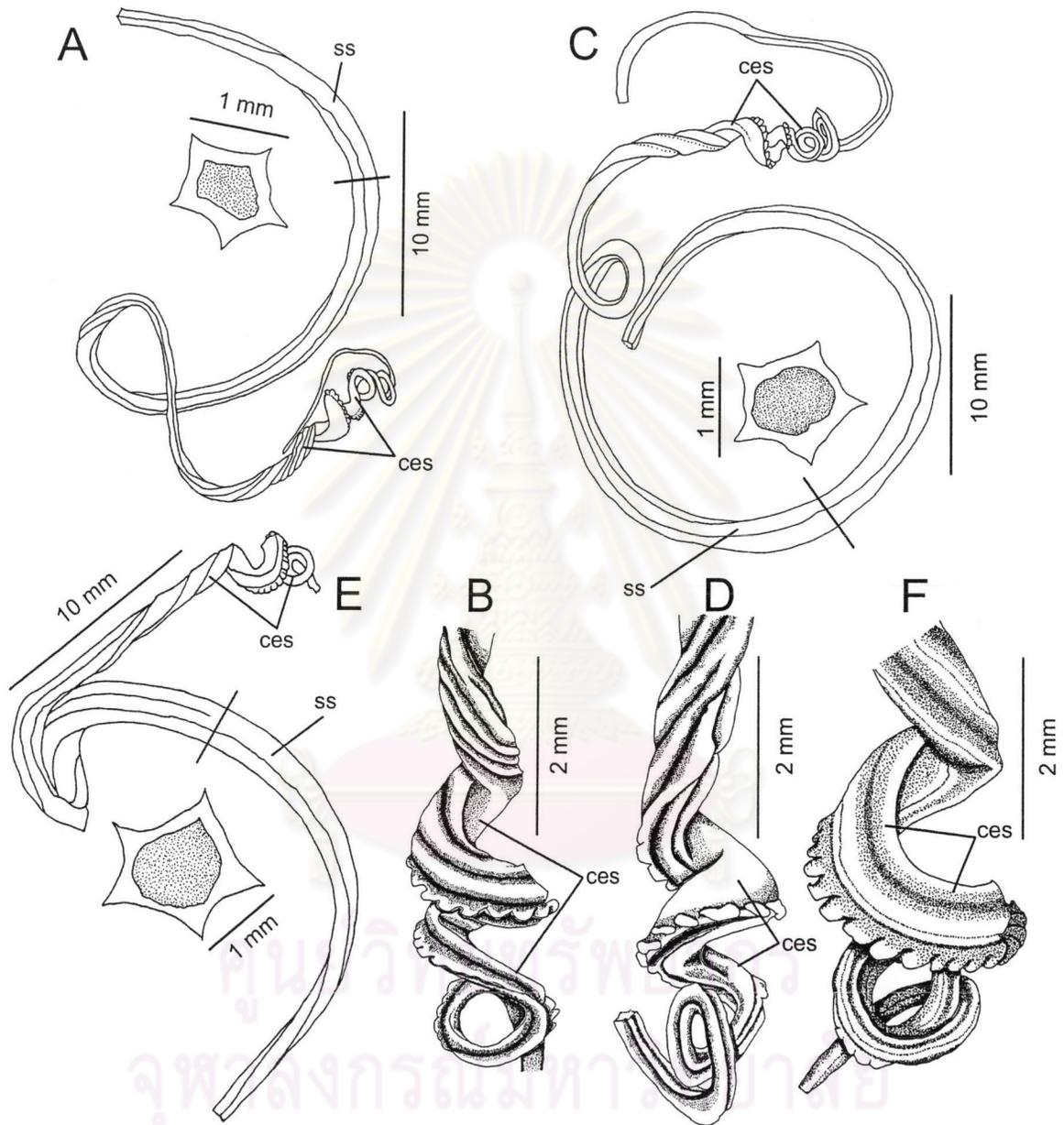
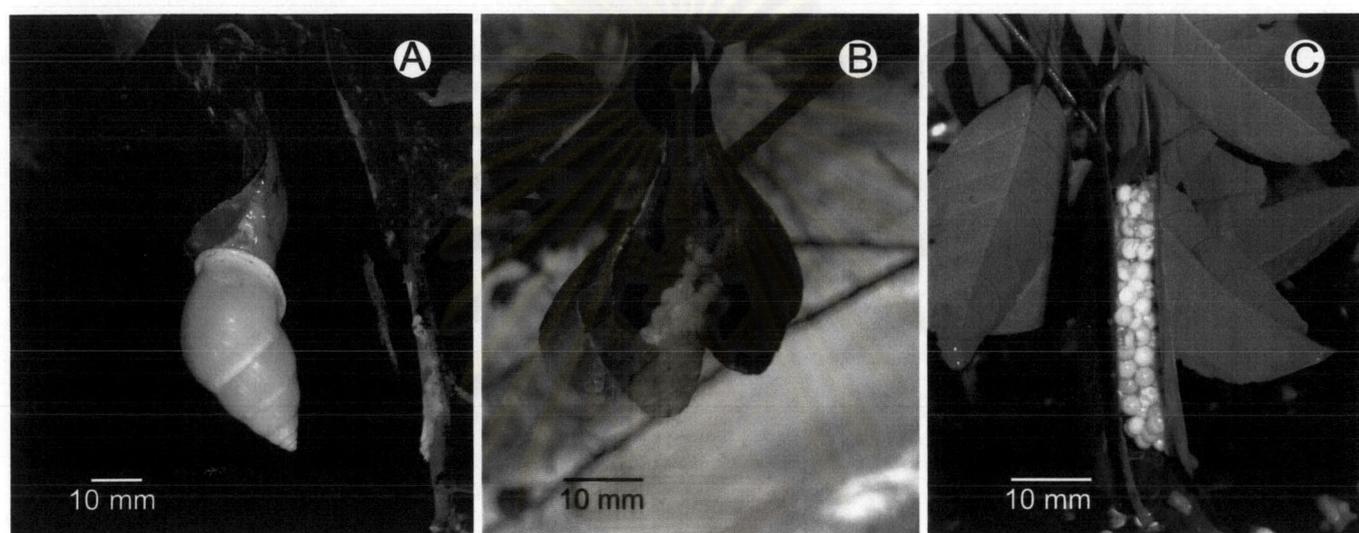


Figure 4.14 Comparative entire body of spermatophores including cross-section at the middle of sperm sac and posterior coiled expanded sections. **A, B.** The nominotypical subspecies. **C, D.** *A. atricallosus leucoxanthus*. **E, F.** *A. atricallosus* ssp.



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Figure 4.15 **A.** Egg laying behavior of *A. (A.) atricallosus atricallosus* from Ban Takhun Suratthani observed in September, 2003. Snail using pomelo leaves (*Citrus maximus* (Burm.f.) Merr.) constructed egg nest. **B.** The intact clutch after egg laying. **C.** The egg clutch of *A. (A.) atricallosus leucoxanthus* from Makhm district, Chantaburi were observed in September, 2003. Rambutan leaves (*Nephelium lappaceum* L.) were used as the egg nest.

