

# Systematic revision of the arboreal snail *Satsuma albida* species complex (Mollusca: Camaenidae) with descriptions of 14 new species from Taiwan

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The taxonomy of the endemic arboreal snail *Satsuma albida* species complex from Taiwan was unclear due to the animals' highly similar morphology, and their nocturnal and strict arboreal behaviour, leading to difficulties in collecting living specimens. This article is the first comprehensive comparative study on the systematics and taxonomy of this species complex using external morphology, anatomy of the reproductive system and molecular phylogeny. Consequently, two subspecies of *S. albida* are raised to species status, namely *S. insignis* and *S. mollicula*. Fourteen new species are also described. Fourteen of the 17 species showed polymorphism in banding pattern amongst populations and other species retained the whitish unity as seen in *S. albida*. Distributions of almost all taxa are geographically limited, with the exception of *S. polymorpha* sp. nov. The phylogeny of these species was reconstructed using 20 morphological characters and molecular data from the partial sequences of mtDNA CO1 and 16S rRNA genes, and the complete ITS2 sequence. The molecular phylogeny revealed three subclades (west, east and polymorpha clade) and revealed that these snails are monophyletic, originating from a ground-dwelling ancestor. © 2008 The Linnean Society of London, *Zoological Journal of the Linnean Society*, 2008, 154, 437–493.

ADDITIONAL KEYWORDS: anatomy – phylogeny – Pulmonate – Stylommatophora – taxonomy.

## INTRODUCTION

The endemic camaenid arboreal snail *Satsuma albida* (Adams, 1870) was first collected in the south-west of Taiwan by R. Swinhoe, a British consul. This whitish conic snail was described as a new species by Adams (1870), who provided a concise description and a distinct hand drawing but without anatomical description. Two subspecies, *S. a. insignis* (Pilsbry & Hirase, 1906 [1905]) and *S. a. mollicula* (Pilsbry & Hirase, 1909 [1908]), were described later based on morphological characters. However, living specimens are difficult to collect because of their arboreal and

nocturnal behaviour. Consequently, a clear taxonomy of these highly similar animals has not until now been provided.

The land snail genus *Satsuma* A. Adams, 1868 is a varied group that is distributed throughout East Asia including Taiwan and Japan (Kuroda, 1958; Wu & Wu, 1998; Hsieh, Hwang & Wu, 2006). Taiwanese *Satsuma* species exhibit strict terrestrial, arboreal or semi-arboreal behaviour (Hsieh *et al.*, 2006). Owing to the whitish and highly conical shell, the strict arboreal snails have been suggested to be placed within the genus *Ganesella* Blandford, 1863 (Pilsbry & Hirase, 1906 [1905]) or the subgenus *Luchuhadra* Kuroda & Habe, 1949 (Kuroda & Habe, 1949; Minato, 1976) together with some species distributed in the

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Ryukyu Islands. Habe (1955) placed *Luchuhadra* as a subgenus under *Satsuma* with definitive descriptions of the reproductive system of *S. (Luchuhadra) largillierti* (Pfeiffer, 1849), the type species of the subgenus. Minato (1976) reported the reproductive system of *S. (Luchuhadra) amanoi* (Kuroda, 1960), which accorded with Habe's (1955) viewpoint. However, the reproductive system of *S. albida* from northern Taiwan (Chang, Chang & Hwang, 1996) and *S. a. mollicula* from Kenting, southern Taiwan (Sinagawa, 1980), showed a swelling on the posterior epiphallus and a small flagellum, suggesting that the Taiwanese taxa should be removed from *Luchuhadra* (Chang *et al.*, 1996). Furthermore, in line with Pilsbry & Hirase' (1906 [1905]) view, Chang *et al.* (1996) doubted the Taiwanese species belonged to the genus *Ganesella*, distributed from China to India, owing to the thin, highly pyramidal and white-coloured shell and angulated periphery. Nevertheless, their systematic status remains unclear.

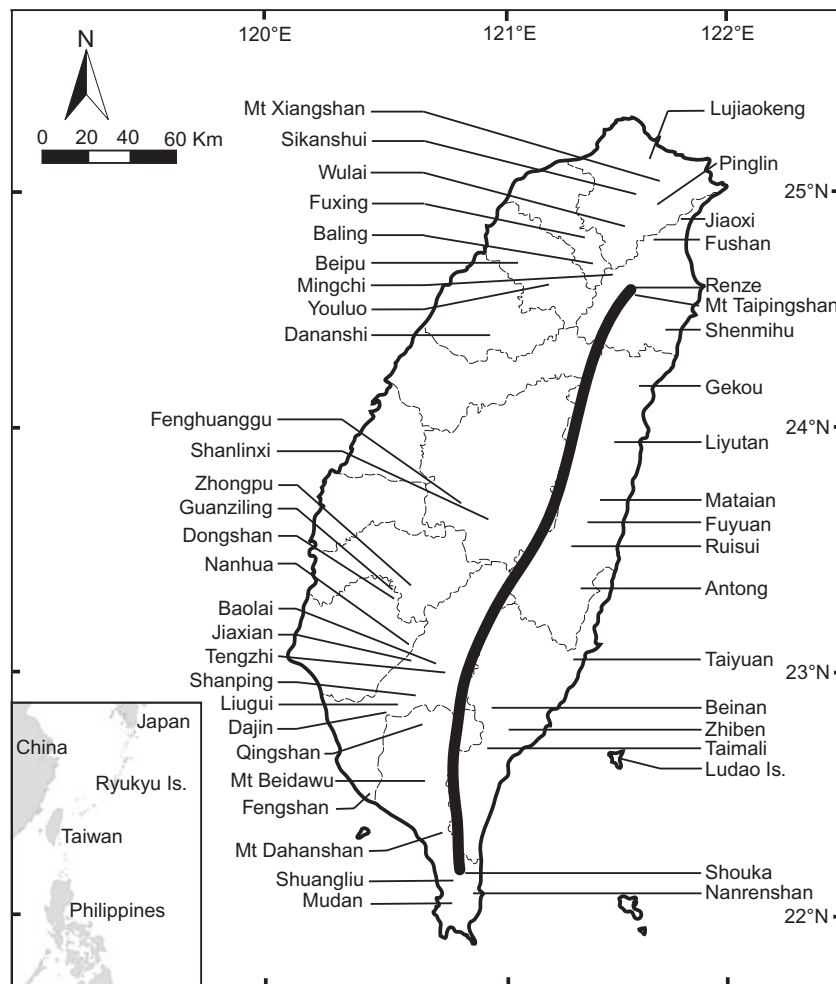
The systematic and taxonomic revision of this group can now be undertaken based on extensive

collection in Taiwan since 1995. Sufficient numbers of living specimens were obtained for detailed examinations. This article first revises the taxonomy of the *S. albida* species complex using morphological and anatomical characteristics. The phylogeny of the species complex is also reconstructed using morphological and molecular characters to understand the relationships amongst these highly similar species.

## MATERIAL AND METHODS

### SPECIMEN COLLECTION AND MORPHOLOGICAL DATA

Snails were collected from representative sites in Taiwan (Fig. 1, Table 1). The collected snails were anaesthetized using menthol in water, killed in hot water and then fixed and preserved in 70% ethanol. The soft bodies of sexually mature specimens, e.g. with fully expanded lips, were pulled out carefully and subjected to dissection for examination of the reproductive system. The dissections were performed using a stereo microscope (Leica MZ7.5) with a



**Figure 1.** Sampling localities of all taxa in Taiwan. Bold line, Central Range; thin line, administrative boundary.

**Table 1.** List of the sampling localities showing altitude (metres) and WGS84 coordinate

Locality	Altitude	WGS84 coordinate
<i>Satsuma albida</i> species complex from Taiwan		
Wulai, Taipei	450	24°46'35.1"N, 121°30'11.6"E
Sikanshui, Taipei	280	24°54'03.9"N, 121°34'03.0"E
Pinglin, Taipei	360	24°56'28.7"N, 121°42'51.4"E
Lujiaokeng, Mt Yangmingshan, Taipei	370	25°11'28.4"N, 121°33'50.2"E
Mt Xiangshan, Taipei	120	25°01'38.1"N, 121°34'34.7"E
Jiaoxi, Yilan	30	24°49'44.1"N, 121°45'59.9"E
Fushan, Yilan	640	24°45'29.3"N, 121°35'34.2"E
Mt Taipingshan, Yilan	1600	24°29'43.6"N, 121°32'08.3"E
Renze, Yilan	600	24°32'36.9"N, 121°30'29.0"E
Shenmihu, Yilan	1300	24°22'43.5"N, 121°44'50.4"E
Baling, Taoyuan	690	24°40'43.3"N, 121°23'07.7"E
Mingchi, Taoyuan	1130	24°39'06.5"N, 121°28'18.3"E
Fuxing, Taoyuan	430	24°49'26.2"N, 121°21'19.4"E
Youlue, Hsinchu	430	24°41'07.5"N, 121°08'59.8"E
Beipu, Hsinchu	520	24°39'41.6"N, 121°04'28.9"E
Dananshi, Miaoli	540	24°35'48.7"N, 121°02'37.5"E
Shanlinxi, Nantou	1800	23°38'22.3"N, 120°47'31.7"E
Fenghuanggu, Lugu, Nantou	700	23°43'52.2"N, 120°47'22.2"E
Guanziling, Tainan	320	23°19'43.3"N, 120°30'59.5"E
Nanhua, Tainan	320	23°07'16.8"N, 120°34'07.6"E
Dongshan, Tainan	180	23°16'50.6"N, 120°25'50.7"E
Jiaxian, Kaohsiung	380	23°07'20.8"N, 120°36'59.4"E
Baolai, Kaohsiung	510	23°06'33.1"N, 120°42'10.9"E
Shanping, Kaohsiung	800	22°58'06.4"N, 120°41'10.8"E
Dajin, Kaohsiung	300	22°53'31.5"N, 120°38'50.1"E
Tengzhi, Kaohsiung	1360	23°03'24.9"N, 120°43'15.5"E
Liugui, Kaohsiung	350	22°59'24.3"N, 120°38'36.6"E
Gekou, Taroko National Park, Hualien	180	24°09'28.0"N, 121°37'20.1"E
Liyutan, Hualien	145	23°56'09.8"N, 121°30'42.8"E
Mataian, Hualien	180	23°40'22.0"N, 121°25'13.9"E
Ruisui, Hualien	1150	23°29'40.4"N, 121°22'33.3"E
Antong, Hualien	420	23°17'20.1"N, 121°20'42.7"E
Fuyuan, Hualien	200	23°35'15.4"N, 121°21'12.7"E
Taiyuan, Taitung	580	23°07'17.2"N, 121°16'46.0"E
Beinan, Taitung	1250	22°47'56.2"N, 121°02'13.6"E
Zhiben, Taitung	200	22°42'22.5"N, 121°02'07.0"E
Taimali, Taitung	900	22°36'36.8"N, 120°59'54.6"E
Mt Huoshaoshan, Ludao Is., Taitung	20	22°39'10.6"N, 121°29'03.4"E
Mt Beidawu, Taiwu, Pingtung	1400	23°09'29.4"N, 120°42'29.3"E
Mt Dahanshan, Pingtung	1200	22°24'39.1"N, 120°45'19.8"E
Qingshan, Sandimen, Pingtung	1000	22°48'54.0"N, 120°40'34.1"E
Shuangliu, Pingtung	280	22°13'07.3"N, 120°47'35.9"E
Shouka, Pingtung	450	22°14'35.6"N, 120°50'36.9"E
Mudan, Pingtung	225	22°07'55.4"N, 120°47'18.5"E
Nanrenshan, Kenting National Park, Pingtung	240	22°04'55.3"N, 120°51'08.3"E
Outgroup		
<i>Satsuma nux</i>		
Zhongpu, Chiayi, Taiwan	340	23°22'44.2"N, 120°32'58.2"E
<i>Satsuma succincta</i>		
Fengshan, Kaohsiung, Taiwan	30	22°32'34.3"N, 120°23'29.7"E
<i>Satsuma pekanensis</i>		
Beinan, Taitung, Taiwan	1250	22°47'56.2"N, 121°02'13.6"E

**Table 1.** *Continued*

Locality	Altitude	WGS84 coordinate
<i>Satsuma largillierti</i> Okinawa Island, Japan		
<i>Satsuma myomphala</i> Shimane, Honshu, Japan		
<i>Moellendorffia hiraseana</i> Beinan, Taitung, Taiwan	500	22°47'13.6"N, 121°03'0.1"E
<i>Camaena longsonensis</i> Langson, N. Vietnam	1155	4°37'24.7"N, 108°36'51.7"E

camera lucida attachment for drawing. Shell measurements including shell height, shell diameter (the greatest breadth) and number of whorls were made following Kerney & Cameron (1979), using a digital calliper to an accuracy of 0.1 mm. The type materials of H. Adams and H. Pilsbry and additional materials were inspected.

The major portion of the collection was selected as type materials and general vouchers, and were deposited in the National Taiwan Museum (TMNT), the National Museum of Natural Science, Taiwan (NMNS), the Natural History Museum, London (BMNH), the Academy of Natural Sciences of Philadelphia (ANSP) and the Naturmuseum Senckenberg, Frankfurt am Main (SMF). Specimens in the Nishinomiya Shell Museum, Japan, and Museum of Zoology, National Taiwan University, Taiwan (NTUM), were also examined.

The following abbreviations for genitalia are used in the figures: ag, albumen gland; at, atrium; bc, bursa copulatrix; bs, bursa stalk; dp, distal penis; ep, epiphallus; fl, flagellum; fo, free oviduct; hd, hermaphrodite duct; mp, middle penis; pc, penial caecum; pp, proximal penis; prm, penial retractor muscle; pv, proximal vagina, mv, middle vagina, dv, distal vagina; so, spermoviduct; vd, vas deferens.

The *Satsuma albida* species complex maintains a polymorphic banding pattern of varied width, coloration and shapes. For simplification, the banding pattern is coded using eight digits, modified from the system used for other taxa (Jones, Leith & Rawlings, 1977; Lai, 1981). Besides the spiral bands on whorls, additional purple–black stains on the umbilicus, the lip or the apex are also coded. A number (1–8) indicates that the band is present, whereas a '0' means no bands or stains are observed. A band formula may be ranged from 00000000 for a shell of no band to 12345678 for a shell of eight bands and stains. Digits in parentheses denote a smear displayed between and connected with the bands or stains. The smears were usually paler than bands and blurred the margins of

bands. A '0' or zeros in parentheses means a zone of smear without definite sharp band or stain.

*Digit 1*: an apical spot usually covering the embryonic whorls only, sometimes extended to the anterior part of the subsequent whorl.

*Digit 2*: a sub-sutural band that is close to or immediately in contact with the suture.

*Digit 3*: a supra-peripheral band between the suture and periphery.

*Digit 4*: a peripheral band covering the angulated area of the periphery.

*Digit 5*: a sub-peripheral band, sometimes contacting band 4.

*Digit 6*: a basal band positioned close to the umbilicus.

*Digit 7*: an umbilicus spot covering the umbilicus and columellar lip.

*Digit 8*: inferior lip stain covering the inferior lip and area surrounding it.

Three stains or bands were not coded in this study because of their ambiguity and rarity. (1) A stain on the outer lip was also observed, but it was pale pink and unclear. (2) A short and thin band along the suture, comprising 1/4–1/8 of the body whorl anterior to the upper insertion of the outer lip was seen occasionally. The band is covered by or closely contacted with the two bands surrounding the periphery and is difficult to be coded. (3) The columella is stained when the apex spot is present for the most broken shells observed. In some cases, the columellar stain is absent even when the apical spot is present. Owing to difficulty in observing the columellar stain, it is omitted herein.

In order to reconstruct a morphological phylogeny, potentially phylogenetically informative characters were selected. Ambiguous (e.g. number of internal folds in genitalia and length of genital organ) and highly polymorphic (e.g. banding pattern of shell) characters were omitted. The selected characters were solely used for species-level taxonomy. Charac-

ter states for continuous variables were determined by natural gaps of measurements between species. Twenty morphological characters from shell, soft body and genitalia were selected as follows:

1. Shell shape (shell height/shell diameter): 0, < 0.8; 1, 0.8–1.1; 2, 1.1–1.3; 3, > 1.3
2. Periostracum colour of shell spire: 0, brown; 1, white; 2, yellowish; 3, golden
3. Periostracum colour of shell base: 0, brown; 1, white; 2, yellowish; 3, golden; 4, greenish
4. Pre-apertural constriction behind inferior lip: 0, absent; 1, present
5. Pre-apertural constriction behind outer lip: 0, absent; 1, present
6. Aperture shape (aperture height/aperture diameter): 0, < 1; 1, > 1
7. Peripheral keel: 0, absent; 1, present
8. Shell size (shell height x shell diameter in mm): 0, < 400; 1, > 400
9. Soft body colour: 0, dark grey; 1, white; 2, yellowish
10. Dark pedal stripe: 0, absent; 1, present
11. Relative length of distal vagina to whole vagina: 0, 0 (= distal vagina absent); 1, 0–0.25; 2, 0.25–0.5
12. Bursa stalk base: 0, tapering smoothly; 1, swollen or conic
13. Bursa stalk/spermoviduct length ratio: 0, > 0.75 (equal length); 1, < 0.75 (short bursa stalk)
14. Spinules: 0, absent; 1, present
15. Flagellum base (ratio of maximum flagellum width/flagellum length): 0, slender (ratio < 0.25); 1, swollen (ratio > 0.25)
16. Penial caecum: 0, absent; 1, slender; 2, conic
17. Surface of penis near to epiphallus: 0, smooth; 1, strongly corrugated
18. Deep groove on proximal penis: 0, absent; 1, present
19. Principal pilaster: 0, absent/short; 1, medium (the same length as penial caecum); 2, long (longer than penial caecum)
20. Ratio of penial caecum/epiphallus between penial retractor muscle and insertion to penial caecum: 0, < 0.2; 1, 0.2–2.0; 2, > 2.0

#### MOLECULAR DATA

Whole genomic DNA was extracted from pedal muscle tissue of fresh, frozen or ethanol-preserved specimens using the HotSHOT method (Truett *et al.*, 2000). Fragments of the partial cytochrome oxidase subunit 1 (CO1) and 16S rRNA gene were amplified using primer pairs LCO1491/HCO2198 (Folmer *et al.*, 1994) and 16Sar/16Sbr (Palumbi, 1996). Sequences of the complete ITS2 gene were amplified according to Wade & Mordan (2000). Each 30- $\mu$ L PCR mixture consisted

of 3  $\mu$ L 10 $\times$  reaction buffer containing 15 mM MgCl<sub>2</sub>, 0.2 mM dNTP, 0.1 units of *Taq* polymerase (Super-Therm), 0.5 mM of each primer, 1  $\mu$ L template DNA and ddH<sub>2</sub>O. The conditions for thermal cycling, performed on a Biometra Uno II, was 5 min at 95 °C for pre-denaturing, 35 cycles of 1 min at 95 °C, 1 min at 50 °C and 1 min at 72 °C, and a final extension at 72 °C for 7 min for both the CO1 and the 16S rRNA genes. The amplicons were examined on a 2% agarose gel for quality and fragment size, then purified using Geneaid PCR Extraction Kit and sequenced on an ABI 3730 automated sequencer. Chromatographs and sequences were examined, initially compiled, aligned and edited in BIOEDIT 7.0.1. (Hall, 1999) and CLUSTAL X (Thompson *et al.*, 1997).

#### PHYLOGENETIC ANALYSIS

Congruence between different gene sequences was tested by performing the incongruence length test (ILD) (Mickey & Farris, 1981) with the homogeneity partition command of the program PAUP\* 4.0b10 (Swofford, 2003). Invariable sites were removed before applying the test (Cunningham, 1997). The test was performed by heuristic search with TBR branch-swapping and 1000 replicates. Gaps were treated as missing. The best-fitting model for the aligned sequences of these genes was determined using a hierarchical likelihood ratio test performed in the program Modeltest 3.7 (Posada & Crandall, 1998). The selected substitution model was then adopted in the reconstruction of phylogeny based on the neighbour-joining method (NJ) (Saitou & Nei, 1987). The NJ analysis was conducted in PAUP using the maximum-likelihood distance. Parsimony analysis was conducted in PAUP by heuristic search under TBR branch swapping, random taxa addition of ten replicates and MulTrees option in effect. Gaps within the alignment were treated as missing. Support for nodes was evaluated by bootstrap analysis of 1000 replicates (Felsenstein, 1985). *Satsuma* (*L.*) *largillerti* from Okinawa Island was included for comparison, as species of the subgenus *Luchuhadra* are thought to be closely related to the *S. albida* species complex. Representative species of *Satsuma* from Taiwan and Japan were also included, i.e. *S. pekanensis* (Rolle, 1911), *S. succincta* (Adams, 1866) and *S. myomphala* (Martens, 1865) (Table 1). *Camaena longsonensis* (Morlet, 1891) collected from north Vietnam and *Moellendorffia hiraseana* Pilsbry, 1905 were used as outgroups.

The morphological dataset was analysed by parsimony analysis using a branch-and-bound search with default settings in PAUP. All characters were treated as unordered and equally weighted. Multiple states in the same species were interpreted as polymorphism.



Agreement among equally parsimonious trees was evaluated by the 50% majority rule consensus. Support for nodes was tested by bootstrap analysis (Felsenstein, 1985) with 1000 replicates. Because of the incomplete anatomical data on most *Satsuma* species, two species, *S. nux* and *S. largillierti*, were included for comparisons. Character states for *S. nux* were obtained from unpublished data of the present authors. Characters, especially of the genitalia, of *S. largillierti* were compiled from literature researches (Kuroda & Habe, 1949; Habe, 1955; Azuma, 1995). Due to the lack of anatomical information for *C. longsonensis*, character states for the outgroup genus *Camaena* were compiled from the literature, including the anatomy of *C. cicatricosa* (Müller, 1774) and *C. xanthoderma* (Moellendorff, 1882) (Pilsbry, 1895; Sinagawa, 1979; Hwang, 1995). Unavailable character states were treated as missing, which were usually genital characters.

## RESULTS

### SYSTEMATIC DESCRIPTION

#### FAMILY CAMAENIDAE PILSBRY, 1895

#### GENUS *SATSUMA* A. ADAMS, 1868

#### *SATSUMA ALBIDA* SPECIES COMPLEX

*Diagnosis:* The colour of shell, periostracum and soft body is white to yellowish, never brownish as seen in other *Satsuma*. The shell is conical with shell height/shell diameter ratios of 1.0–1.8.

*Description:* Shell dextral, conical, thin to thick, small to medium size (see Table 2 for shell measurements). Shell white or yellowish with or without coloured bands and stains; shell of some species with greenish or golden tint. Bands highly polymorphic, pink, reddish purple or dark purple, variable in width and shape (Fig. 2). Whorls not obviously expanded. Periphery bluntly angulated to keeled. Base expanded or flattened. Surface glossy with curved striae and thin periostracum. Aperture diagonally tetragonal or ovate-lunate. Peristome thin, reflected. Pre-apertural constriction behind outer and inferior lips present on some species. Insertion of columellar lip dilated, not connected with insertion of outer lip. Callus between insertions thin, present only on some species. Umbilicus narrow, half to mostly covered by dilated columellar lip. Colour of soft body in accordance with shell, either white or yellowish. Longitudinal pedal stripe of grey colour present on ventral side of foot in white-coloured individuals. Yellow-shelled species do not exhibit such pedal stripe.

The vagina and penis can be divided into three segments, namely proximal, middle and distal parts

for convenience of description. Boundaries between parts can be recognized by apparent changes of the external and internal morphologies, such as the strength of parts and the number, shape and strength of internal folds. However, some species showed no apparent boundary between these parts. The verge around the epiphallic pore forms two to three strong pilasters (called caecal pilasters hereafter in this article) tapering to the apex of the penial caecum and usually fused as a single principal pilaster extending distally to the proximal penis.

Bursa stalk long with 8–15 smooth and straight internal folds. Free oviduct short. Proximal vagina muscular, swollen, smooth with strong internal folds. Middle vagina constrictive with wiggly and dense internal folds in some species. Distal vagina and atrium villous, dull externally with fine corrugations internally. Flagellum slender or conical. Penis and epiphallus bundled by thin and semi-transparent penial muscle. Proximal penis absent, short or long, with variable morphology. Middle and distal penis thin, slender with strong pilasters to fine wrinkles internally. In some species, a few to numerous variably sized, tiny, flexible and nearly regular tetrahedral spinules were born on the surfaces of pilasters in part of the penial caecum, penis and vagina. A representative figure of the spinules is supplied only for *Satsuma mollicula* as the morphology of spinules is similar between species under the stereo microscope.

#### *SATSUMA ALBIDA* (H. ADAMS, 1870) (FIGS 3, 4)

*Helix (Satsuma) albida* H. Adams, 1870: 378, pl. 27, fig. 9. (Nov., 1870)

*Helix albida*, Pfeiffer, 1876: 379–380; Moellendorff, 1884: 335–336; Tryon, 1887: 218, pl. 51, fig. 53.

*Helix (Satsuma) albida*, Schmacker & Boettger, 1891: 159.

*Ganesella albida*, Pilsbry, 1895: 169; Pilsbry & Hirase, 1906 [1905]: 736; Kuroda, 1941: 144; Kuroda, 1958: 145.

*Satsuma albida*, Minato, 1976: 84; Richardson, 1985: 268; Chang *et al.*, 1996: 25–30 [non *albida*]; Hsieh *et al.*, 2006: 231.

*Coniglobus (Luchuhadra) albida*, Chang, 1984: 15, pl. 5, fig. 28.

*Satsuma albidum*, Lai, 1990: 49. [incorrect gender ending]

*Satsuma (Coniglobus) albida*, Ohara & Otani, 2002: 83.

#### *Material examined*

*Type specimen:* Only one specimen originally collected by R. Swinhoe was found and is here designated as the lectotype (BMNH 1878.1.28.229,

**Table 2.** *Satsumaalbida* species complex showing measurements of holotype/lectotype (*italic*)

Species	<i>N</i>	SH (mm)	SD (mm)	SH/SD	Whorls
<i>S. albida</i>	5	<i>15.0</i> 15.1 (15.0–15.8)	<i>14.0</i> 13.7 (12.8–14.3)	<i>1.07</i> 1.11 (1.07–1.23)	<i>5.8</i> 5.5 (5.3–5.8)
<i>S. hagiomontis</i>	6	<i>17.7</i> 15.3 (14.0–17.7)	<i>16.2</i> 15.3 (14.0–16.2)	<i>1.09</i> 1.01 (0.99–1.09)	<i>6.8</i> 5.9 (5.1–6.8)
<i>S. swinhoei</i>	10	<i>18.5</i> 17.2 (16.3–18.5)	<i>16.5</i> 16.2 (14.6–17.0)	<i>1.12</i> 1.07 (1.01–1.18)	<i>6.3</i> 5.9 (5.8–6.3)
<i>S. insignis</i>	5	<i>16.8</i> 16.8 (16.1–20.2)	<i>14.3</i> 14.8 (12.5–15.6)	<i>1.17</i> 1.17 (1.10–1.35)	<i>6.0</i> 6.1 (6.0–6.8)
<i>S. lini</i>	4	<i>17.6</i> 17.3 (14.2–18.6)	<i>14.9</i> 14.8 (12.3–15.1)	<i>1.19</i> 1.17 (1.15–1.23)	<i>5.8</i> 5.8 (5.3–6.0)
<i>S. phoenicis</i>	6	<i>19.4</i> 18.1 (17.4–19.4)	<i>16.0</i> 15.5 (14.3–16.3)	<i>1.21</i> 1.19 (1.10–1.25)	<i>6.0</i> 5.9 (5.8–6.0)
<i>S. careocaecum</i>	18	<i>19.1</i> 17.8 (16.3–19.1)	<i>14.8</i> 14.6 (13.6–15.6)	<i>1.29</i> 1.23 (1.16–1.30)	<i>6.6</i> 6.1 (5.6–6.8)
<i>S. polymorpha</i>	31	<i>14.2</i> 13.9 (11.5–17.1)	<i>13.9</i> 13.4 (11.0–16.8)	<i>1.03</i> 1.06 (0.99–1.16)	<i>5.5</i> 5.0 (4.5–5.9)
<i>S. mollicula</i>	7	<i>21.2</i> 21.8 (20.4–23.5)	<i>15.1</i> 16.3 (15.1–16.7)	<i>1.40</i> 1.34 (1.28–1.44)	<i>6.5</i> 6.5 (6.5–6.9)
<i>S. huberi</i>	12	<i>20.3</i> 17.7 (16.5–20.7)	<i>12.4</i> 12.2 (11.5–14.5)	<i>1.64</i> 1.44 (1.39–1.64)	<i>6.8</i> 6.1 (5.8–6.8)
<i>S. auratibasis</i>	16	<i>20.1</i> 20.0 (17.5–22.2)	<i>15.8</i> 14.6 (13.0–15.8)	<i>1.27</i> 1.37 (1.27–1.54)	<i>6.3</i> 6.5 (5.9–7.0)
<i>S. katipolensis</i>	9	<i>18.2</i> 16.3 (15.9–18.9)	<i>12.1</i> 12.2 (12.0–13.2)	<i>1.50</i> 1.36 (1.24–1.50)	<i>6.0</i> 5.8 (5.5–6.0)
<i>S. luteolella</i>	18	<i>23.5</i> 21.0 (16.3–23.5)	<i>15.3</i> 13.9 (11.1–15.3)	<i>1.54</i> 1.50 (1.40–1.64)	<i>6.6</i> 6.5 (5.9–6.9)
<i>S. kanoi</i>	8	<i>29.7</i> 28.3 (25.9–29.7)	<i>18.4</i> 17.1 (15.9–18.6)	<i>1.61</i> 1.62 (1.51–1.81)	<i>7.3</i> 7.1 (6.9–7.8)
<i>S. vallis</i>	6	<i>18.5</i> 17.4 (16.0–18.5)	<i>12.8</i> 12.7 (12.4–13.2)	<i>1.45</i> 1.37 (1.24–1.45)	<i>6.1</i> 5.8 (5.5–6.1)
<i>S. viridibasis</i>	5	<i>22.4</i> 21.4 (20.8–23.3)	<i>14.6</i> 14.4 (13.9–15.8)	<i>1.54</i> 1.50 (1.44–1.55)	<i>6.5</i> 6.3 (6.0–6.5)
<i>S. pilsbryi</i>	10	<i>17.9</i> 16.9 (14.8–17.9)	<i>12.3</i> 12.1 (11.1–13.2)	<i>1.46</i> 1.40 (1.28–1.46)	<i>5.8</i> 5.9 (5.6–6.1)

SH, shell height; SD, shell diameter; SH/SD, shell height/shell diameter ratio; Whorls, number of whorls; *N*, sample size of all type specimens for new species or type(s) and additional specimens measured in this study for the three already described species, *S. albida*, *S. insignis* and *S. mollicula*; median (*bold*), minimum and maximum (parentheses).

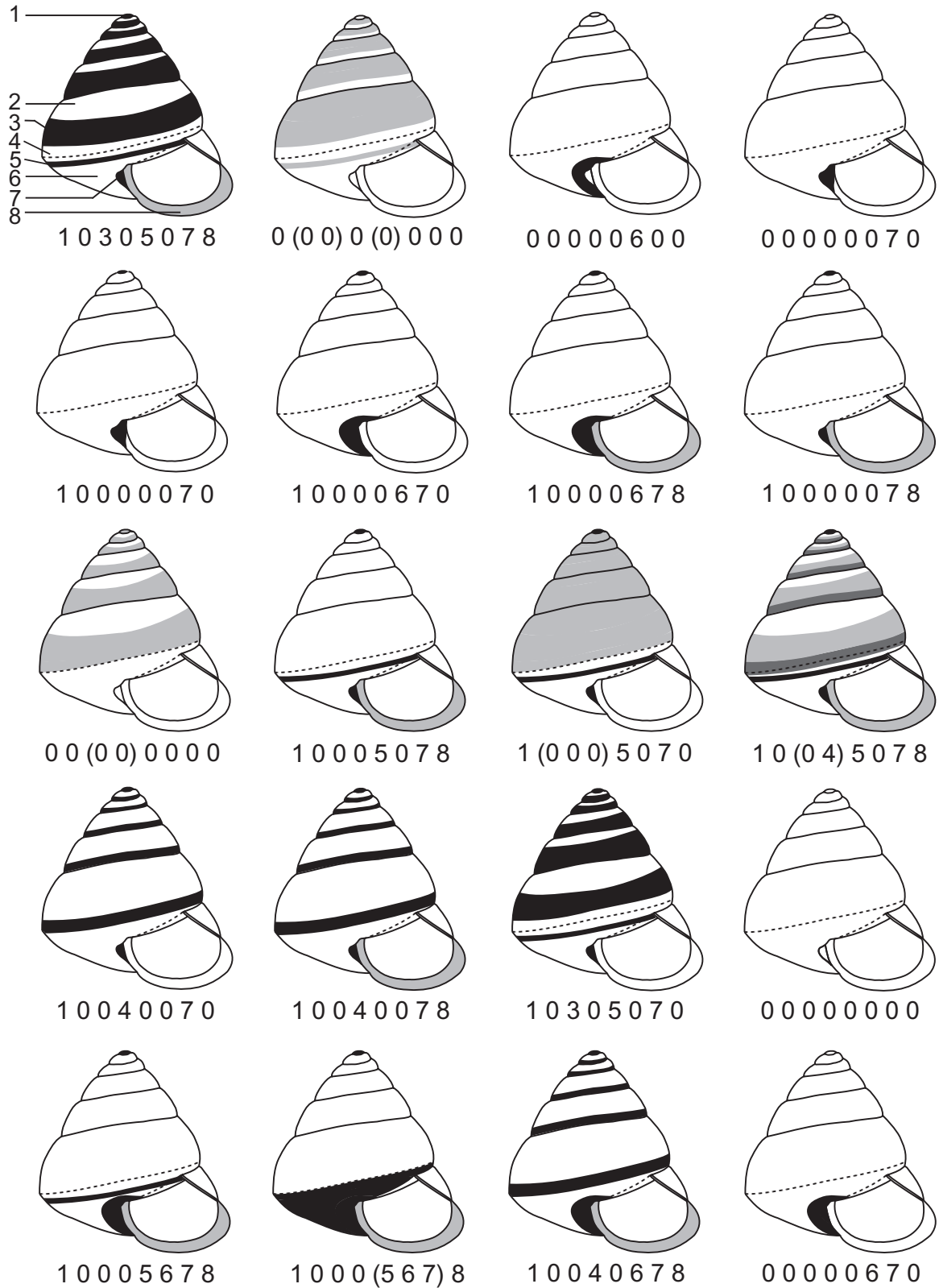
Fig. 3A–D), which was part of H. Adams' collection purchased by the Natural History Museum, London. The number of specimens was not mentioned in Adams' description, but a later mark on the case, 'paratype', indicated that there was probably more than one specimen examined by H. Adams although no specimen and designation of types can be traced. Therefore, we prefer to designate the single specimen as lectotype.

*Additional material:* Nineteen specimens were collected from Nanhua (*N* = 1), Jiashian (*N* = 2), Baolai (*N* = 5), Shanping (*N* = 1) and Dajin (*N* = 10). Three specimens from Dajin were deposited as vouchers,

TMMT P-0277 (dissected, in alcohol), BMNH 20060782 (shell) and ANSP 413693 (shell).

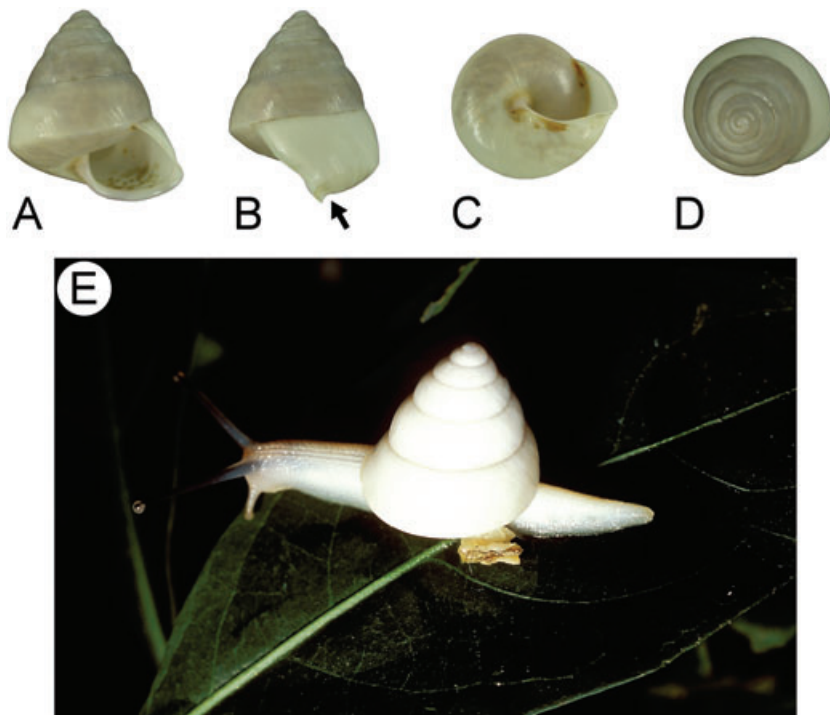
#### *Type locality*

Taiwan, Formosa. The locality 'Taiwan' indicated the 'Taiwan Hsien (County), Taiwan Fu' on south-west Formosa at that time (Swinhoe, 1864), which is equivalent approximately to part of Tainan County and Kaohsiung County at present. The label accompanying with the specimen is marked as 'Takow, Formosa' and is incongruent with H. Adams' description. Takow (or Takao) located at Qijin, coastal part of Kaohsiung City nowadays, is less likely to have this species. We suggest that it is either mislabelled by



**Figure 2.** Band formula and colour stain demonstrating polymorphism of banding patterns. Numbers 1–8 show the position of the band. A '0' means no bands or stains present. Digits in parentheses denoted a smear displayed between and connected with the bands or stains. See text for definition of bands and stains in detail.





**Figure 3.** *Satsuma albida*. A–D, lectotype (BMNH 1878.1.28.229, shell height = 15 mm). E, living specimen. Arrow indicates the pre-apertural constriction.

H. Adams or was used as a convenient way to represent part of the 'Taiwan Hsien' area, like some of H. Adams' species (1866, 1870).

#### *Diagnosis*

Shell and soft body white with grey pedal stripe; shell height equal to shell diameter; penis smooth-surfaced, slender; penial caecum long, slender.

#### *Etymology*

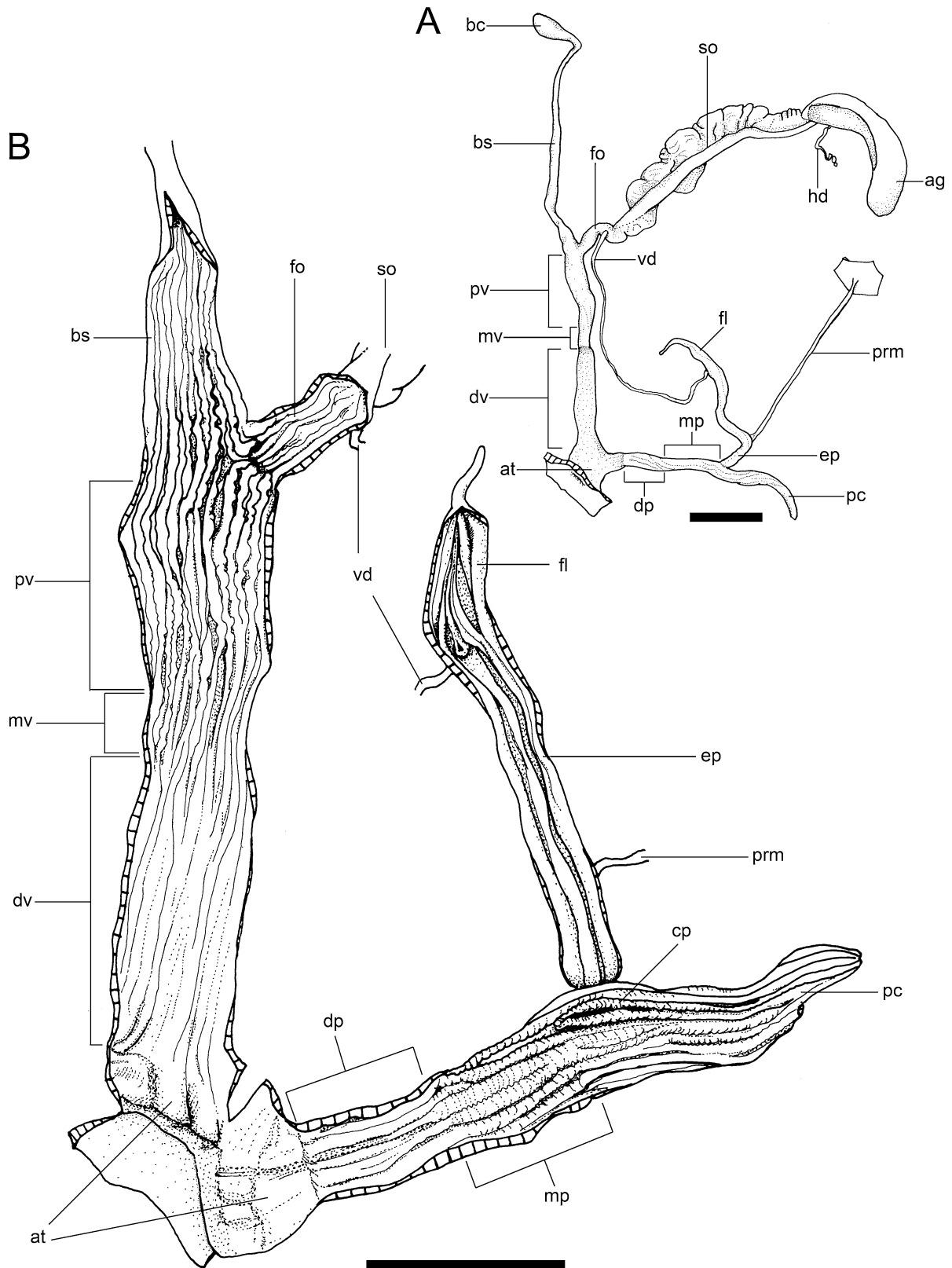
*L. albidus*: white

#### *Description*

**Shell** (Fig. 3): dextral, conical, thin but rigid, medium to small, higher than wide. Apex obtuse. Whorls expanded; periphery bluntly angulated. Base inflated. Pre-apertural constriction behind outer and inferior lips present. Surface smooth, glossy with faint axial and spiral striae. Shell white or white milky with fine periostracum. Aperture diagonal, ovate-lunate. Peristome thin, expanded; inferior lip convex, reflected; outer lip expanded at periphery but simple near to insertion, straight in right-lateral view; superior end of columellar lip vertical, distinctly dilated, covering most of umbilicus; inferior end of columellar lip oblique. Junction of columellar and inferior lips angulated. Umbilicus narrow, covered by dilated columellar lip, left only crevice.

**Band or stain:** Without any band or stain. Band formula = 0 0 0 0 0 0 0.

**Reproductive system** (Fig. 4): Bursa stalk swollen at base, shorter than spermoviduct. Bursa copulatrix oval or clavated. Proximal vagina muscular, gross and smooth externally, bearing about 15 strong and wiggly folds internally; middle vagina constrictive; distal vagina long, one-third to half length of vagina, finely wrinkled inside. Flagellum long, tapering, not swollen at base. Epiphallus with three wide but weak pilasters inside. Penial caecum long, slender, almost equal in width until blunt tip. Cecal pilaster two in number, weak, barely any more prominent than other pilasters, which number about seven. Principal pilaster absent; proximal penis not identified; middle penis long, slender, muscular, approximately same strength as penial caecum, with six to seven low, well-defined, wiggly, corrugated pilasters inside; distal penis slender, same strength as middle penis, bearing weak and smooth pilasters that reduce gradually as fine wrinkles towards atrium internally. Walls of penis and penial caecum smooth, thin, semi-translucent; internal pilasters visible from outside. Three individuals dissected, each from Dajin, Baolai and Shanping. Specimen from Baolai with weakly swollen middle penis. Specimen from Shanping with weakly swollen distal penis.



**Figure 4.** Reproductive system of *Satsuma albida* (TMMT P-0277, Dajin). A, whole genitalia; B, interior of genitalia. Scale bar = 5 mm. See text for abbreviations.

*Distribution*

This species was found in south-east Tainan and northern Kaohsiung County including Nanhua, Jiaxian, Baolai, Liugui, Shanping and Dajin (Fig. 1, Table 1).

*Remarks*

These animals exhibit arboreal and herbivorous behaviour, perching 2–4 m above the ground (Fig. 3E).

Because it is hard to distinguish this species from similar species without examination of specimens, the reliability of identification of most literature sources (Pfeiffer, 1876; Moellendorff, 1884; Schmacker & Boettger, 1891; Kuroda, 1941; Chang, 1984; Lai, 1990) was left for further consideration. The specimens dissected by Chang *et al.* (1996) were collected from Taipei County, and have different morphologies on shell and reproductive characters. Our dissected individual had a shell height of 19.2 mm, diameter of 14 mm and height/diameter ratio of 1.37. The illustrated reproductive system revealed a short flagellum with a strongly expanded base and digitate tip, a conical penial caecum, a strongly swollen proximal vagina and an expanded proximal penis, similar to *Satsuma viridibasis* described below. The photographed shell in Chang *et al.* (1996) has larger shell dimensions (height

17.7 mm, diameter 16 mm, height/diameter ratio 1.11) than *S. albida*. This is, in fact, a shell of *S. phoenicis* (described below) collected from the type locality of the species by one of the authors C. C. Hwang. The authors were not aware of the species diversity in this species complex.