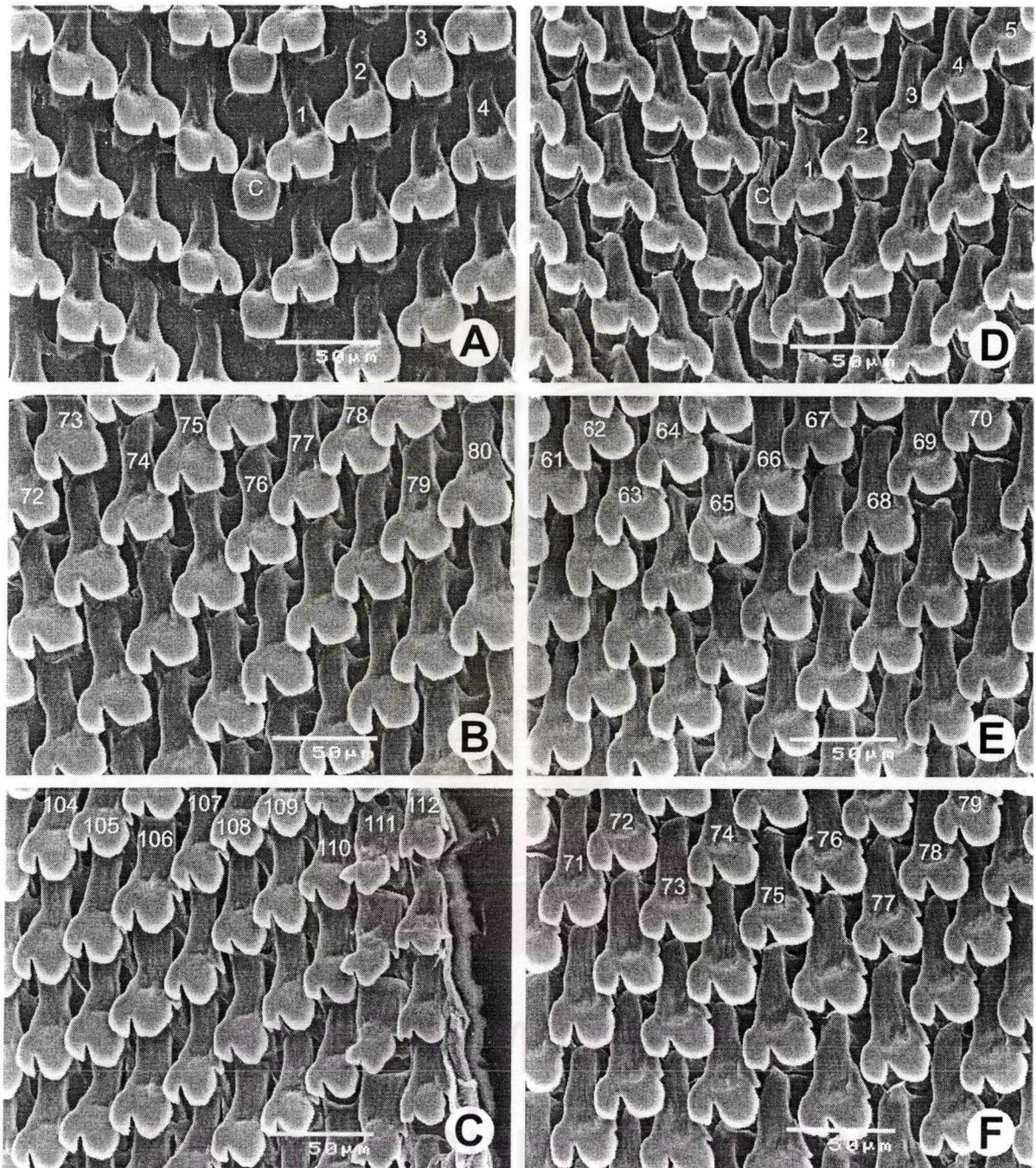


Figure 4.16 SEM images of the radula. A-C. A. (*A.*) *schomburgki schomburgki* (2001), (A) central tooth with the first to the fourth lateral teeth, (B) lateral teeth with the tricuspid marginal teeth transition, and (C) outermost marginal teeth. D-F. A. (*A.*) *schomburgki ssp.* (2017), (D) central tooth with the first to the fifth lateral teeth, (E) lateral teeth with the tricuspid marginal teeth transition, and (F) outermost marginal teeth. Numbers indicated order of lateral and marginal teeth. Central tooth indicated by 'C'.