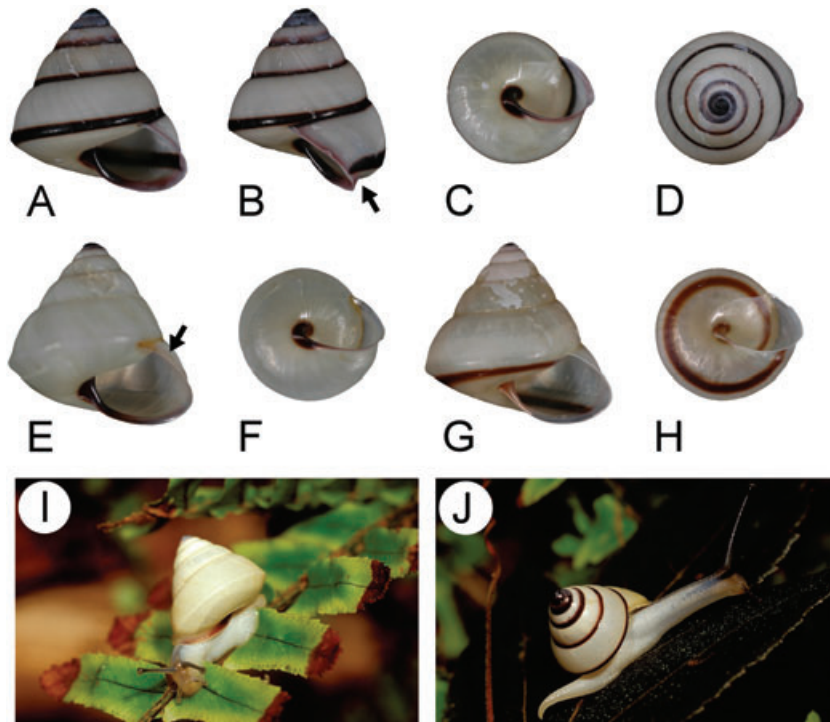
*SATSUMA HAGIOMONTIS SP. NOV.* (FIGS 5, 6)*Material examined*

*Type specimen:* Holotype: TMMT 0604 (from type locality, dry shell, tissue in alcohol). Five paratypes: all from type locality, TMMT 0615 (dry shell, tissue in alcohol, dissected); TMMT 0616 (dry shell, tissue in alcohol); BMNH 20060751, BMNH 20060752, ANSP 413674 (dry shell).

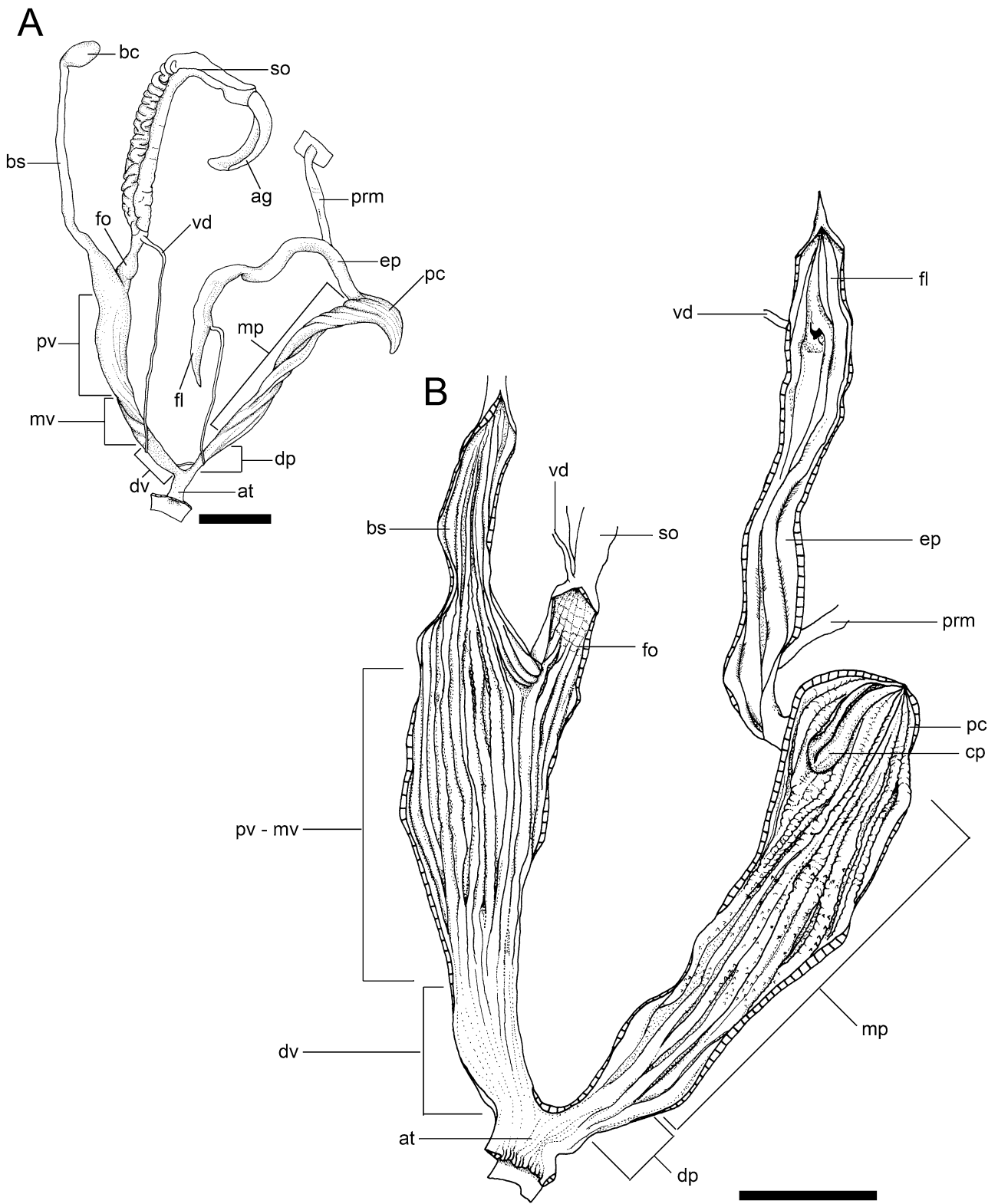
*Additional material:* Museum of Zoology, National Taiwan University (NTUM): two dry shells, collected from Kuwarusu (= Taiwu, Pingtung County, southern Taiwan) in 1918.

*Type locality*

M. Beidawushan, Pingtung County, southern Taiwan (Fig. 1, Table 1).



**Figure 5.** *Satsuma hagiomontis* sp. nov. A–D, holotype (TMMT 0604, shell height = 17.7 mm). E, F, paratype (TMMT 0615, shell height = 14 mm). G, H, paratype (TMMT 0616, shell height = 14 mm). I, J, living specimens. Arrow indicates the pre-apertural constriction.



**Figure 6.** Reproductive system of *Satsuma hagiomontis* sp. nov. (paratype, TMMT 0615). A, whole genitalia; B, interior of genitalia. Scale bar = 5 mm. See text for abbreviations.

*Diagnosis*

Shell and soft body white with grey pedal stripe; periphery keeled; shell height/diameter ratio close to 1.0; distal vagina short; penis corrugated on surface; penial caecum conical; genitalia with or without spinules.

*Etymology*

*L. hagio*: holy, *L. montis*: mountain. The type locality, Mt Beidawushan, is a holy mountain of two aboriginal tribes, the Paiwan and Rukai.

*Description*

*Shell* (Fig. 5): dextral, conical, thin, fragile, semi-translucent, medium sized. Apex obtuse. Whorls inflated. Peripheries bluntly angulated with keel extended to peristome. Base inflated. Pre-apertural constriction behind outer and inferior lips present. Shell surface smooth, glossy, with spiral striae. Shell colour white milky with thin periostracum. Aperture diagonal, ovate-lunate. Peristome thin, expanded, reflected at curved inferior lip. Superior columellar lip vertical, reflected, covering most of umbilicus. Inferior columellar lip oblique, continual to inferior lip.

*Band or stain*: Polymorphism exists in this taxon. Some individuals exhibit a red-brown to black-purple stain around the umbilicus, columellar, columellar lip, inferior lip and apex, others have spiral colour band around the whorls or at the base. The outer lip exhibits no coloration. Band formula = 1 0 0 0 0 0 7 8; 1 0 0 0 5 0 7 0; 1 0 0 4 0 0 7 0; 1 0 0 4 0 0 7 8.

*Reproductive system* (Fig. 6): Bursa stalk long, with apparently expanded and conical base, regularly tapering towards oval bursa copulatrix. Proximal vagina muscular, swollen, smooth externally, with 14–17 strong, smooth folds internally. Middle vagina less muscular, distinctly constrictive, twisted. Distal vagina short, one-quarter of vagina in length. Flagellum long, tapering, not swollen at base. Pilaster in epiphallus wide, weak, three in number. Penial caecum long, depressed-conical. Cecal pilaster two in number, moderately weak, not strongly corrugated on surfaces. Principal pilaster and proximal penis absent. Middle penis long, twisted, depressed, with seven to nine moderately strong, wiggly, corrugated pilasters inside. Distal penis short, constrictive, with three wide and low pilasters vanishing towards atrium internally. Of the two dissected specimens one (TMMT 0615) has many spinules on the surface of the pilasters in the middle penis.

*Distribution*

The species was found only in a narrow area of mid-altitude (1000–1400 m) forest near Mt Beidawushan, Pingtung County, southern Taiwan (Fig. 1, Table 1).

*Remarks*

These arboreal herbivores are nocturnal, perching under leaves more than 2 m above ground. Adults were found during summer (Fig. 5I, J). The species differs from *S. albida* in having a keeled periphery, lower spire with shell height/diameter ratio close to 1.0, short distal vagina; corrugated penis externally, conical penial caecum and spinules inside genitalia. The conical penial caecum and strongly corrugated penis are unique among white-shelled species in west Taiwan.

**SATSUMA SWINHOEI SP. NOV.** (FIGS 7, 8)*Material examined*

*Type specimen*: Holotype: TMMT 0605 (from type locality, dry shell, tissue in alcohol). Nine paratypes: all from type locality, NMNS 005405-1 (dry shell, tissue in alcohol, dissected); TMMT 0617–0620 ( $N = 4$ , dry shell, tissue in alcohol); BMNH 20060754, BMNH 20060755, ANSP 413675, SMF 329384 (dry shell, tissue in alcohol).

*Type locality*

Qingshan, Pingtung County, southern Taiwan (Fig. 1, Table 1).

*Diagnosis*

Shell and soft body white with grey pedal stripe; periphery keeled; base of bursa stalk slender; distal vagina short; penis surface smooth.

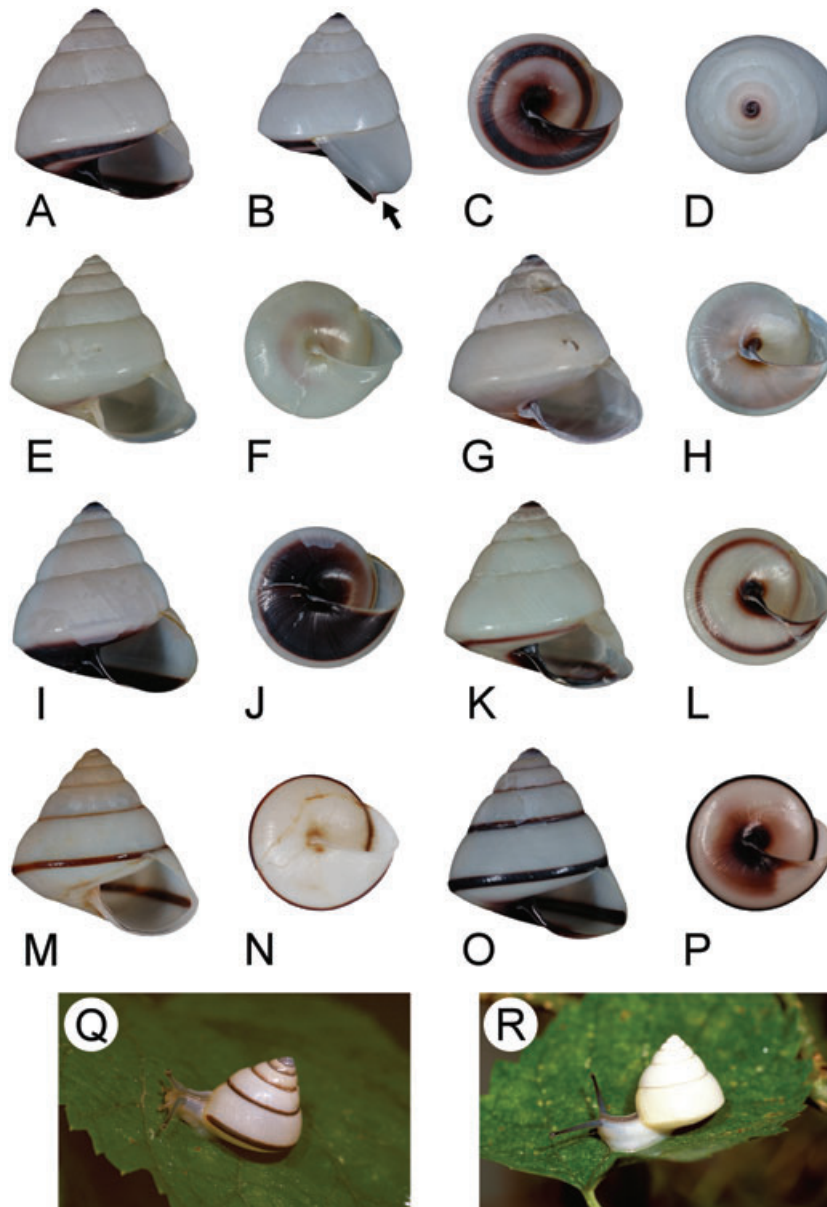
*Etymology*

In memory of the prominent naturalist, Mr Robert Swinhoe (1836–1877) who discovered the first *S. albida*.

*Description*

*Shell* (Fig. 7): Dextral, conical, thin, rigid, medium sized. Apex obtuse. Whorls expanded. Periphery bluntly angulated, keeled. Base inflated. Pre-apertural constriction behind outer and inferior lips present. Surface smooth, glossy with spiral striae. Shell colour milky white with fine periostracum. Aperture diagonal, ovate-lunate to tetragonal. Peristome thin, expanded, reflected at curved inferior lip. Superior columellar lip vertical, reflected, covering



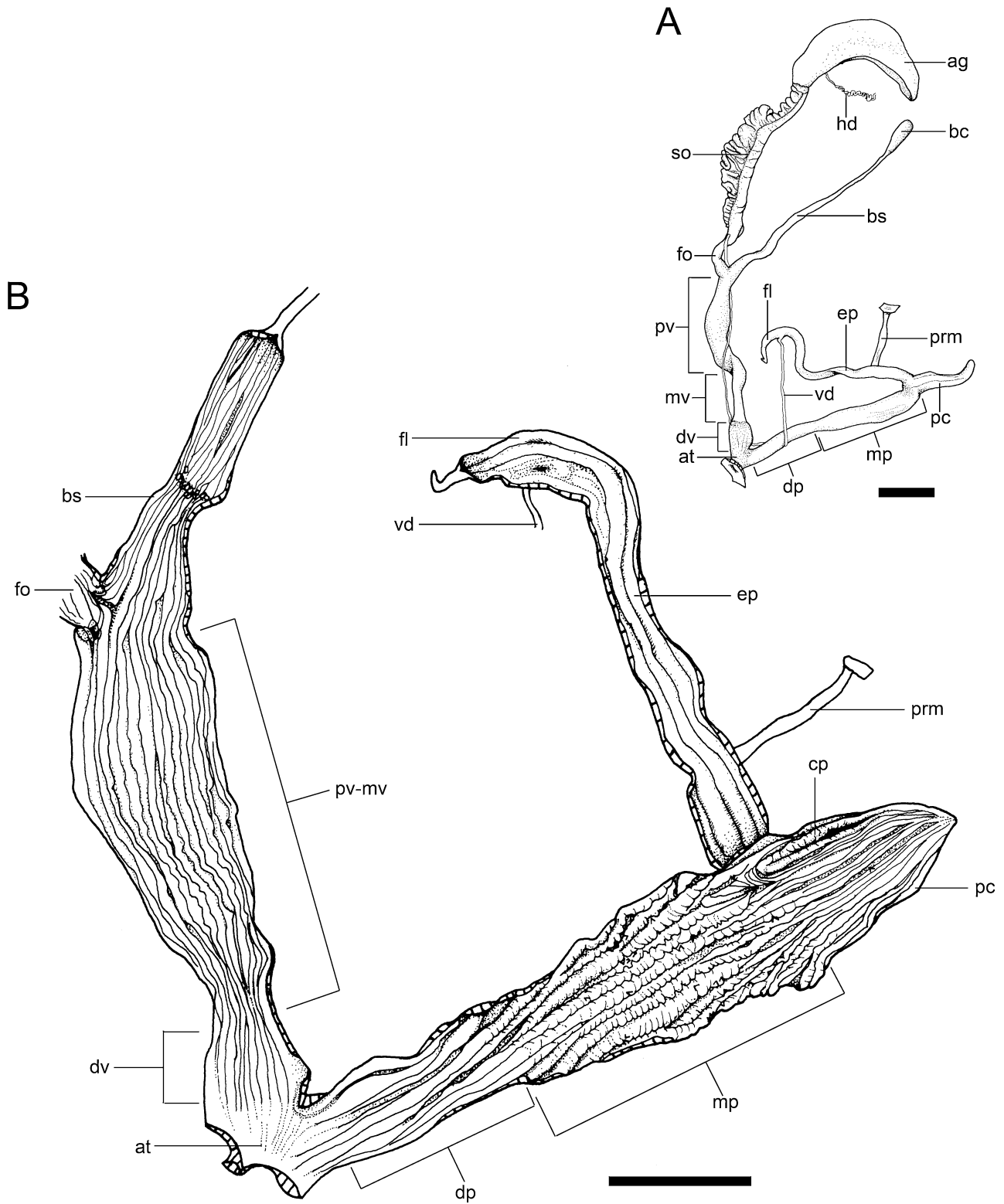


**Figure 7.** *Satsuma swinhoei* sp. nov. A–D, holotype (TMMT 0605, shell height = 18.5 mm). E, F, paratype (BMNH 20060754, shell height = 16.3 mm). G, H, paratype (TMMT 0617, shell height = 17.2 mm). I, J, paratype (TMMT 0618, shell height = 17.3 mm). K, L, paratype (TMMT 0619, shell height = 17.3 mm). M, N, paratype (NMNS 005405-1, shell height = 16.3 mm). O, P, paratype (TMMT 0620, shell height = 18.2 mm). Q, R, living specimens. Arrow indicates the pre-apertural constriction.

umbilicus mostly. Inferior columellar lip oblique, obtusely angulated at junction with inferior lip.

**Band or stain:** Polymorphism exists in this taxon. Some individuals exhibit a light red-brown to purple stain around and in the umbilicus. Band formula = 0 0 0 0 0 0 0 0; 0 0 0 4 0 0 0 0; 0 0 0 0 0 6 0 0; 0 0 0 0 6 7 0; 1 0 0 0 5 0 7 8; 1 0 0 0 5 6 7 8; 1 0 0 0 (5 6 7) 8; 1 0 0 4 0 6 7 8.

**Reproductive system** (Fig. 8): The genital morphology of the present species is similar to that of *S. hagiomontis* sp. nov. but with following exceptions: (1) the base of the bursa stalk is expanded only, not conical; (2) the two cecal pilasters are weak, merely stronger than the ridges in the penial caecum and (3) the distal vagina is swollen and short, one-seventh the length of the vagina. One individual was dissected.



**Figure 8.** Reproductive system of *Satsuma swinhoei* sp. nov. (paratype, NMNS 005405-1). A, whole genitalia; B, interior of genitalia. Scale bar = 5 mm. See text for abbreviations.

*Distribution*

The species was only found in a limited area of mid-altitude (1000–1200 m) forest near Qingshan Village, Pingtung County, southern Taiwan (Fig. 1, Table 1).

*Remarks*

Inhabits from 2 m above the ground to the canopy. Adults were found in summer and autumn (Fig. 7Q, R).

The present species is close to *S. albida* genetically, but the shell and genitalia morphologies resemble *S. hagiomontis* sp. nov. (see Phylogeny). The species differs from *S. albida* in having a keeled periphery, short distal vagina and larger shell dimensions (Table 2). *Satsuma swinhoei* sp. nov. differs from *S. hagiomontis* sp. nov. in the opaque shell, straight inferior columellar lip, tetragonal aperture, angulated junction between the inferior lip and the columellar lip, slender base of the bursa stalk and slender penial caecum.

**SATSUMA INSIGNIS** (PILSBRY & HIRASE, 1906)  
(FIGS 9, 10)

*Ganesella albida insignis* Pilsbry & Hirase, 1906 [1905]: 736. (15 Jan 1906)

*Ganesella albida insignis*, Kuroda, 1941: 144, No. 1062.

*Coniglobus (Luchuhadra) albida insignis*, Chang, 1984: 15.

*Satsuma albida insignis*, Richardson, 1985: 268; Hsieh *et al.*, 2006: 232.

*Satsuma albidum insignis*, Lai, 1990: 49. [incorrect gender ending]

*Material examined*

*Type specimen*: Lectotype: ANSP 89989 (dry shell), subsequently designated by Baker (1963). One paratype: ANSP 412186 (dry shell).

*Additional material*: Five specimens were collected from Tengzhi, north-east Kaohsiung, southern Taiwan and deposited as vouchers: TMMT P-0280-1 (dry shell, tissue in alcohol, dissected); TMMT P-0278–P-0280 (dry shell, tissue in alcohol); BMNH 20060783, ANSP 413694 (dry shell).

*Type locality*

Hotawa, Taiwan (near Jiashian, Kaohsiung County, southern Taiwan at present).

*Diagnosis*

Shell and soft body white with grey pedal stripe; shell thick; body whorl suddenly widened anterior to peristome; aperture height smaller than width.

*Etymology*

*L. insignis*: distinguished.

*Description*

*Shell* (Fig. 9): Dextral, conical, thick, rigid, medium sized. Apex obtuse. Whorls inflated. Periphery bluntly angulated. Base flat. Pre-apertural constriction behind outer and inferior lips present. Shell colour porcelain white. Surface smooth, with axial and spiral striae. Body whorl suddenly widened anterior to peristome. Aperture subvertical, trapeziform to ovate-lunate. Peristome thin. Inferior lip expanded, reflected; outer lip less expanded and reflected, in right-lateral view curved forward; junction between outer lip and inferior lip angulated acutely. Superior columellar lip reflected. Umbilicus covered by columellar lip mostly, crevice-like. Junction between vertical columellar lip and curved inferior lip angulated.

*Band or stain*: Polymorphism exists in this taxon. Most individuals exhibit a black-purple stain around the columella, columellar lip and inferior lip. The outer lip is paler in colour. Band formula = 0 0 0 0 0 0 0; 0 0 0 0 0 6 7 8; 1 0 0 0 0 6 7 8; 1 0 0 4 0 0 7 8.