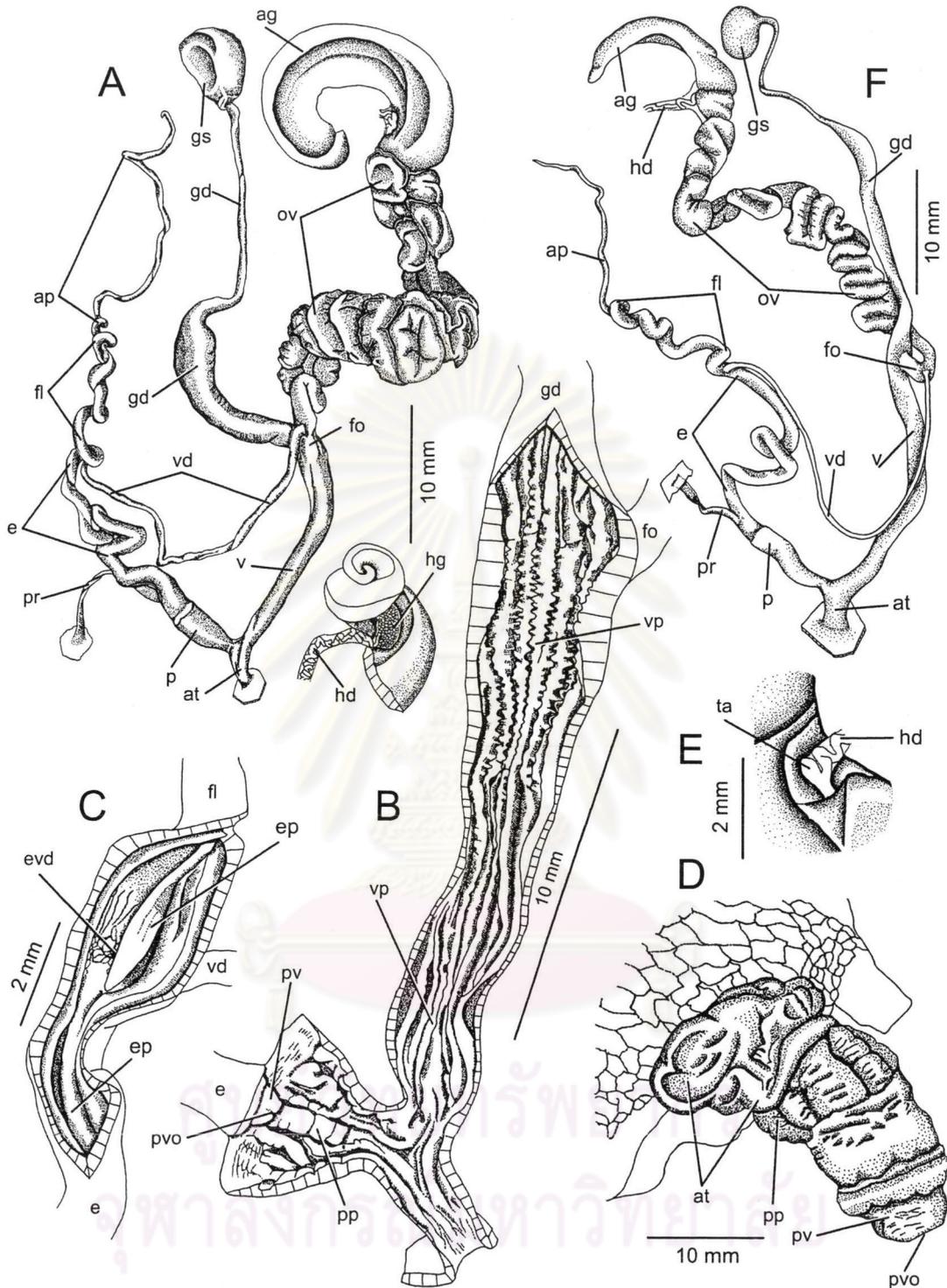


Figure 4.17 *Amphidromus (A.) schomburgki schomburgki* (CUMZ 2001, 12-13 August 2000)—Anatomy. **A.** The whole genital system. **B.** Interior structure of penis, atrium and vagina chamber. **C.** Interior structure of epiphallus. **D.** Protruded penis specimen, which represented the everted internal wall of the atrium, the penial verge and penial pilaster on a prolonged proboscis-like, and truncated at the tip. **E.** Details of hermaphroditic duct and talon junction. **F.** The whole genital system of *A. (A.) schomburgki ssp.* (2017, 12 September 2002).