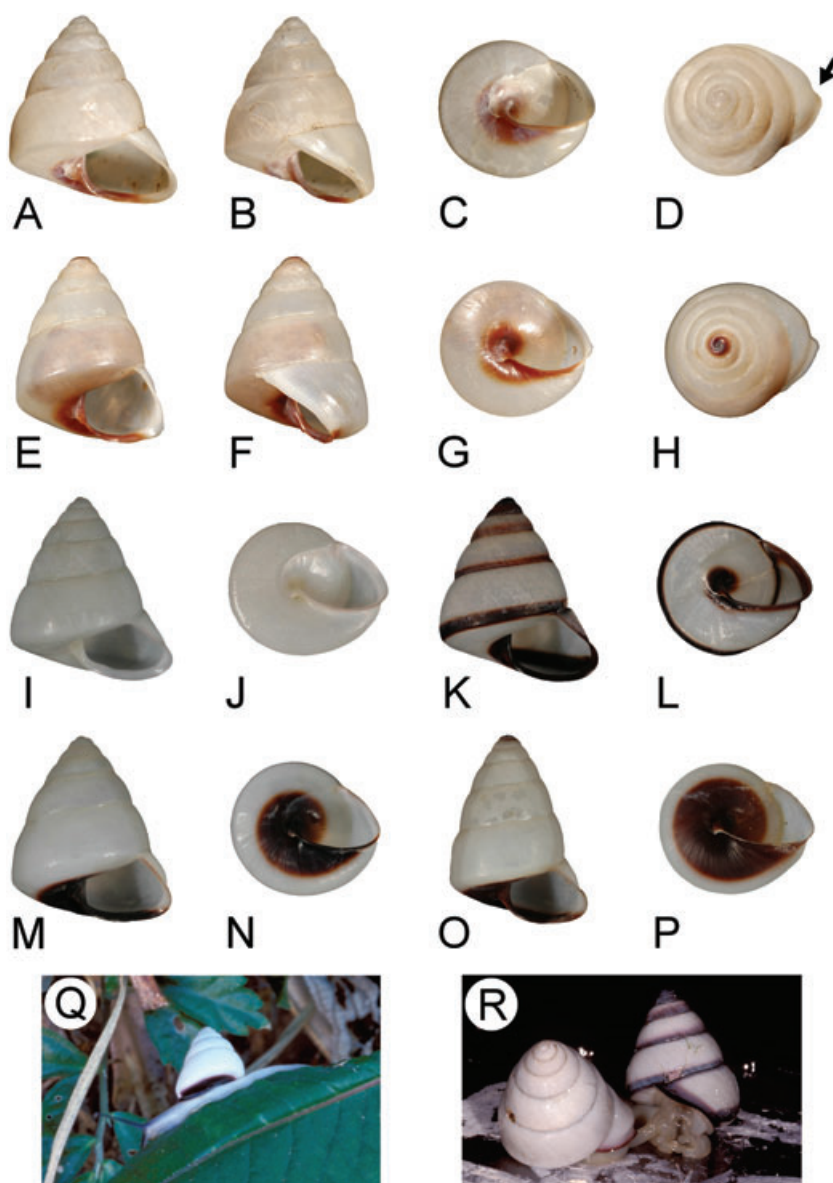
*Reproductive system* (Fig. 10): Bursa stalk long, regularly tapering towards bursa copulatrix. Proximal vagina moderately muscular, gross, smooth externally, with 13 wavy folds inside; middle vagina also muscular, more constrictive than proximal part, with 12 moderate, smooth folds inside; distal vagina one-third length of vagina. Flagellum long, tapering. Epiphallus with three wide but weak pilasters inside. Penial caecum short, tapering with a blunt tip; cecal pilaster two in number, weak but still prominent compared with ridges in penial caecum. Principal pilaster and proximal penis absent; middle penis moderately swollen, muscular, obviously striated externally, with equally strong and elevated internal pilasters six to eight in number; junction between the middle and distal penis constrictive expeditiously; distal penis swollen, muscular, with one strong, high pilaster and four to seven wide but weak pilasters. Three specimens were dissected.

*Distribution*

The animals were only found in the Tengzhi area, north-east Kaohsiung, southern Taiwan (Fig. 1, Table 1).

*Remarks*

Inhabits from above 5 m (Fig. 9Q, R). Life span is probably more than 1 year. Mature individuals were often observed during winter. The correct date of publication was emended based on Clench & Turner (1962). This species differs from *S. albida* in having a



**Figure 9.** *Satsuma insignis*. A–D, lectotype (ANSP 89989, shell height = 16.8 mm). E–H, paralectotype (ANSP 412186, shell height = 15.8 mm). I, J, (TMMT P-0278, shell height = 16.5 mm). K, L, (TMMT P-0279, shell height = 18 mm). M, N, (BMNH 20060783, shell height = 17 mm). O, P, (TMMT P-0280, shell height = 20 mm). Q, living specimen. R, copulation. Arrow indicates the pre-apertural constriction.

more flattened base, more angulated periphery, more protruding body whorl anterior to peristome, thicker shell, larger shell size and greater number of whorls. The protruding body whorl and thick shell can differentiate this species from other white-shelled species in west Taiwan.

***SATSUMA LINI* SP. NOV.** (FIGS 11, 12)

*Material examined*

*Type specimen:* Holotype: TMMT 0602 (from type locality, dry shell, tissue in alcohol, dissected). Three paratypes: all from type locality, TMMT 0621 (imma-

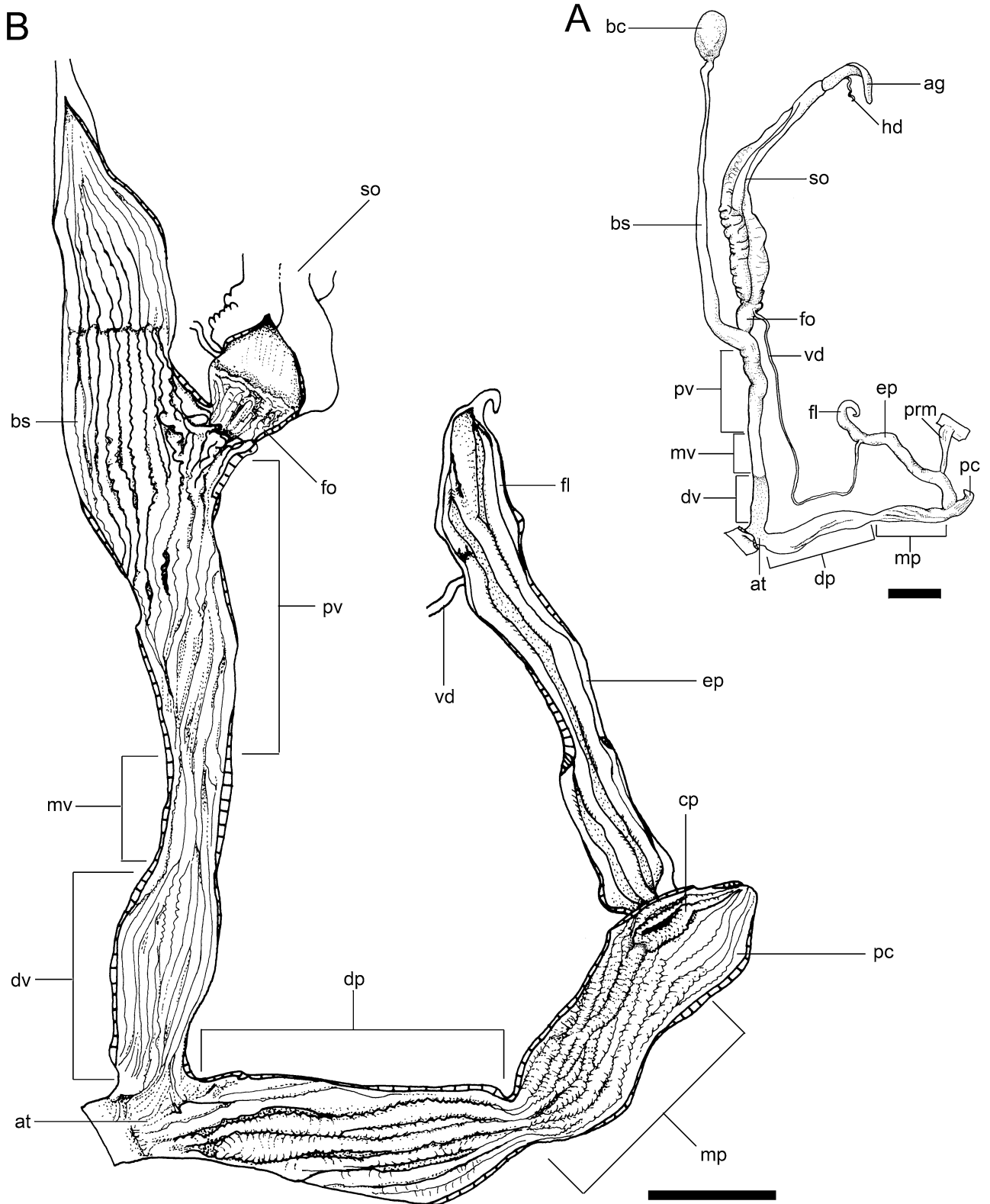
ture, in alcohol); ANSP A21015 (shell with tissue in alcohol); BMNH 20060753 (dry shell).

*Type locality*

Shanlinxi, Nantou County, central Taiwan (Fig. 1, Table 1)

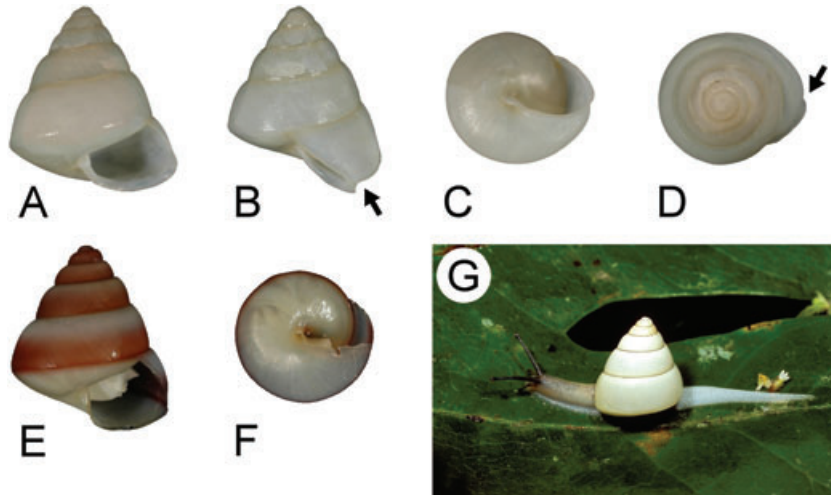
*Diagnosis*

Shell and soft body white with grey pedal stripe; periphery angulated but not keeled; junction between columellar and inferior lips angulated. Because of a

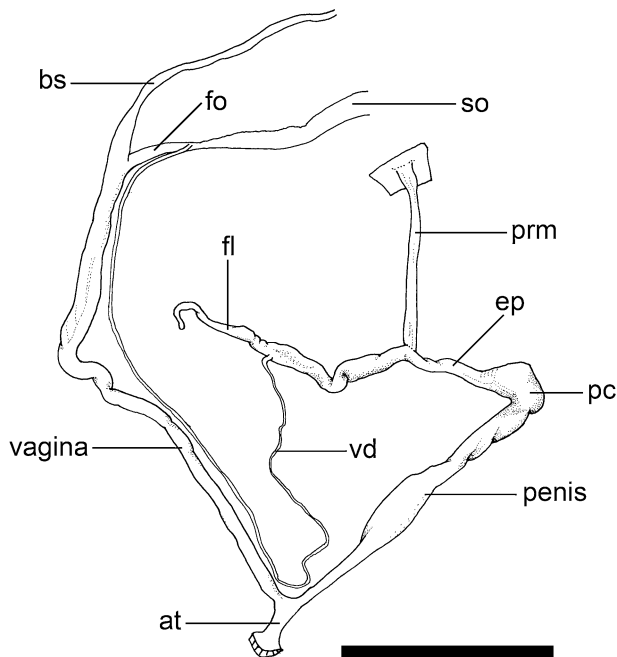


**Figure 10.** Reproductive system of *Satsuma insignis* (TMMT P-0280-1, Tengzhi). A, whole genitalia; B, interior of genitalia. Scale bar = 5 mm. See text for abbreviations.





**Figure 11.** *Satsuma lini* sp. nov. A–D, holotype (TMMT 0602, shell height = 17.6 mm). E, F, paratype (TMMT 0621, shell height = 17 mm). G, living specimen. Arrow indicates the pre-apertural constriction.



**Figure 12.** Reproductive system of *Satsuma lini* sp. nov. (holotype, TMMT 0602), immature genitalia. Scale bar = 5 mm. See text for abbreviations.

lack of knowledge of its genitalia, distinguishing this species from similar species based on shell characteristics only is difficult.

#### Etymology

*L. lini*: the name is dedicated to the late Professor Lin, Fei-Jan (1934–2004), a pioneering evolutionary biologist from Taiwan.

#### Description

**Shell** (Fig. 11): Dextral, conical, medium sized. Apex obtuse. Whorls inflated. Periphery bluntly angulated. Base expanded. Pre-apertural constriction behind outer and inferior lips present. Surface smooth, glossy with spiral striae. Shell colour whitish. Periostracum thin. Aperture diagonal, ovate-lunate angled between outer lip and inferior lip. Peristome thin, expanded, reflected at curved inferior lip. Superior columellar lip reflected. Umbilicus covered by columellar lip mostly, crevice-like. Columellar lip vertical to subvertical, angulated at junction with inferior lip.

**Band or stain:** Polymorphism exists in this taxon. The majority of individuals do not possess band or colour stain, and display a whitish coloration. A rare form exists with pink stain and smear from the third to the fourth band position. Band formula = 0 0 0 0 0 0 0; 0 0 (0 0) 0 0 0 0 (very rare).

**Reproductive system** (Fig. 12): No reproductively mature specimens were collected. An immature genitalia is figured to demonstrate its basic configuration.

#### Distribution

The species was found only in a narrow area of mid-altitude forest (1600–1800 m) near Shanlinxi, Nantou County, central Taiwan (Fig. 1, Table 1).

#### Remarks

Inhabits typically above 3 m. Adults were found during winter (Fig. 11G). Only four specimens are available; two of these have adult shell morphology but genital development is incomplete. The other individuals are sub-adults.

This species is morphologically similar to *S. albida*, *S. swinhoei* sp. nov. and *S. insignis*, but its genetic relationship is closer to *S. insignis* (see Phylogeny). Compared with *S. albida*, *S. lini* has a larger, thinner and more rigid shell, higher spire and more oblique aperture. The species differs from *S. swinhoei* in having a periphery that is not keeled, smaller shell diameter and higher spire.

**SATSUMA PHOENICIS SP. NOV.** (FIGS 13, 14)

*Satsuma albida* (H. Adams), Chang *et al.*, 1996: 25–30, fig. 1 (shell). [non *albida*]

*Material examined*

*Type specimen*: Holotype: TMMT 0601 (from type locality, dry shell, tissue in alcohol). Five paratypes: all from type locality, NMNS 005405-6 (dry shell, tissue in alcohol, dissected); TMMT 0645 (dry shell, tissue in alcohol); BMNH 20060772, ANSP 413687, SMF 329395 (dry shell).

*Type locality*

Fenghuanggu, Lugu, Nantou County, central Taiwan (Fig. 1, Table 1).

*Diagnosis*

Shell and soft body white with grey pedal stripe; proximal penis present, swollen, grooved; principal pilaster present, bifurcate, not formed in single strong pilaster.

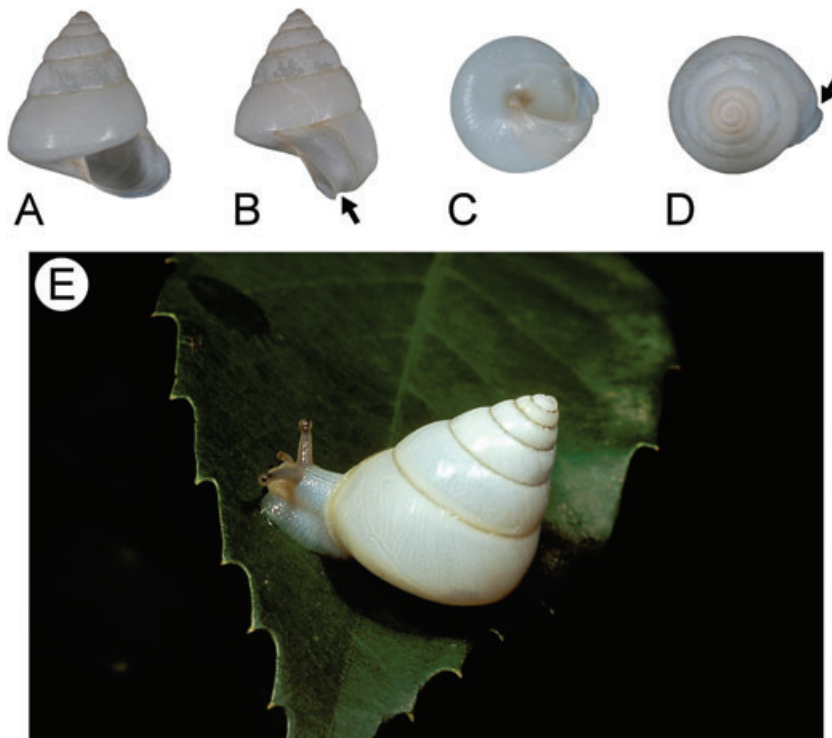
*Etymology*

*L. phoenicis*: phoenix, translation of the type locality 'phoenix valley' (Fenghuanggu).

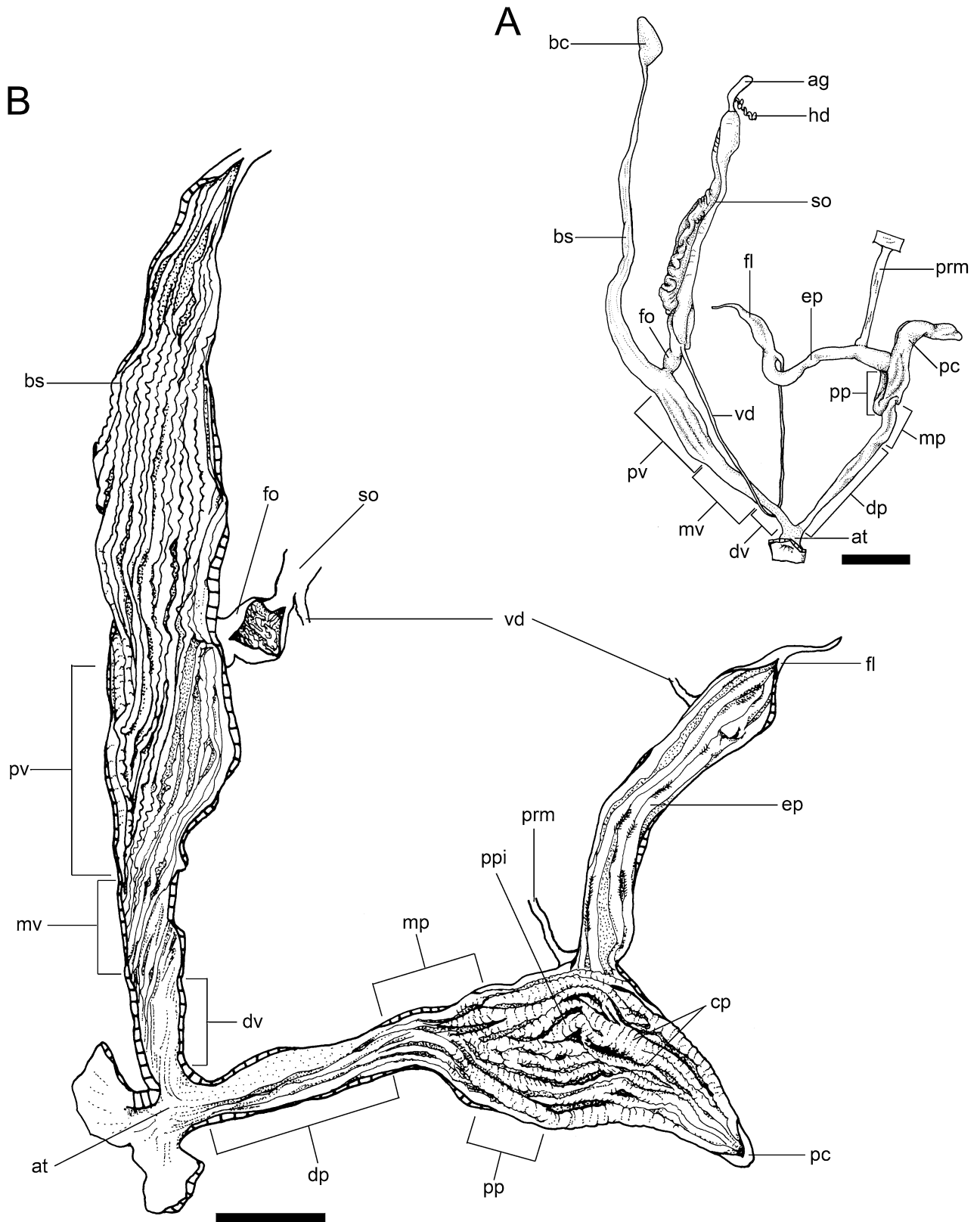
*Description*

*Shell* (Fig. 13): Dextral, conical, medium sized. Apex obtuse. Whorls expanded. Periphery bluntly angulated, extending to peristome. Base expanded. Pre-apertural constriction behind outer and inferior lips present. Surface glossy, with spiral striae. Shell colour milky white, covered with fine periostracum. Aperture diagonal, ovate-lunate. Peristome thin, expanded. Inferior lip reflected, curved downward. Superior columellar lip vertical, reflected. Umbilicus covered by columellar lip, crevice-like. Junction between oblique inferior columellar lip and inferior lip smoothly curved.

*Band or stain*: Band or stain is not present in this species. Band formula = 0 0 0 0 0 0 0.



**Figure 13.** *Satsuma phoenicis* sp. nov. A–D, holotype (TMMT 0601, shell height = 19.4 mm). E, living specimen. Arrow indicates the pre-apertural constriction.



**Figure 14.** Reproductive system of *Satsuma phoenicis* sp. nov. (NMNS 005405-6). A, whole genitalia; B, interior of genitalia. Scale bar = 5 mm. See text for abbreviations.

**Reproductive system** (Fig. 14): Bursa stalk long, tapering with wiggly folds internally. Proximal vagina muscular, furrowed externally; middle vagina muscular, constrictive, with weak folds inside; distal vagina one-quarter length of vagina. Flagellum long, tapering smoothly towards tip. Penial caecum long, tapering with blunt tip; cecal pilasters two or three in number, surrounding epiphallic pore. Principal pilaster present, bifurcate, weak, not merged as single strong pilaster. Proximal penis widened, muscular, furrowed with a deep groove externally corresponding to strong, elevated, corrugated internal pilasters; middle penis short, suddenly constrictive from proximal penis, with weak and smooth pilasters inside; distal penis moderately slender, with one to two weak internal pilasters gradually weakened towards atrium. Three specimens were dissected.

**Distribution**

Lugu area, Nantou County, central Taiwan (Fig. 1, Table 1).

**Remarks**

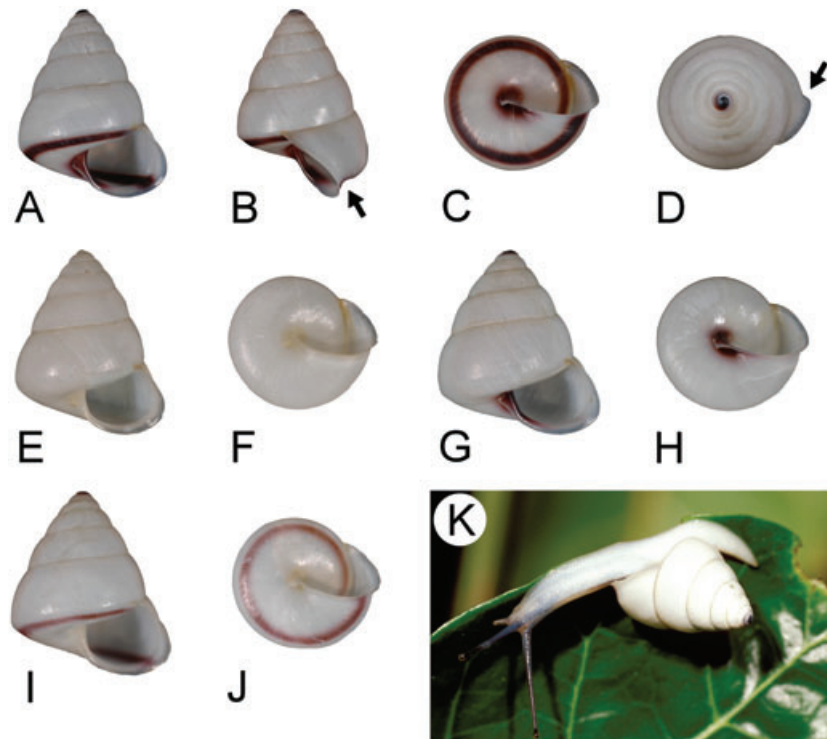
Animals are arboreal, herbivores and nocturnal perching under leaves 2–3 m above ground. Adults were found during summer and autumn (Fig. 13E).

The swollen and grooved proximal penis and bifurcate principal pilaster is unique among species in west Taiwan. The shell of the present species differs from that of *S. albida* in its larger size, and being thinner, translucent and more rigidness; differs from that of *S. lini* in larger measurements (Table 2), more flattened base and inferior lip, more blunt periphery, more curved downward inferior lip and, hence, smooth junction between the inferior lip and the columellar lip. This species is morphologically similar to *S. lini* sp. nov., but the genetic relationship was calculated to be closer to *S. careocaecum* sp. nov. The photographed shell in Chang *et al.* (1996, Fig. 1) belongs to this species (see remarks in *S. albida*.)

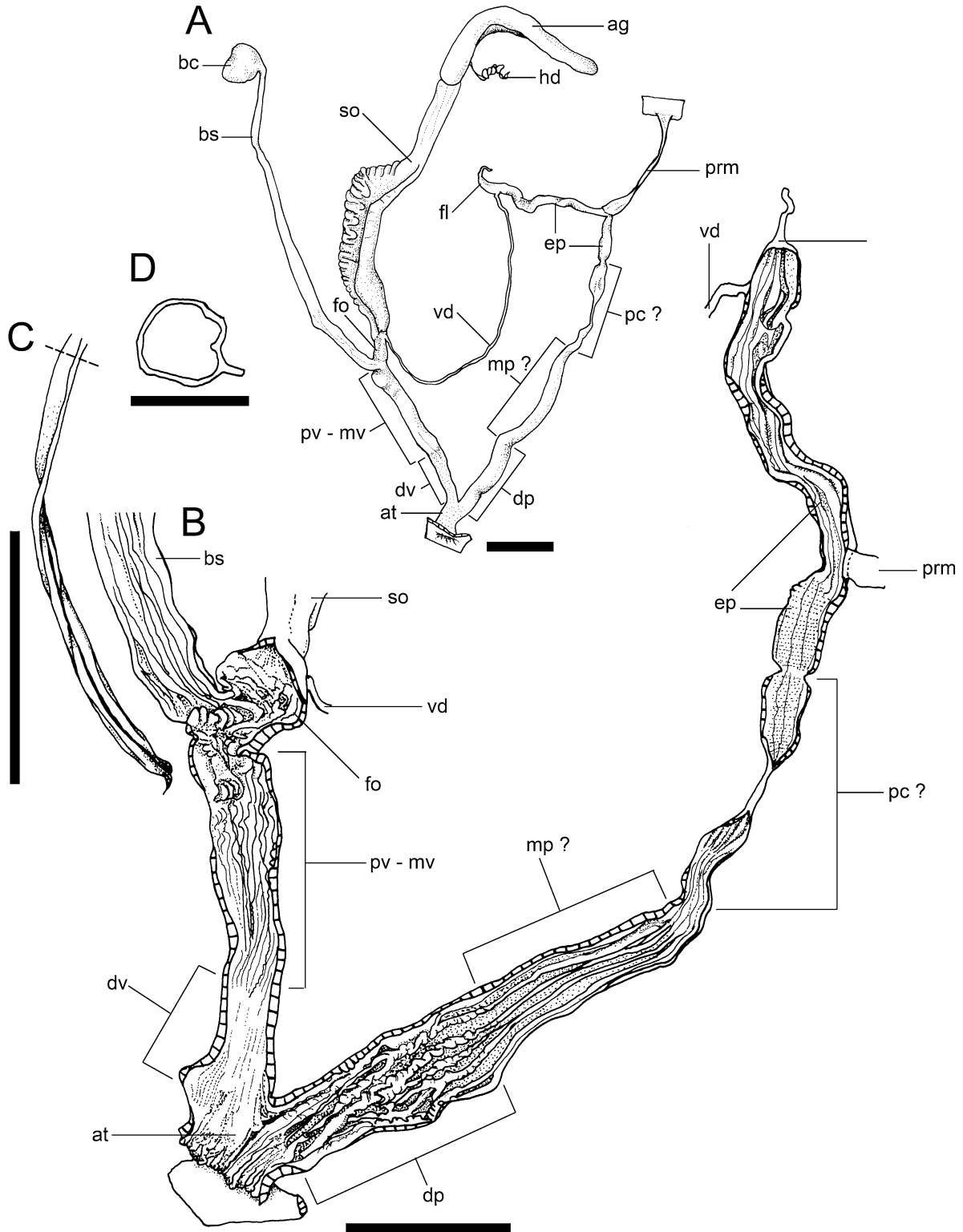
**SATSUMA CAREOCAECUM SP. NOV. (FIGS 15, 16)**

**Material examined**

**Type specimen:** Holotype: TMMT 0603 (from type locality, dry shell, tissue in alcohol). Seventeen paratypes: all from type locality, TMMT 0651 (dry shell, tissue in alcohol, dissected); TMMT 0622–0624, TMMT 0646–0650 (dry shell, tissue in alcohol); BMNH 20060769–20060771, ANSP 413686 ( $N = 3$ ), SMF 329393–329394 (dry shell).



**Figure 15.** *Satsuma careocaecum* sp. nov. A–D, holotype (TMMT 0603, shell height = 19.1 mm). E, F, paratype (TMMT 0622, shell height = 17.8 mm). G, H, paratype (TMMT 0623, shell height = 17.9 mm). I, J, paratype (TMMT 0624, shell height = 17.7 mm). K, living specimen. Arrow indicates the pre-apertural constriction.



**Figure 16.** Reproductive system of *Satsuma careocaecum* sp. nov. (paratype, TMMT 0651). A, whole genitalia; B, interior of genitalia. C, part of spermatophore showing its position in the female genitalia. D, cross-section of spermatophore at dash line. Scale bar for A–C = 5 mm, for D = 0.5 mm. See text for abbreviations. An abbreviation with a question mark indicates a tentative portion of genitalia.



*Type locality*

Guanziling, Tainan County, southern Taiwan (Fig. 1, Table 1).

*Diagnosis*

Shell and soft body white with grey pedal stripe; base expanded; penial caecum absent.

*Etymology*

*L. careo*: lack; *caeca*: caecum, referring to the lack of a penial caecum.

*Description*

*Shell* (Fig. 15): Dextral, conical, thin, rigid, medium sized. Apex obtuse. Whorls inflated. Periphery bluntly angulated to arc-like. Base expanded. Pre-apertural constriction behind outer and inferior lips present. Surface sheen with spiral striae. Shell colour white or white milky. Periostracum fine. Aperture diagonal, ovate-lunate. Peristome thin, expanded, reflected. Inferior lip curved downwards. Columellar lip oblique, reflected covering most of umbilicus. Junction of columellar lip and inferior lip roundly angulated.

*Band or stain*: Polymorphism exists in this taxon. Most individuals exhibit a red-brown to black-purple stain around the umbilicus, columellar, columellar lip and apex; a sub-peripheral band is present in some specimens. The outer lip and inferior lip lack such coloration. Band formula = 0 0 0 0 0 0 0; 1 0 0 0 0 0 7 0; 1 0 0 0 5 0 0 0; 1 0 0 0 5 0 7 0.

*Reproductive system* (Fig. 16): Bursa stalk long, almost slender. Proximal and middle vagina equally thin without conspicuous boundary between them, smooth externally, bearing 8–12 smooth, irregular strength folds internally; distal vagina one-third length of vagina. Flagellum long, tapering, with slender tip. Epiphallus with four weak pilasters inside. Penial caecum absent. Segment corresponding to penial caecum with three weak pilasters inside; then continued by slender tubule to penis. No verge or apparent internal constriction observed. Penis weak, gradually becoming robust towards atrium; middle penis with five clear, smooth, thin pilasters; distal penis with five strong, irregular, wiggly pilasters. Spermatophore (Fig. 16C) found in bursa stalk of figured individual (TMMT 0651); apical end partly digested in bursa copulatrix (not shown); tail tip remains in proximal vagina; cross-section at middle part (Fig. 16D) with three shallow valliculae and a projected fold. Six specimens were dissected.

*Distribution*

From Guanziling to Dongshan, northern Tainan County, southern Taiwan (Fig. 1, Table 1).

*Remarks*

The perching distance is typically from 3 m above ground to the canopy. Mature individuals often appear during winter (Fig. 15K).

The absence of a penial caecum is the most distinct character among species of this species complex. Some *Satsuma* species, e.g. *S. nux paiwanis* (Kuroda, 1941), showed a reduced penial caecum (Chang, 1989), whilst others, e.g. *Pancala batanica pancala* (Schmacker & Boettger, 1891) and *Pancala bacca* (Pfeiffer, 1866 [1865]), showed a lack of a penial caecum with an apparent verge at insertion of the epiphallus (Chang, 1992; Hwang, 1995). A totally degenerated penial caecum as seen in *S. careocaecum* sp. nov. was not recorded in *Satsuma*.

The species differs from *S. lini* in having a greater number of whorls, apical spot, sub-peripheral band and umbilicus spot; from *S. hagiomontis* sp. nov. and *S. swinhoei* sp. nov. in having bluntly angulated periphery; and from *S. insignis* in having thinner shell and regularly expanded body whorl.

**SATSUMA POLYMORPHA SP. NOV. (FIGS 17–20)***Material examined*

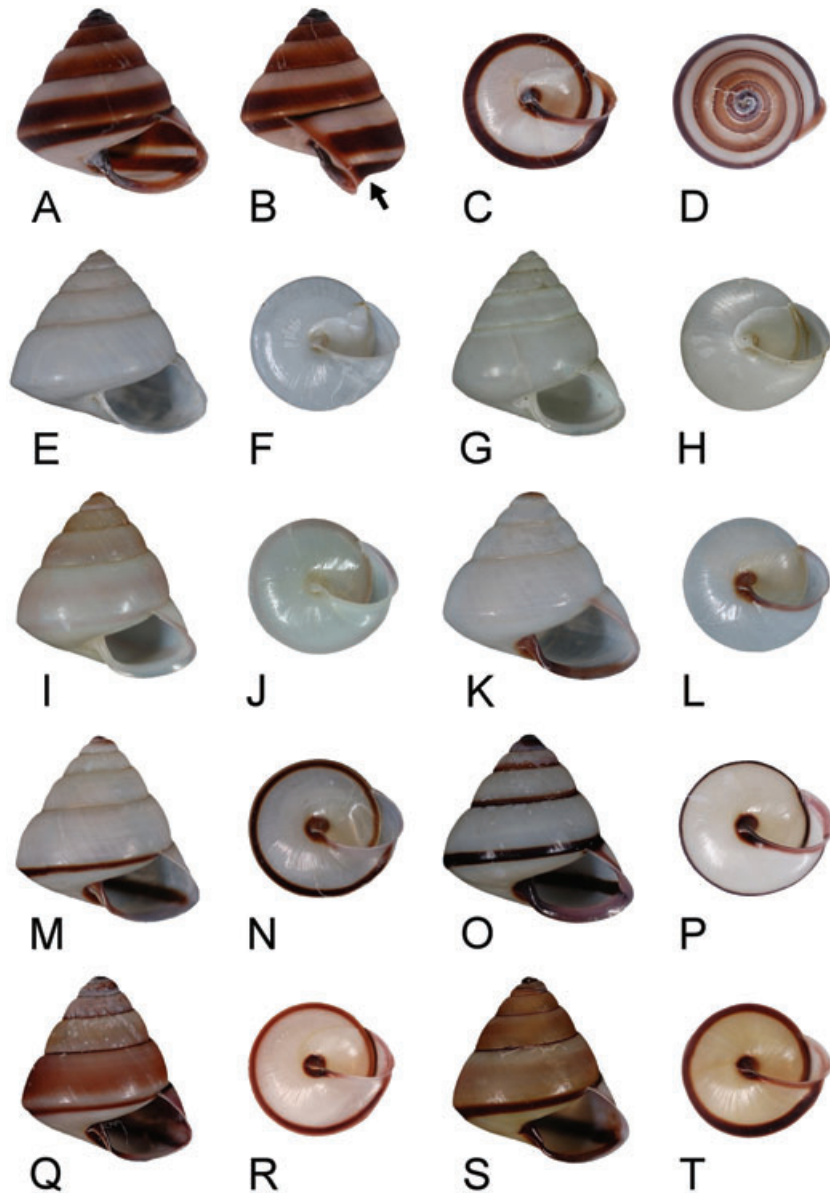
*Type specimen*: Holotype: TMMT 0606 (from type locality, dry shell, tissue in alcohol). Thirty-four paratypes: 27 paratypes from type locality: TMMT 0680 (dry shell, tissue in alcohol, dissected); TMMT 0627–0630, TMMT 0632, TMMT 0673–0674 (dry shell, tissue in alcohol); NMNS 005405-7–005405-11, BMNH 20060776–20060781, ANSP 413689, ANSP 413690 ( $N = 2$ ), ANSP 413691 ( $N = 2$ ), ANSP 413692, SMF 329397–329398 (dry shell); two paratypes from Mataian, Hualien: TMMT 0631, TMMT 0671 (dry shell, tissue in alcohol); one paratype from Ruisui, Hualien: TMMT 0633 (dry shell, tissue in alcohol); two paratypes from Fushan, Yilan: TMMT 0625 (dry shell, tissue in alcohol), BMNH 20060775 (dry shell); one paratype from Youluo, Hsinchu: TMMT 0626 (dry shell, tissue in alcohol); one paratype from Shenmihu, Yilan: TMMT 0672 (dry shell, tissue in alcohol, dissected).

*Type locality*

Beinan, Taitung County, eastern Taiwan (Fig. 1, Table 1).

*Diagnosis*

Shell and soft body white with grey pedal stripe; shell height/diameter ratio close to 1.0; number of whorls few, five in most individuals; proximal penis and



**Figure 17.** *Satsuma polymorpha* sp. nov. A–D, holotype (TMMT 0606, shell height = 14.2 mm). E, F, paratype (TMMT 0625, shell height = 16.7 mm). G, H, paratype (TMMT 0626, shell height = 16 mm). I, J, paratype (TMMT 0627, shell height = 14.6 mm). K, L, paratype (TMMT 0628, shell height = 14 mm). M, N, paratype (TMMT 0629, shell height = 14.5 mm). O, P, paratype (TMMT 0630, shell height = 15.1 mm). Q, R, paratype (TMMT 0631, shell height = 13.8 mm). S, T, paratype (TMMT 0632, shell height = 14.9 mm). Arrow indicates the pre-apertural constriction.

principal pilaster distinctly short, weak, almost vanishing, absent in individuals from Shenmihu; internal spinules absent in most individuals, present only in a specimen from Shenmihu.

#### *Etymology*

*Gr. polus*: much; *Gr. morph*: shape, referring to the high polymorphism of banding patterns.

#### *Description*

*Shell* (Figs 17, 18): Dextral, conical, thin, medium sized. Apex obtuse. Whorls inflated. Periphery bluntly angulated. Base expanded. Pre-apertural constriction behind outer and inferior lips present. Surface even, glossy, with faint spiral striae. Shell colour milky white. Periostracum fine, with polymorphic banding patterns in most individuals. Aperture diagonal, ovate-lunate to rectangular. Peristome thin, inflated,

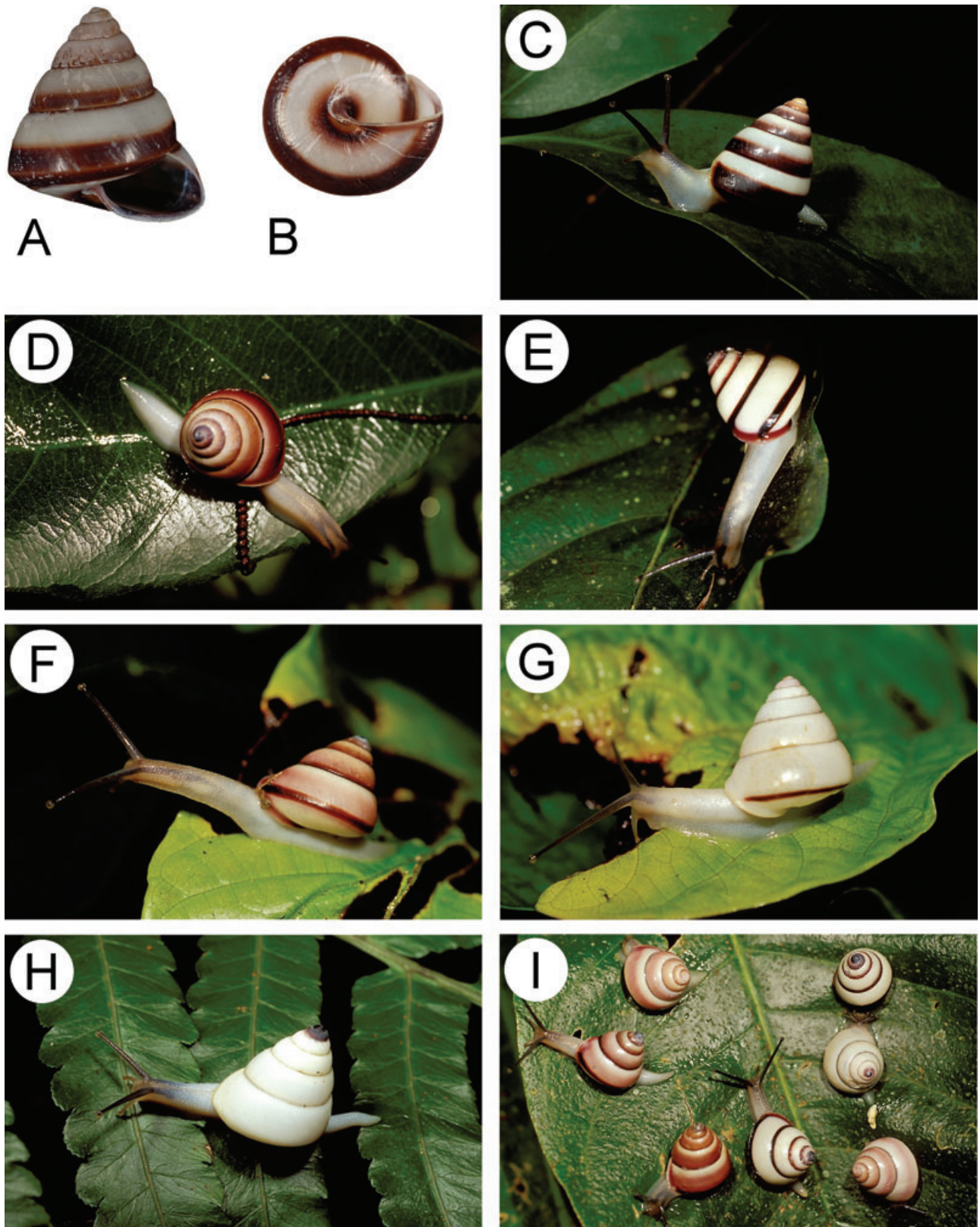
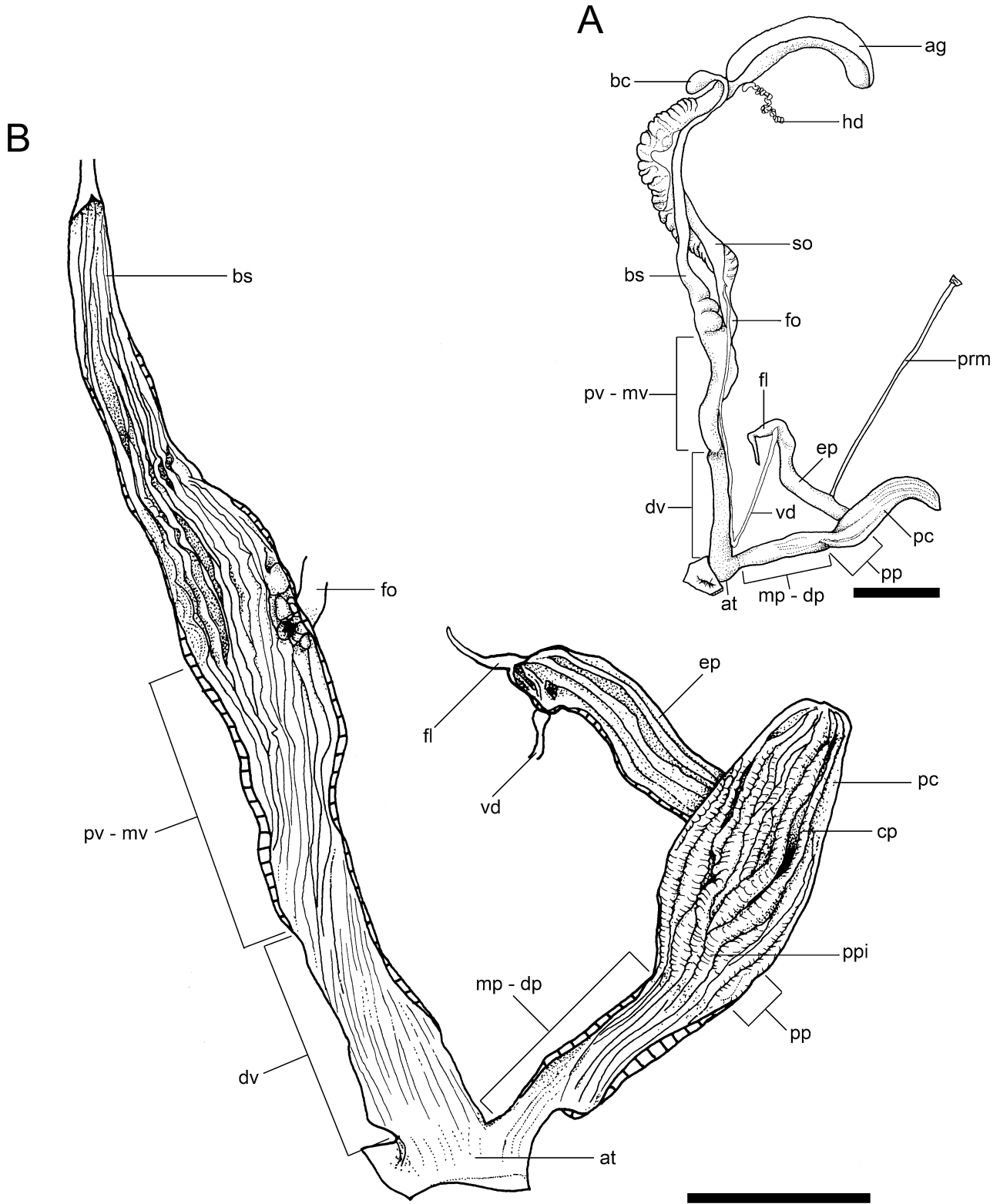
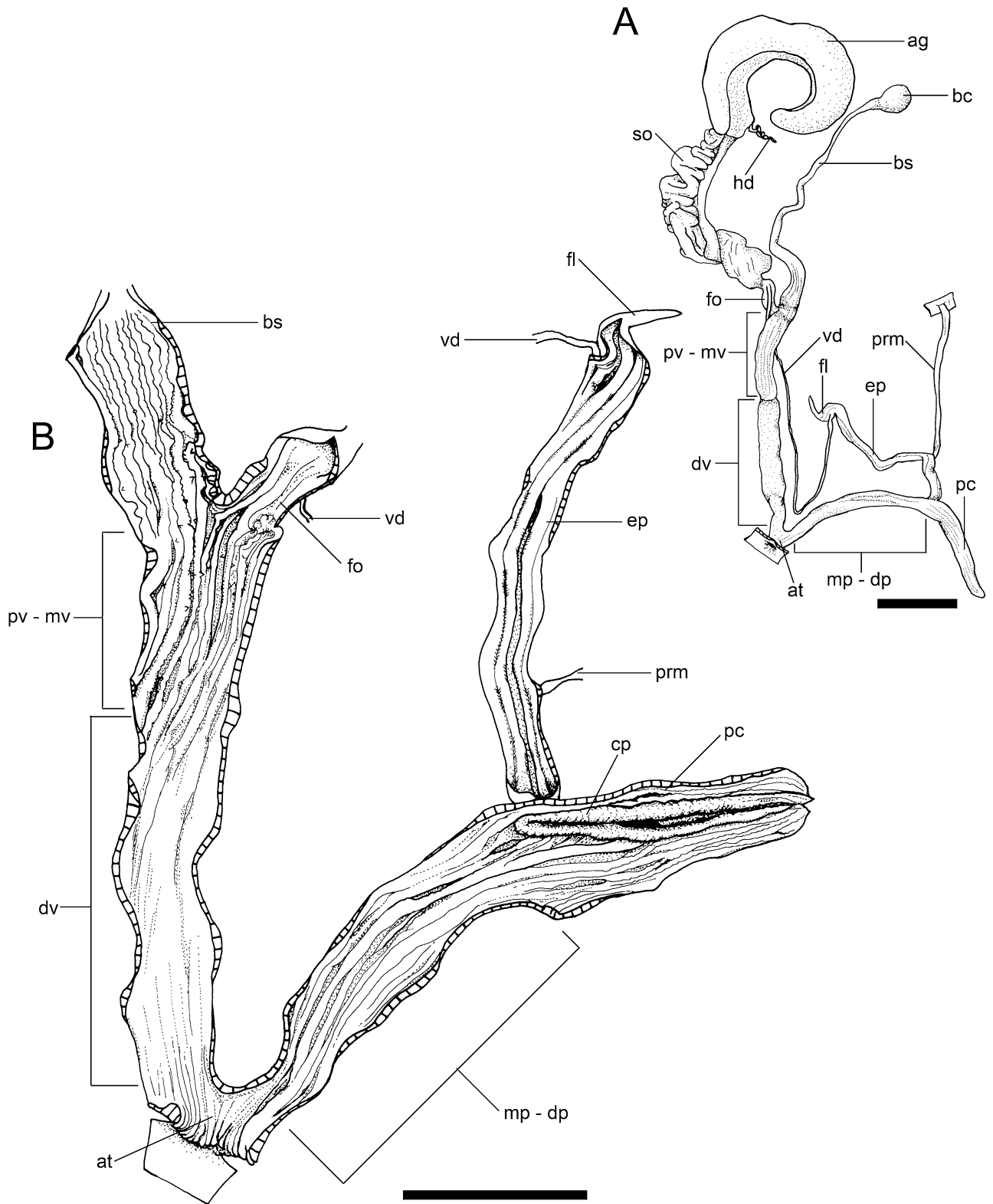


Figure 18. *Satsuma polymorpha* sp. nov. A, B, paratype (TMMT 0633, shell height = 17.1 mm). C–I, living specimens.