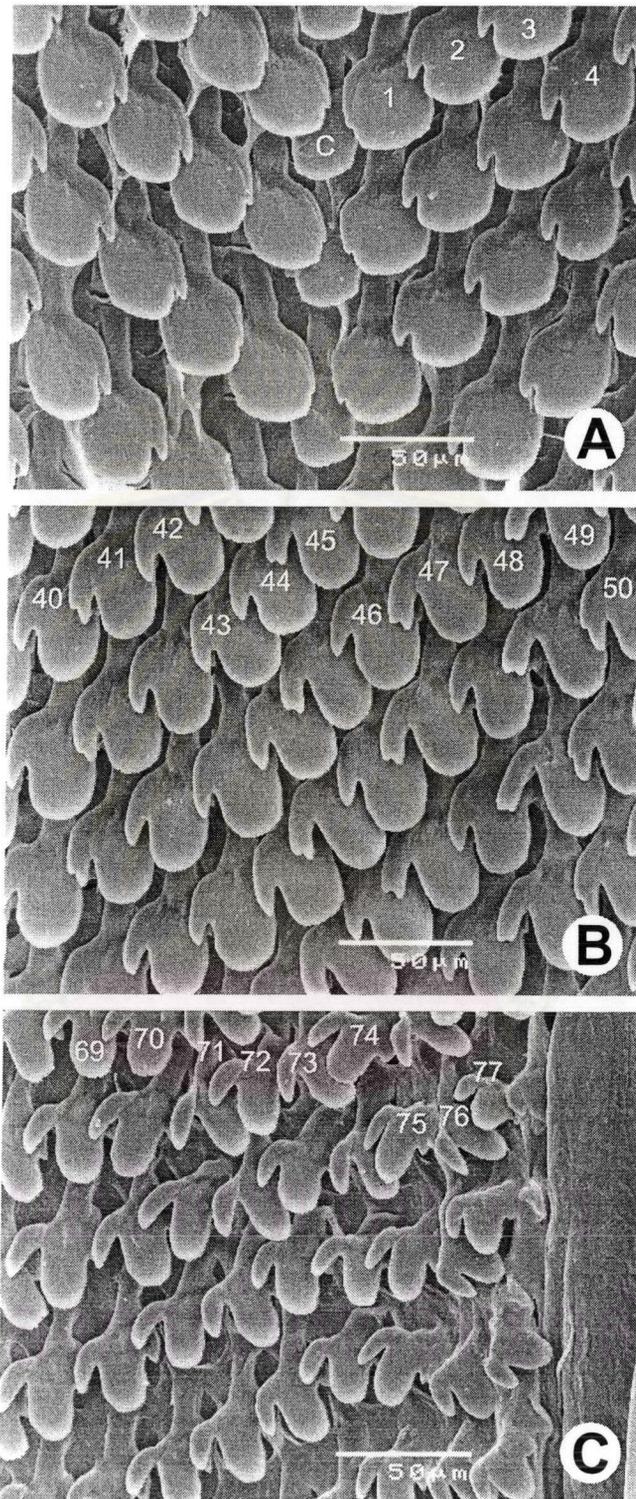


Figure 4.18 SEM images of the radula of *A. (A.) givenchy* (2158). **A.** Central tooth with the first to the fourth lateral teeth. **B.** Lateral teeth with the tricuspid marginal teeth transition. **C.** Outermost marginal teeth. Numbers indicated order of lateral and marginal teeth. Central tooth indicated by 'C'.