**Figure 19.** Reproductive system of *Satsuma polymorpha* sp. nov. from Beinan, Taitung (paratype, TMMT 0680). A, whole genitalia; B, interior of genitalia. Scale bar = 5 mm. See text for abbreviations.



**Figure 20.** Reproductive system of *Satsuma polymorpha* sp. nov. from Shenmihu, Yilan (paratype, TMMT 0672). A, whole genitalia; B, interior of genitalia. Scale bar = 5 mm. See text for abbreviations.



reflected at inferior lip. Superior columellar lip slanted, reflected covering most of umbilicus. Junction between oblique columellar lip and inferior lip angulated.

**Band or stain:** The taxon demonstrates the highest polymorphism of its group. The banding patterns and stains are varied among individuals. Band formula = 0 0 0 0 0 0 0 0; 0 (0 0) 0 (0) 0 0 0; 0 0 0 0 0 0 7 0; 1 0 0 0 0 0 7 0; 1 0 0 0 0 0 7 8; 1 0 0 0 5 0 7 8; 1 0 (0 4) 5 0 7 8; 1 0 0 4 0 0 7 0; 1 0 0 4 0 0 7 8; 1 0 3 0 5 0 7 8; 1 0 3 0 5 6 0 0; 1 0 3 0 5 0 7 8.

**Reproductive system** (Figs 19, 20): Bursa stalk long, slender, with expanded base. Proximal vagina barely widened, furrowed externally, with 11–15 strong, wiggly folds internally; middle vagina varied in length, not as distinguishable as proximal vagina, usually muscular sometimes with thick walls, constrictive, with ten weak, dense folds inside; distal vagina long, two-fifths to three-fifths length of vagina. Flagellum long, tapering, not swollen at base. Pilaster in epiphallus three in number, wide, low. Penial caecum long, robust, tapering, with blunt tip; cecal pilaster two in number, weakly to strongly prominent. Principal pilaster short, almost vanishing. Proximal penis short, muscular, twisted, unevenly furrowed externally, with principal pilaster and eight to ten strong, corrugated pilasters; middle and distal penis short, constrictive near atrium, with gradually vanishing pilasters inside. Spinules observed only in a dissected individual from Shenmihu, Yilan (TMMT 0672, Fig. 20). Five individuals from the type locality, Beinan (Fig. 19), two from Fushan, two from Shenmihu and one immature specimen from Ruisui were dissected. The samples from Shenmihu are different in having (1) an indistinct middle vagina where only a short constriction was seen, (2) weak pilasters in the penial caecum, (3) spinules and in lacking (4) a proximal penis and principal pilaster (Fig. 20).

#### Distribution

This is the most widespread taxon of its group, distributed in mid-altitude (800–1600 m) forest in east Taiwan (from Shenmihu, Yilan County, to Taimali, Taitung County) and in north Taiwan of lower altitude (from Dananshi, Miaoli County, to Fushan, Yilan County) (Fig. 1, Table 1).

#### Remarks

Perches 5 m above the ground; at times animals are active in the tree canopy. Adults were found in summer. Brood is frequently 20 (Fig. 18C–I).

The shells of northern populations (Miaoli, Hsinchu, Taoyuan, Taipei and north Yilan County) are solely white. Regardless of anatomical characters,

they share a common genetic structure with the polymorphic populations distributed in eastern Taiwan (data not shown).

The species has a similar shell height/diameter ratio to *S. hagiomontis* sp. nov., but the shell dimensions are smaller than that of the latter species. Most specimens of this species have a smaller shell and lower number of whorls than other white-shelled species in west Taiwan.

#### *SATSUMA MOLLICULA* (PILSBRY & HIRASE, 1909) (FIGS 21, 22)

*Ganesella albida mollicula* Pilsbry & Hirase, 1909 [1908]: 593–594 (3 March 1909)

*Ganesella albida mollicula*, Kuroda, 1941: 145, no. 1062; Sinagawa, 1980: 6–8, figs 4, 5.

*Coniglobus (Luchuhadra) albida mollicula*, Chang, 1984: 15.

*Satsuma albida mollicula*, Richardson, 1985: 268; Hsieh *et al.*, 2006: 232.

*Luchuhadra albida*, Chang, 1985: 7. [wrong identification]

*Satsuma albidum molliculum*, Lai, 1990: 49. [incorrect gender ending]

#### Material examined

**Type specimen:** Holotype: ANSP 95753 (dry shell), fixed by monotypy (Baker, 1963).

**Additional material:** Specimens were collected from Nanrenshan, eastern Hengchun peninsula, Pingtung County, southern Taiwan. Four specimens were deposited as vouchers: TMMT P-0282 (dry shell, tissue in alcohol, dissected); TMMT P-0281 (dry shell, tissue in alcohol); BMNH 20060784, ANSP 413695 (dry shell).

#### Type locality

Toshun, South Cape of Formosa (south-east of Hengchun Peninsula, Pingtung County, southern Taiwan at present).

#### Diagnosis

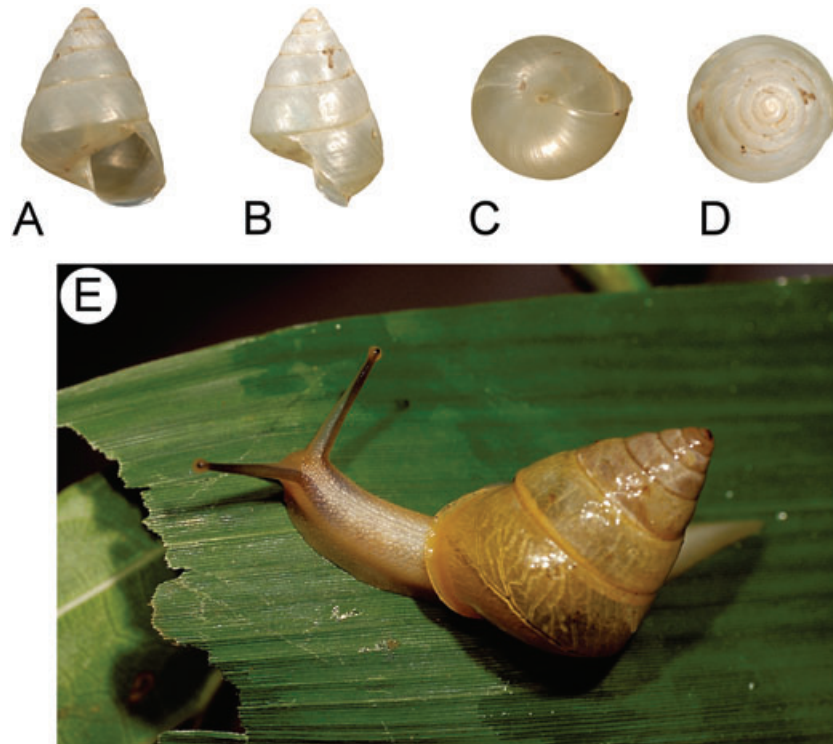
Shell colour honey yellowish to greenish gold; soft body yellowish without pedal stripe; periphery keeled; number of whorls more than six; base of bursa stalk conic; bursa stalk shorter than spermoviduct; principal pilaster long.

#### Etymology

*L. mollis*: soft; *-cula*: diminutive suffix.

#### Description

**Shell** (Fig. 21): Dextral, conical, thin, fragile, semi-translucent, medium sized. Apex obtuse. Whorls inflated. Periphery angulated with keel. Base



**Figure 21.** *Satsuma mollicula*. A–D, holotype (ANSP 95753, shell height = 21.2 mm). E, living specimen.

inflated. Pre-apertural constriction behind peristome absent. Shell colour honey yellowish to greenish gold, turning pale white when periostracum peeled off. Surface smooth, with fine axial and spiral striae. Aperture diagonal, ovate-lunate. Peristome thin. Inferior lip and outer lip expanded. Junction between outer lip and inferior lip curved. Superior columellar lip slanted towards aperture, reflected covering most of umbilicus. Umbilicus almost closed, only tiny crevice-like behind columellar lip.

*Band or stain:* Most individuals have neither band nor stain; rarely do individuals have red-brown stain on the columellar and the columellar lip. The inferior lip, outer lip, apex and whorls do not have such coloration. Band formula = 0 0 0 0 0 0 0 0; 0 0 0 0 0 0 7 0.

*Reproductive system* (Fig. 22): Bursa stalk short, half length of spermoviduct, tapering, expanded at basal part only. Bursa copulatrix clavated. Proximal vagina muscular, swollen, smooth, with 10–13 internal folds; middle vaginas of equal strength, muscular; distal vagina short, one-third to one-quarter length of vagina, gradually constrictive towards atrium. Flagellum long, conically swollen at base, with digitate tip. Pilaster in epiphallus wide, low, three to four in number. Penial caecum long,

conical, with a blunt tip; cecal pilaster two in number, strong; in one of the two dissected individuals, one cecal pilaster not merged into the principal pilaster after insertion of epiphallus, simply reduced as an independent and weak fold instead; remaining inner walls in penial caecum with eight to ten weak ridges. Proximal penis long, muscular, twisted, strongly furrowed. Principal pilaster twice length of cecal pilasters; middle penis depressed, bent, furrowed externally, with five to nine strong internal pilasters reduced gradually as fine corrugations towards atrium. Spinule present on internal surfaces of vagina, penial caecum and penis. Two individuals were dissected.

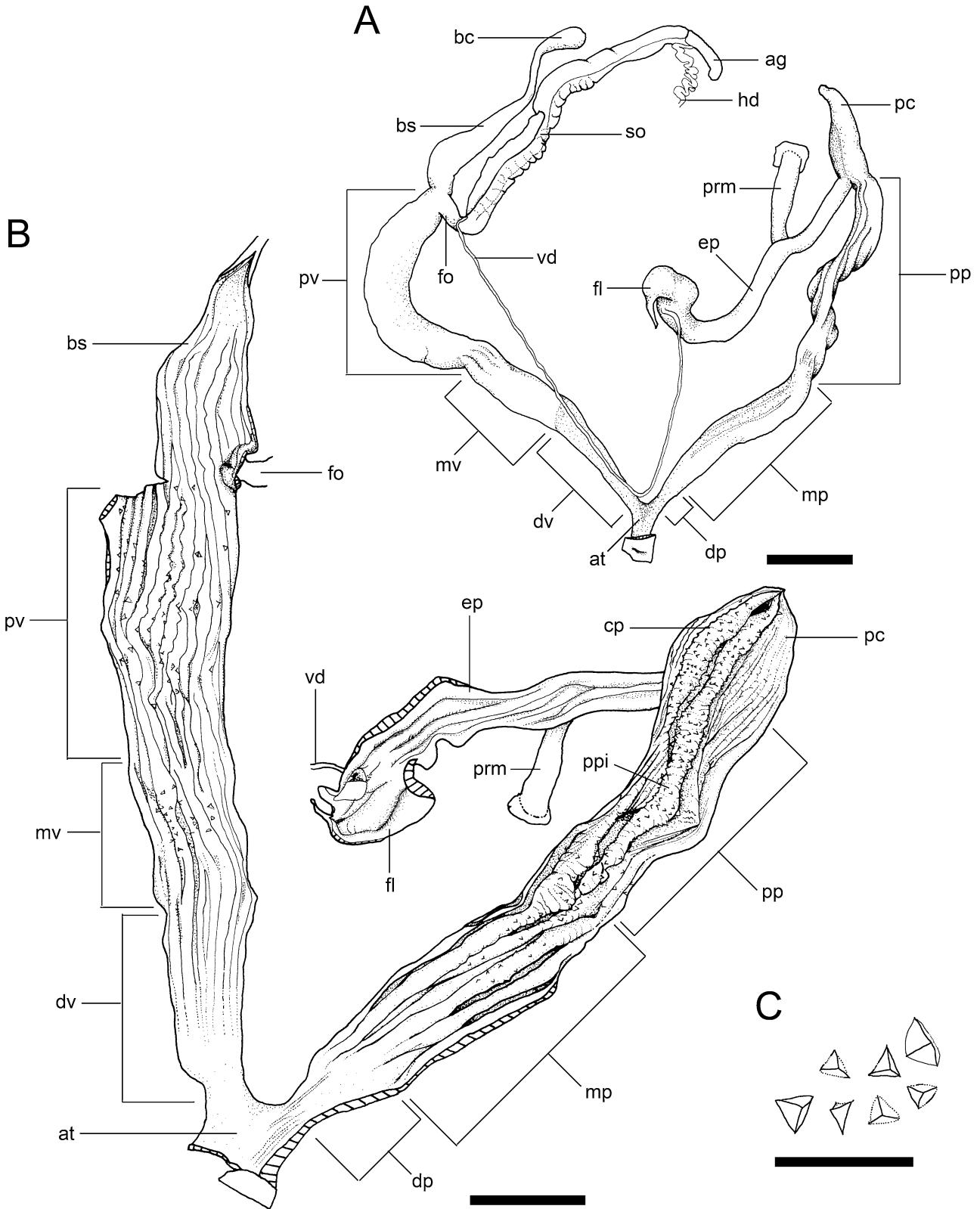
#### *Distribution*

In south Hengchun Peninsula, Pingtung County, southern Taiwan (Fig. 1, Table 1).

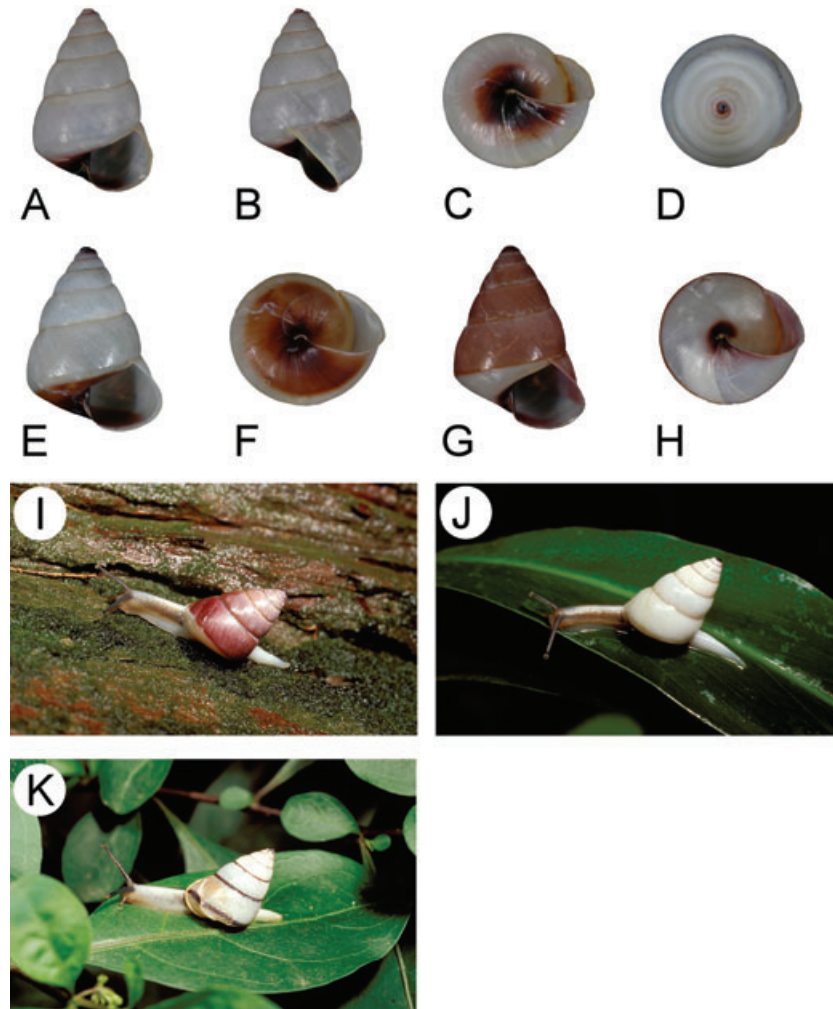
#### *Remarks*

The perching distance from the ground is 2–5 m. Mature individuals are often observed during summer (Fig. 21E). The correct date of publication was emended based on Clench & Turner (1962).

This species is distinct from *S. albida* in having a high spire, yellowish and thin shell, yellowish soft body without grey pedal stripe, swollen flagellum at base, conical penial caecum, long principal pilaster,



**Figure 22.** Reproductive system of *S. mollicula* (TMMT P-0282). A, whole genitalia; B, interior of genitalia. Scale bar = 5 mm. C, spinules (scale bar = 0.5 mm). See text for abbreviations.



**Figure 23.** *Satsuma huberi* sp. nov. A–D, holotype (TMMT 0608, shell height = 20.3 mm). E, F, paratype (TMMT 0634, shell height = 20.7 mm). G, H, paratype (TMMT 0635, shell height = 19.3 mm). I–K, living specimens.

long and corrugated proximal penis, and distinct phylogenetic relationship (see Phylogeny), and hence it is given full species status. The keeled periphery is unique among the yellow-shelled species in east Taiwan. The golden tint to the shell, long principal pilaster, conical base of bursa stalk and short bursa stalk distinguish this species from other species.

**SATSUMA HUBERI SP. NOV.** (FIGS 23, 24)

*Material examined*

*Type specimen:* Holotype: TMMT 0608 (from type locality, dry shell, tissue in alcohol). Eleven paratypes: all from type locality, TMMT 0654 (dry shell, tissue in alcohol, dissected); TMMT 0634–0635, TMMT 0652–0653 (dry shell, tissue in alcohol); NMNS 005405-4, BMNH 20060764–20060765, ANSP 413683 ( $N = 2$ ), SMF 329391 (dry shell).

*Type locality*

Mt Dahanshan, Pingtung County, southern Taiwan (Fig. 1, Table 1).

*Diagnosis*

Shell and soft body yellowish or white without pedal stripe; shell thick, robust; distal vagina short; principal pilaster short.

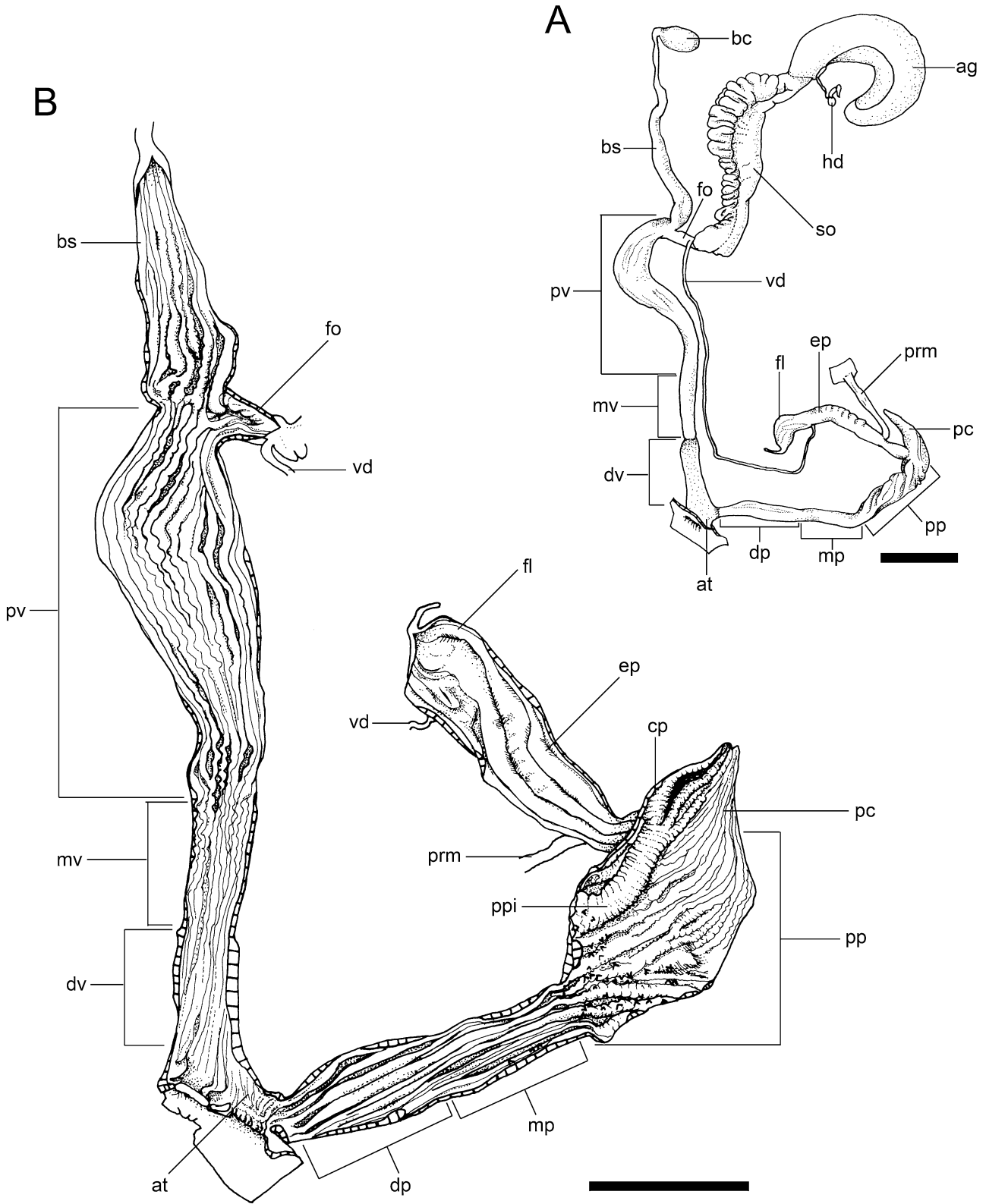
*Etymology*

The name is dedicated to the late Father Franz Huber (1913–1994), an Austrian priest who was also a biologist, in memory of his contribution to biological science education in Taiwan.

*Description*

*Shell* (Fig. 23): Dextral, conical, hard, rigid, medium sized. Apex obtuse. Whorls expanded. Periphery curved, barely angulated. Base inflated. Pre-apertural





**Figure 24.** Reproductive system of *Satsuma huberi* sp. nov. (paratype, TMMT 0654). A, whole genitalia; B, interior of genitalia. Scale bar = 5 mm. See text for abbreviations.



constriction behind peristome absent. Shell colour ivory-white to pale yellow. Surface even, with fine axial and spiral striae. Aperture subvertical, elliptical to ovate. Junction between outer lip and inferior lip curved. Peristome thin, expanded. Columellar lip vertical, reflected, covering umbilicus. Umbilicus fully closed.

*Band or stain:* Polymorphism exists in this taxon. Most individuals are tinged with pale red-brown spiral stain extending around the darkly stained umbilicus. The apex has the same colour as the umbilicus. Such coloration is not observed at the inferior lip and outer lip. Band formula = 1 0 0 0 0 6 7 0; 1 0 0 0 (0 6 7) 0; 1 (0 0 0) 0 0 7 0 (very rare); 1 0 0 4 0 0 7 0 (very rare).

*Reproductive system* (Fig. 24): Bursa stalk tapering, expanded at base, shorter than spermoviduct. Bursa copulatrix oval. Proximal vagina muscular, swollen, smooth, with 13–14 internal folds; middle vaginas constrictive, slender, muscular; distal vagina short, one-fifth length of vagina, swollen with one major internal fold in addition to fine corrugations. Flagellum conical, swollen at base, with short and digitate process. Penial caecum long and conical; cecal pilasters two to three in number, strong; remaining inner walls contained 15 weak ridges. Proximal penis long, muscular, twisted, with unevenly ridged surface, internally with seven strong and corrugated folds; principal pilaster medium in length, equal to or barely longer than cecal pilasters; middle penis obviously constrictive, smooth externally, with moderate and smooth internal folds; distal penis of same width as middle penis, with wide and low pilasters inside. Boundary between middle penis and distal penis not clear. Spinule present on pilasters of proximal and middle penis, not seen in vagina. Three individuals were dissected.

#### *Distribution*

This species was recorded only at Mt Dahanshan, Pingtung County, southern Taiwan (Fig. 1, Table 1).

#### *Remarks*

The perching distance from ground is typically more than 2 m. Adults can be found in winter and eventually breed in spring. Brood size is less than 30 (Fig. 23I–K).

The thick and robust shell is unique among the *Satsuma albida* species complex. Some specimens of *S. insignis* also have thick shells, but never as thick and robust as shells in this species. The polymorphic colour of shell, both white and yellow, is also unique.

#### *SATSUMA AURATIBASIS* SP. NOV. (FIGS 25, 26)

##### *Material examined*

*Type specimen:* Holotype: TMMT 0609 (from type locality, dry shell, tissue in alcohol). Fifteen paratypes: all from type locality, TMMT 0658 (dry shell, tissue in alcohol, dissected); TMMT 0636–0637, 0655–0657 (dry shell, tissue in alcohol); NMNS 005405-3, BMNH 20060760–20060762, ANSP 413679–413681, SMF 329388–329389 (dry shell).

##### *Type locality*

Mudan, Pingtung County, southern Taiwan (Fig. 1, Table 1).

##### *Diagnosis*

Spires and soft body yellowish without pedal stripe; base and sometimes the entire last whorl pale gold; number of whorls more than six; bursa stalk shorter than spermoviduct; base of bursa stalk expanded; principal pilaster long.

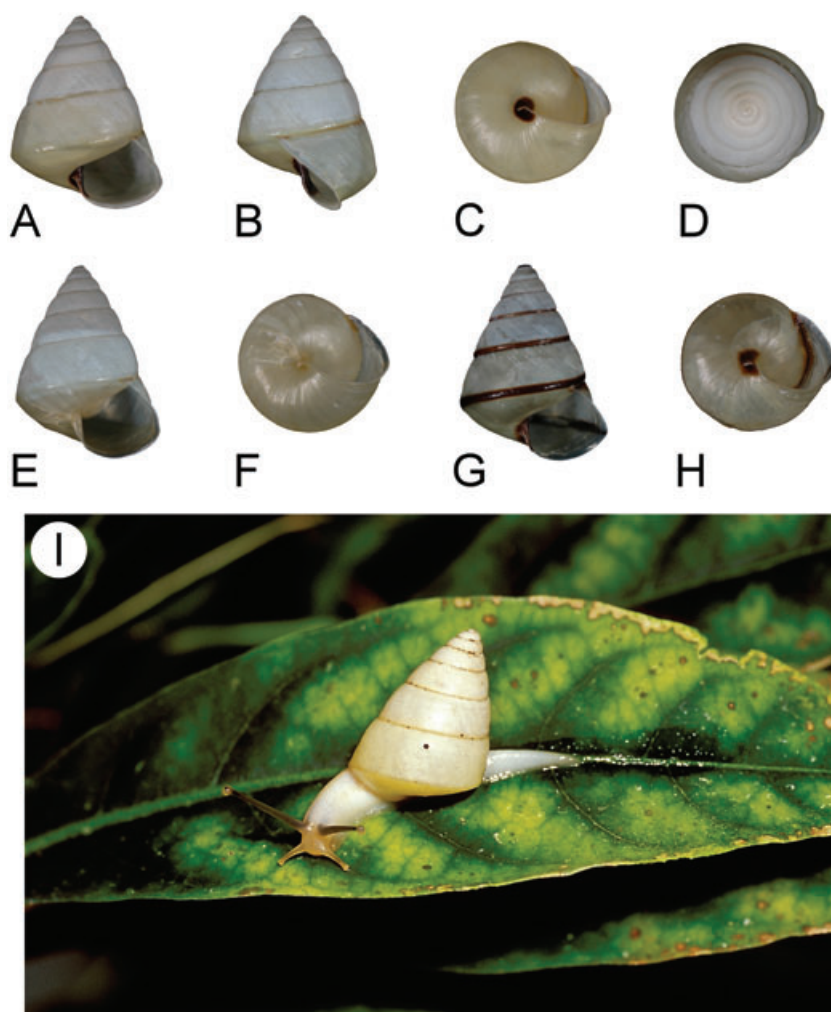
##### *Etymology*

*L. aurat:* golden; *L. basis:* base, referring to its pale golden base.

##### *Description*

*Shell* (Fig. 25): Dextral, conical, thin, fragile, semi-translucent, medium sized. Apex obtuse. Whorls inflated to flat. Periphery roundly curved. Base inflated. Pre-apertural constriction behind peristome absent. Shell colour on upper whorls light yellow; base and sometimes the entire last whorl pale gold, turning white when periostracum peeled away. Shell surface smooth, with fine axial and spiral striae. Aperture diagonal, ovate-lunate to trapezoid. Inferior lip curved; outer lip almost straight. Junction between outer lip and inferior lip curved. Peristome thin, expanded. Columellar lip vertical to subvertical, reflected covering umbilicus. Umbilicus mostly covered by columellar lip, crevice-like. Junction between columellar lip and inferior lip roundly angulated.

*Band or stain:* This taxon shows polymorphism. Some individuals do not exhibit any colour band or stain whilst others have a red-brown umbilicus and columellar lip; otherwise, the apex, inferior lip and outer lip lack such coloration. Some individuals have a short and thin band immediately behind the insertion of the outer lip. A rare colour pattern exists with the peripheral band and the apical and umbilicus spot. Band formula = 0 0 0 0 0 0 0 0; 1 0 0 0 0 0 7 0; 1 0 0 4 0 0 7 0 (rare).



**Figure 25.** *Satsuma auratibasis* sp. nov. A–D, holotype (TMMT 0609, shell height = 20.1 mm). E, F, paratype (TMMT 0636, shell height = 20.8 mm). G, H, paratype (TMMT 0637, shell height = 18.4 mm). I, living specimen.

*Reproductive system* (Fig. 26): The genital morphology is highly similar to that of *S. mollicula* and can be distinguished by (1) the longer bursa stalk of *S. auratibasis*, which is three-fifths the length of the spermoviduct, than that of *S. mollicula*; and (2) the longer epiphallus of *S. auratibasis*, which has a length almost equivalent to the penis. The length of epiphallus in *S. mollicula* is three-fifths that of the penis.

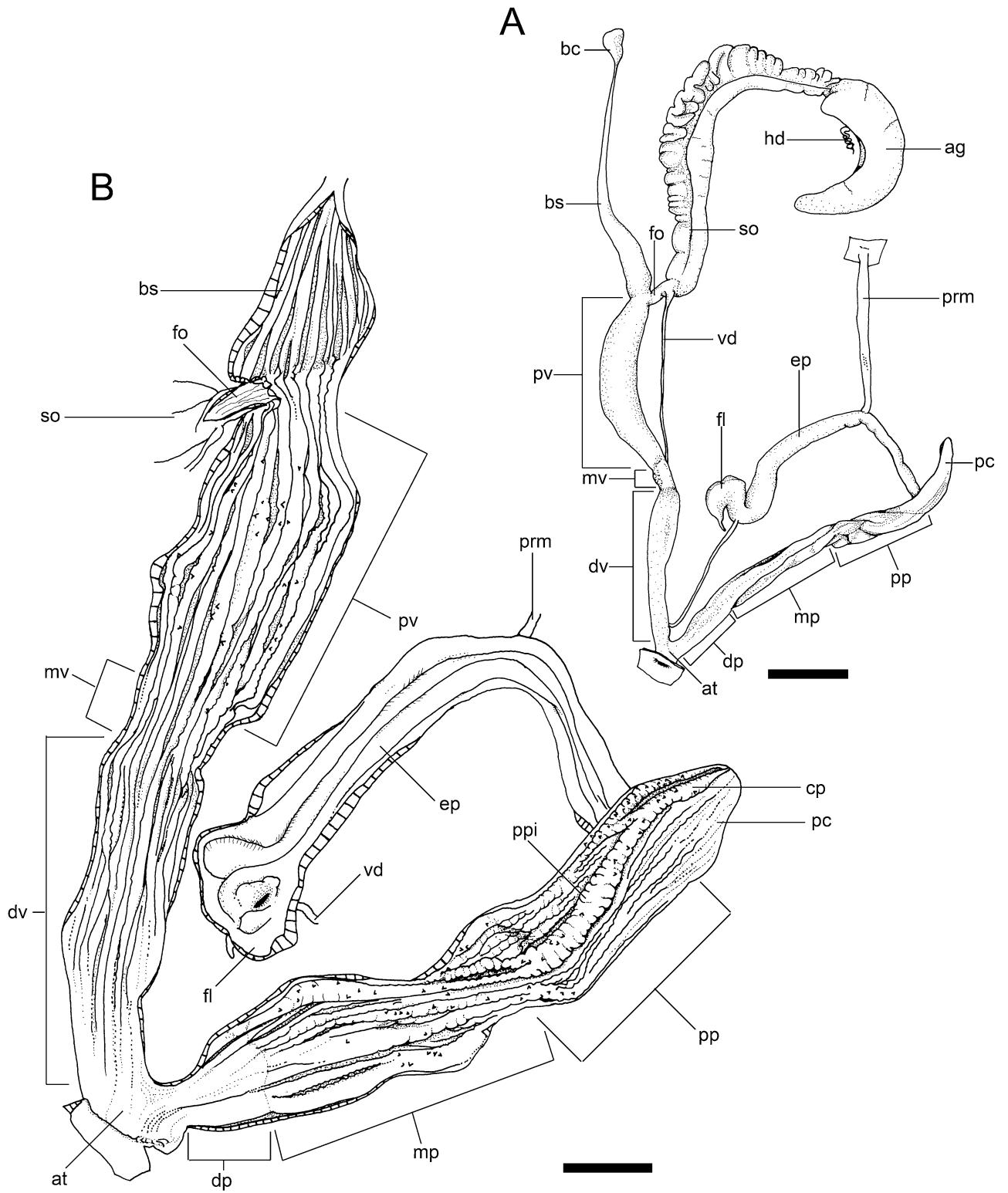
#### *Distribution*

This species is distributed in lowland (< 400 m) broadleaf forest habitats around the north end of Hengchun peninsula, Pingtung County, southern Taiwan, including Mudan, Shuangliu and Shouka (Fig. 1, Table 1).

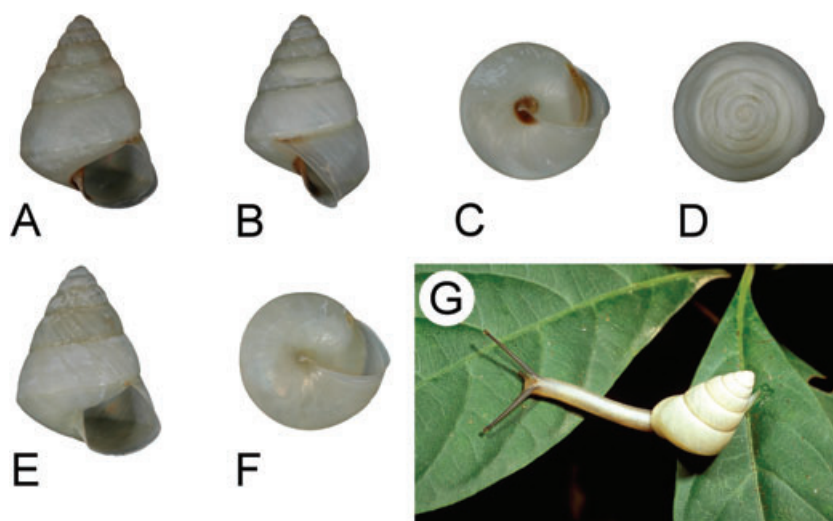
#### *Remarks*

The animals were found from 2 m above ground to the tree canopy. Adults were found in spring and usually perched higher than juveniles (Fig. 25I).

*Satsuma auratibasis* sp. nov. is similar to *S. mollicula* based on the morphological characters of shell and genitalia. Both were found distributed on Hengchun peninsula, southern Taiwan, but their distributions do not overlap. The former species is distributed in the northern part of the area, the latter in the south (Fig. 1). Furthermore, molecular phylogeny indicates *S. auratibasis* is close to *S. huberi* rather than *S. mollicula* despite the morphological similarities. *Satsuma auratibasis* differs from *S. mollicula* in that its shell is larger, angulated at the periphery that is never keeled, pale gold in colour, never greenish gold as seen in *S. mollicula*. Moreover, the golden tint is confined to the base or the last whorl only of *S. auratibasis*. *S. auratibasis* differs morphologically from *S. huberi* in having gold-tinted shell base, conical base of bursa stalk, long bursa stalk and long principal pilaster.



**Figure 26.** Reproductive system of *Satsuma auratibasis* sp. nov. (paratype, TMMT 0658). A, whole genitalia; B, interior of genitalia. Scale bar = 5 mm. See text for abbreviations.



**Figure 27.** *Satsuma katipolensis* sp. nov. A–D, holotype (TMMT 0607, shell height = 18.2 mm). E, F, paratype (TMMT 0638, shell height = 16.1 mm). G, living specimen.

***SATSUMA KATIPOLENSIS* SP. NOV.** (FIGS 27, 28)

*Material examined*

*Type specimen:* Holotype: TMMT 0607 (from type locality, dry shell, tissue in alcohol). Eight paratypes: all from type locality, TMMT 0679 (dry shell, tissue in alcohol, dissected); TMMT 0638 (dry shell, tissue in alcohol); NMNS 005405-5, BMNH 20060773–20060774, ANSP 413688 ( $N = 2$ ), SMF 329396 (dry shell).

*Type locality*

Zhiben, Taitung County, eastern Taiwan (Fig. 1, Table 1).

*Diagnosis*

Shell and soft body yellowish without pedal stripe; base of bursa stalk expanded; distal vagina short; principal pilaster short.

*Etymology*

From Katipol, the type locality name of the Puyuma aboriginal tribe, today known as Zhiben.

*Description*

*Shell* (Fig. 27): Dextral, extremely thin, fragile, translucent, medium to small. Apex obtuse. Whorls inflated. Periphery bluntly angulated to arc-like. Base expanded. Pre-apertural constriction behind peristome absent. Shell colour light yellow, turning pale white when periostracum peeled away. Surface smooth, with fine axial and spiral striae. Aperture diagonal, ovate-lunate to trapezoid. Junction between outer lip and inferior lip angulated obtusely. Peristome thin, expanded. Inferior lip curved downward.

Columellar lip subvertical, slanting to aperture side, reflected covering umbilicus. Umbilicus mostly covered by columellar lip, crevice-like. Junction between columellar lip and inferior lip bluntly angulated.

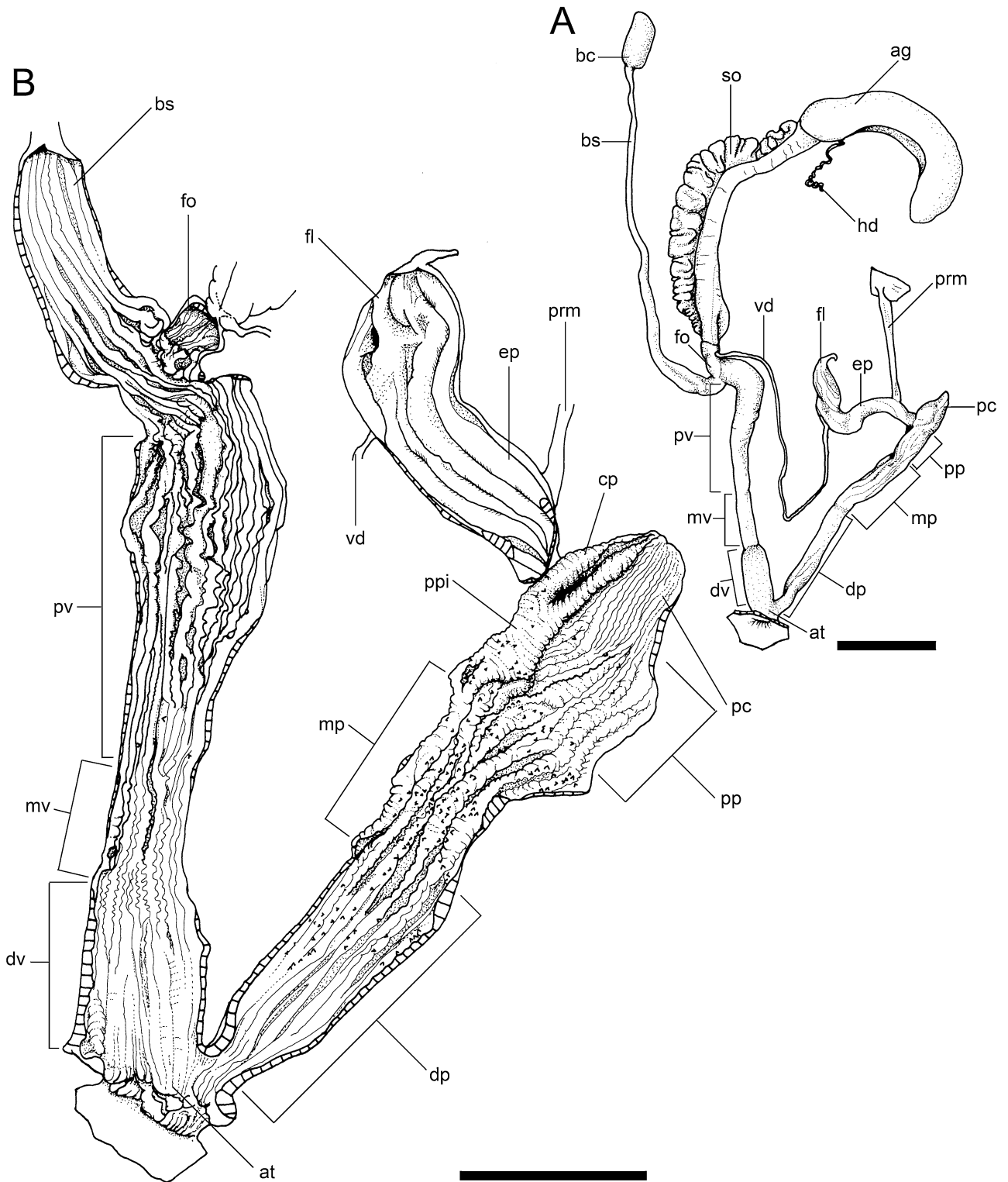
*Band or stain:* Polymorphism exists in this taxon. Band formula = 0 0 0 0 0 0 0 0; 0 0 0 0 0 0 7 0; 1 0 0 4 0 0 7 0 (Rare).

*Reproductive system* (Fig. 28): Bursa stalk expanded at base, slender at apical half. Proximal vagina muscular, swollen, smooth, with 12–18 internal folds; middle vagina muscular, slender, constrictive, with fine, dense and wiggly folds internally; distal vagina swollen, short, one-fifth length of vagina. Flagellum long, conical, swollen at base, tapering at tip. Epiphallus contains four wide, low pilasters inside. Penial caecum depressed, conical, short; cecal pilaster two in number; remaining inner walls contain 17–25 weak ridges. Proximal penis not particularly swollen, with a deep groove externally; principal pilaster medium in length, equal to cecal pilaster; middle penis long, muscular, unevenly furrowed, with five to six strong, wiggly and corrugated pilasters; distal penis smooth externally, with eight moderate and smooth internal folds that reduce gradually as fine wrinkles towards atrium. Spinules present in penis and vagina. Two individuals were dissected.

*Distribution*

This species is distributed in the low-altitude (< 500 m) broadleaf forest habitats around Zhiben, southern Taitung County (Fig. 1, Table 1).





**Figure 28.** Reproductive system of *Satsuma katipolensis* sp. nov. (paratype, TMMT 0679). A, whole genitalia; B, interior of genitalia. Scale bar = 5 mm. See text for abbreviations.



*Remarks*

Inhabiting from 2 to 5 m. Adults were found in autumn (Fig. 27G).