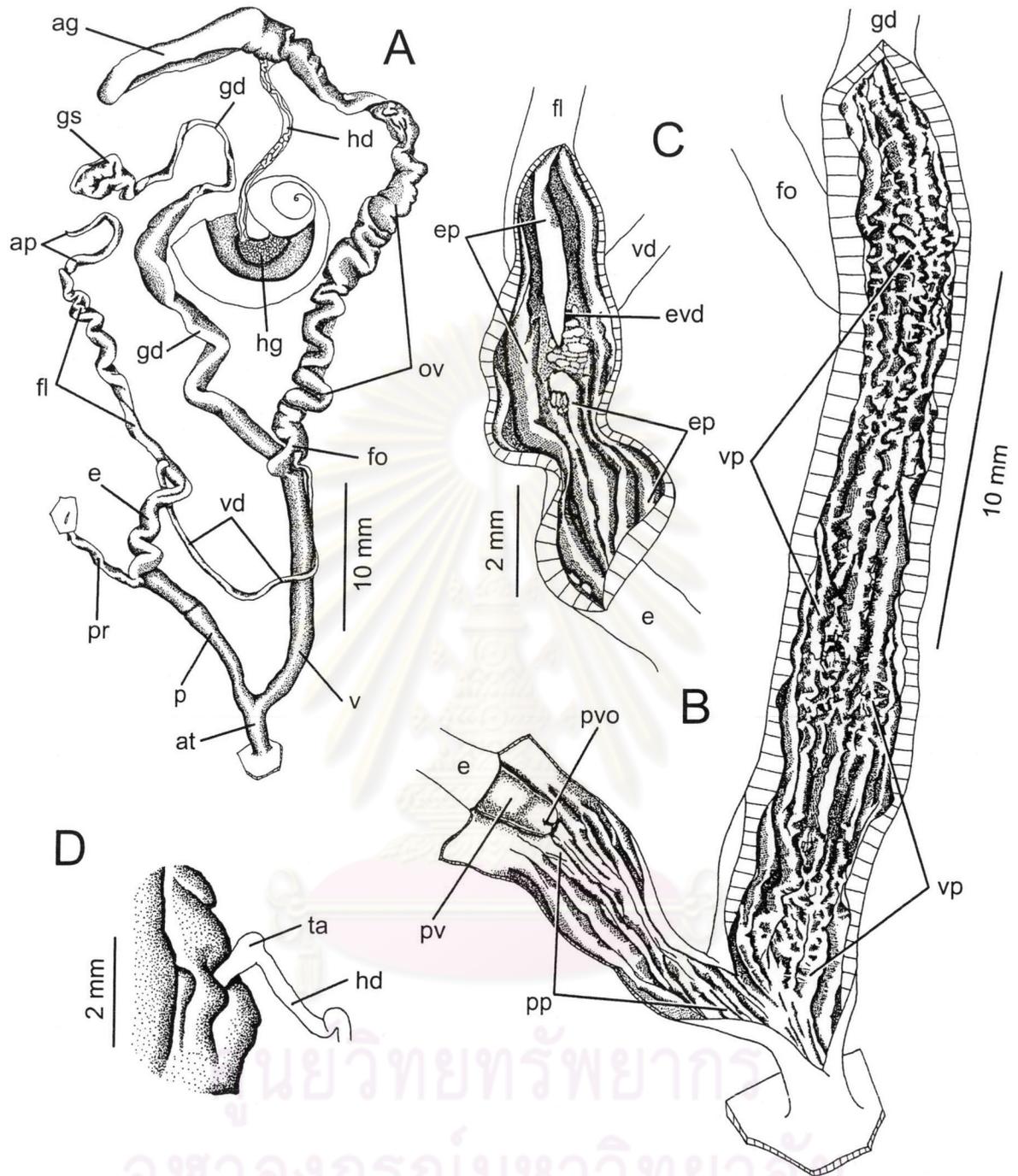


Figure 4.19 *Amphidromus (A.) givenchyi* (2158, 23 August 2002)–Anatomy. **A.** The whole genital system. **B.** Interior structure of penis, atrium and vagina chamber. **C.** Interior structure of epiphallus. **D.** Details of hermaphroditic duct and talon junction.