This species is morphologically similar to *S. huberi* and can be distinguished by the following characteristics: (1) the shell is thinner, (2) the shell colour is never ivory-white, (3) the base of the bursa stalk is expanded, (4) the base of the flagellum is more swollen, (5) the vagina is shorter than the penis and (6) the penial caecum is short.

***SATSUMA LUTEOLELLA* SP. NOV.** (FIGS 29, 30)*Material examined*

*Type specimen:* Holotype: TMMT 0611 (from type locality, dry shell, tissue in alcohol). Total 17 paratypes: seven paratypes from type locality: TMMT 0659 (dry shell, tissue in alcohol, dissected); TMMT

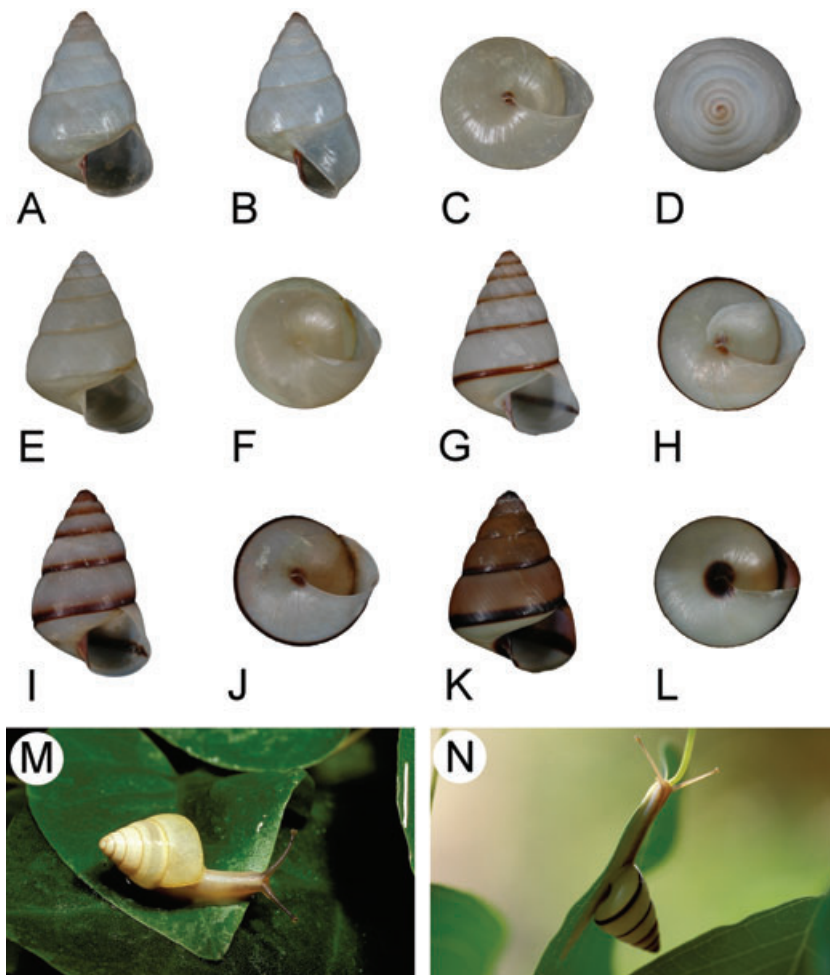
0640–0641, TMMT 0678 (dry shell, tissue in alcohol); BMNH 20060757, ANSP 413678, SMF 329387 (dry shell). Ten paratypes from Antong, Hualien: TMMT 0642 (juvenile, in alcohol); TMMT 0639, TMMT 0676–0677 (dry shell, tissue in alcohol); NMNS 005405-2, BMNH 20060758–20060759, ANSP 413677 ( $N = 2$ ), SMF 329386 (dry shell).

*Type locality*

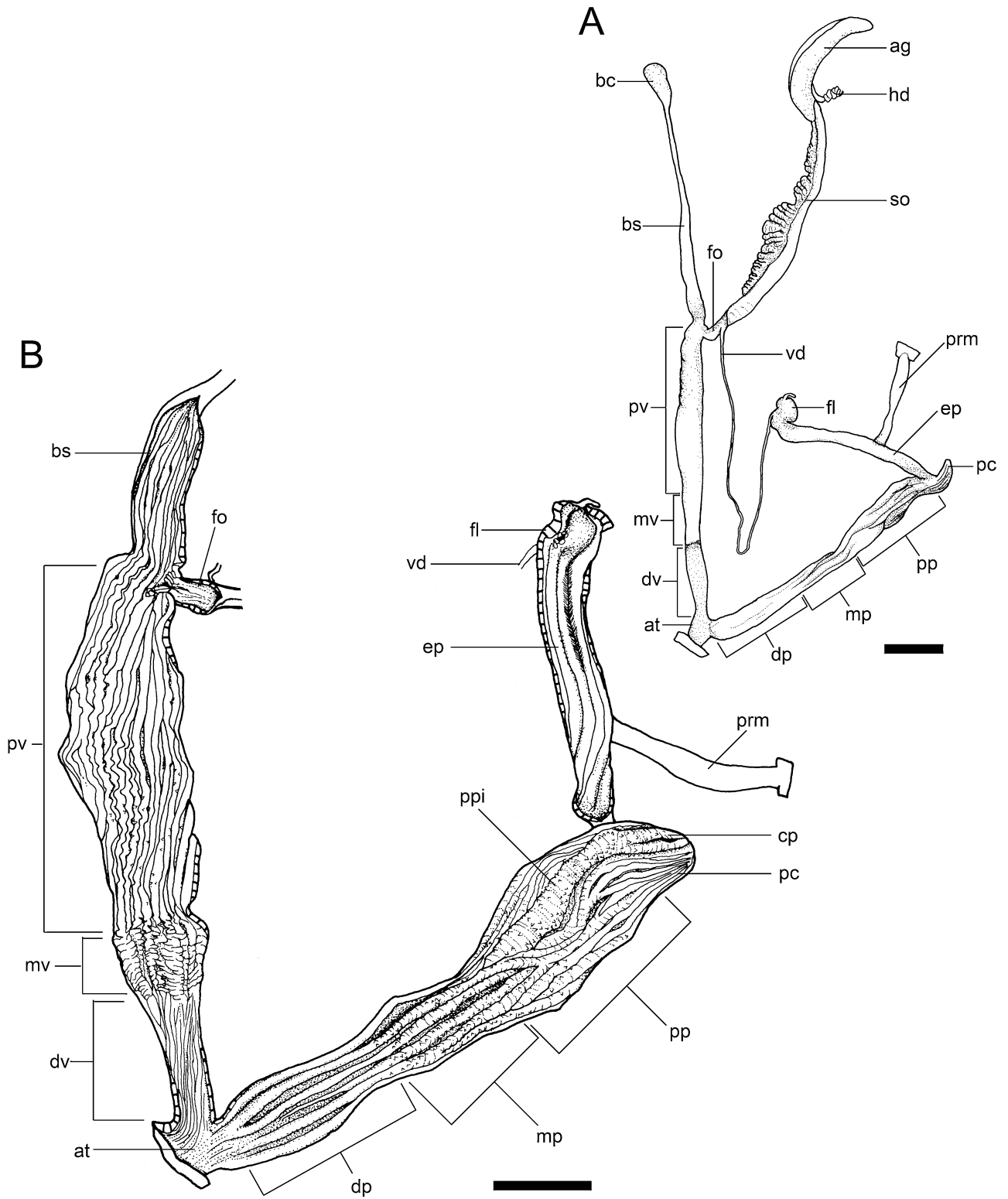
Fuyuan, Hualien County, eastern Taiwan (Fig. 1, Table 1).

*Diagnosis*

Shell and soft body yellowish without pedal stripe; number of whorls more than six; shell highly conical, with shell height/diameter ratio = 1.5.



**Figure 29.** *Satsuma luteolella* sp. nov. A–D, holotype (TMMT 0611, shell height = 23.5 mm). E, F, paratype (TMMT 0639, shell height = 21.9 mm). G, H, paratype (TMMT 0640, shell height = 20.5 mm). I, J, paratype (TMMT 0641, shell height = 21.7 mm). K, L, paratype (TMMT 0642, shell height = 16.3 mm). M, N, living specimens.



**Figure 30.** Reproductive system of *Satsuma luteolella* sp. nov. (paratype, TMMT 0659). A, whole genitalia; B, interior of genitalia. Scale bar = 5 mm. See text for abbreviations.

*Etymology*

*L. luteola*: yellow; *L. -ella*: diminutive suffix, referring to the small and yellowish shell.

*Description*

*Shell* (Fig. 29): Dextral, thin, conical, medium sized to large. Apex obtuse. Whorls inflated. Periphery bluntly angulated, arc-like. Base inflated. Pre-apertural constriction behind peristome absent. Shell colour yellowish white. Surface even, matt, with fine axial and spiral striae. Periostracum thin. Aperture diagonal, ovate, angulated curve between outer lip and inferior lip. Peristome thin. Columellar lip vertical, reflected covering umbilicus. Umbilicus mostly closed, crevice-like.

*Band or stain*: Polymorphism exists in this taxon. Some individuals do not possess any colour band or stain, whilst some exhibit a red-brown umbilicus; however, the inferior lip and outer lip lack coloration. Others have a peripheral or sub-peripheral band around the whorls. Band formula = 0 0 0 0 0 0 0 0; 0 0 0 0 0 0 7 0; 1 0 0 4 0 0 7 0; 1 0 0 0 5 0 7 0; 1 (0 0 0) 5 0 7 0 (very rare).

*Reproductive system* (Fig. 30): Bursa stalk tapering, not enlarged at base, shorter than spermoviduct. Bursa copulatrix oval to ellipsoid. Proximal vagina muscular, swollen, with 12–17 internal folds; middle vaginas of same width or more constricted, muscular; distal vagina medium in length, one-third length of vagina, same width as middle vagina, constricted towards atrium, with fine wrinkles inside. Flagellum conical, swollen at base with short and digitate tip. Penial caecum short, conical, blunt, furrowed externally; cecal pilasters two in number; remaining inner walls contain 12–14 weak ridges. Proximal penis elongated, muscular, twisted, unevenly furrowed externally, with strong folds internally; principal pilaster long, twice to threetimes length of penial caecum; middle penis constrictive, shortly elongated, with well-defined, strong and corrugated pilasters; distal penis of same strength as middle penis, containing strong, smooth pilasters inside. Spinules present in penial caecum, penis and vagina.

*Distribution*

The species was found in lowland broadleaf forest from Liyutan, Mataian, Fuyuan and Antong (Fig. 1, Table 1). It was thus considered to be distributed around the northern parts of the East Rift Valley, eastern Taiwan.

*Remarks*

Found from 2 to 3 m above the ground up to the canopy. Mature individuals are found in summer (Fig. 29M, N).

*Satsuma luteolella* is similar to *S. pilsbryi* (described below) based on morphological characters. The former differs from the latter in having larger shell size, greater number of whorls, paler shell colour, slender base of bursa stalk, long principal pilaster, less expanded proximal penis and lack of a pre-apertural constriction. A dwarf form, which has similar shell dimensions (17.5 mm height, 13.0 mm diameter) to *S. pilsbryi*, was found in the lowland forest around Antong area, southern Hualien County, eastern Taiwan. They can be easily distinguished based on the characters listed above.

**SATSUMA KANOI SP. NOV.** (FIGS 31, 32)

*Ganesella (albida* var. ?) *kasyotonis* Kuroda & Kano in Kuroda, 1941 (*nomen nudum*)

*Ganesella kasyotonis*, Kuroda, 1958 (*nomen nudum*)

*Satsuma albida kasyotonis*, Hsieh *et al.*, 2006: 232.

*Material examined*

*Type specimen*: Holotype: TMMT 0610 (from type locality, dry shell, tissue in alcohol). Seven paratypes: all from type locality, TMMT 0662 (dry shell, tissue in alcohol, dissected); TMMT 0660–0661 (dry shell, tissue in alcohol); BMNH 20060767–20060768, ANSP 413685, SMF 329392 (dry shell).

*Additional material*: Nishinomiya Shell Museum, Japan NCKG 3310: five dry, immature shells, collected by T. Kano from Kasyoto Island (Lutao Island) in 1937.

*Type locality*

Mt Huoshaoshan, Ludao Island, Taitung County, eastern Taiwan (Fig. 1, Table 1)

*Diagnosis*

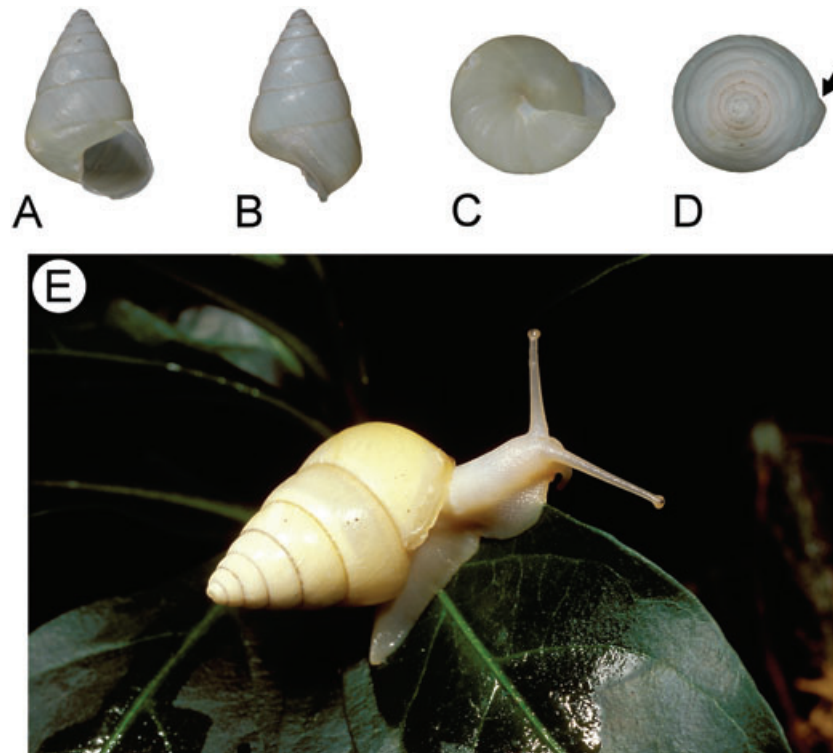
Shell and soft body yellowish without pedal stripe; pre-apertural constriction present behind outer lip; shell large; number of whorls seven.

*Etymology*

The name is dedicated to Mr Tadao Kano (1906–1945), a Japanese explorer and naturalist; he devoted his life to field investigations and disappeared in the rainforest of southern Asia. Mr Kano was the first collector of this species.

*Description*

*Shell* (Fig. 31): Dextral, conical, hard, rigid, medium sized to large. Apex obtuse. Whorls inflated. Periphery bluntly angulated to arc-like. Base inflated. Pre-apertural constriction present behind outer lip only. Shell colour faint yellow. Periostracum thin. Surface smooth, with fine axial and spiral striae. Aperture



**Figure 31.** *Satsuma kanoi* sp. nov. A–D, holotype (TMMT 0610, shell height = 29.7 mm). E, living specimen. Arrow indicates the pre-apertural constriction.

diagonal, ovate. Junction between outer lip and inferior lip angulated curved. Peristome thin, expanded at inferior lip and outer lip. Inferior lip curved downward. Columellar lip subvertical, reflected. Umbilicus mostly covered by columellar lip, crevice-like. Junction between columellar lip and inferior lip obtusely angulated.

*Band or stain:* Band or stain is not present. Band formula = 0 0 0 0 0 0 0.

*Reproductive system* (Fig. 32): Bursa stalk long, tapering. Bursa copulatrix clavated. Proximal vagina muscular, swollen, smooth, with 13–18 internal folds; middle vaginas constricted, slender, muscular; distal vagina short, one-twentieth length of vagina, as wide as or wider than middle vagina, internally with wide and low folds or finely corrugated only. Flagellum short, swollen at base, with suddenly constricted, short and digitate tip. Penial caecum moderately long, conical; cecal pilasters two to three in number, strong, not well merged into principal pilaster; remaining inner walls contain 8–15 weak ridges. Proximal penis long, muscular, twisted, unevenly furrowed externally, with long principal pilaster lengthened twice that of the cecal pilaster. Proximal penis with 15–22 weak ridges; middle penis constricted, slender, with six

irregularly strong, corrugated and wiggly pilasters inside; distal penis of same strength as middle penis, with five to six strong and smooth internal pilasters. Spinules present in penial caecum, proximal penis and vagina. Two individuals were dissected.

#### *Distribution*

The species distributed only in Ludao Island, off Taitung County, eastern Taiwan (Fig. 1, Table 1).

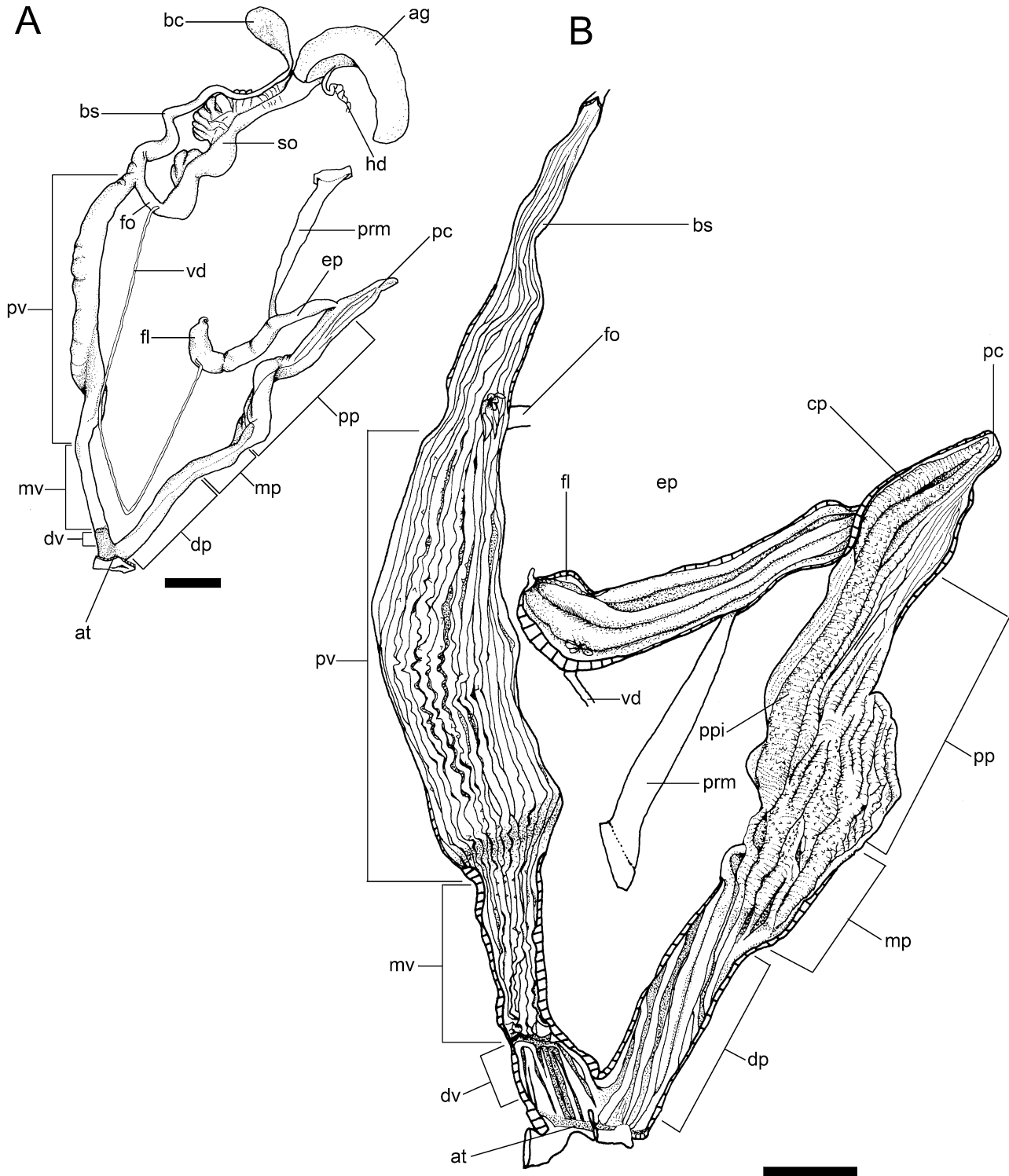
#### *Remarks*

Perching distance from the ground is 2 m to the canopy. Animals were often found inhabiting banyan trees (Fig. 31E). *Satsuma kanoi* has the largest shell dimensions and number of whorls amongst this group. Furthermore, it is confined to Ludao Island and is not sympatric with any species of this group. This species is morphologically and phylogenetically close to *S. luteolella* but differs from the latter in having pre-apertural constriction, larger shell size, greater number of whorls and short distal vagina.

#### **SATSUMA VALLIS SP. NOV.** (FIGS 33, 34)

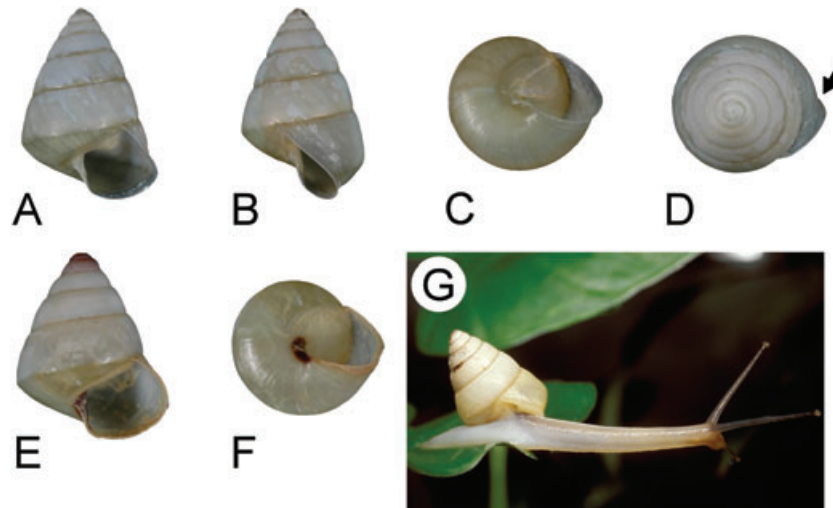
##### *Material examined*

*Type specimen:* Holotype: TMMT 0612 (from type locality, dry shell, tissue in alcohol). Five paratypes: all from type locality, TMMT 0664 (dry shell, tissue in



**Figure 32.** Reproductive system of *Satsuma kanoi* sp. nov. (paratype, TMMT 0662). A, whole genitalia; B, interior of genitalia. Scale bar = 5 mm. See text for abbreviations.





**Figure 33.** *Satsuma vallis* sp. nov. A–D, holotype (TMMT 0612, shell height = 18.5 mm). E, F, paratype (TMMT 0643, shell height = 16 mm). G, living specimen. Arrow indicates the pre-apertural constriction.

alcohol, dissected); TMMT 0643 (dry shell, tissue in alcohol); BMNH 20060763, ANSP 413682, SMF 329390 (dry shell).

#### *Type locality*

Gekou, Taroko National Park, Hualien County, eastern Taiwan (Fig. 1, Table 1).

#### *Diagnosis*

Shell and soft body yellowish without pedal stripe; pre-apertural constriction present behind outer lip; bursa stalk shorter than spermooviduct; spinule absent; principal pilaster short; proximal penis short, apparently expanded.

#### *Etymology*

*L. vallis*: a valley, after the type locality, 'Taroko valley'.

#### *Description*

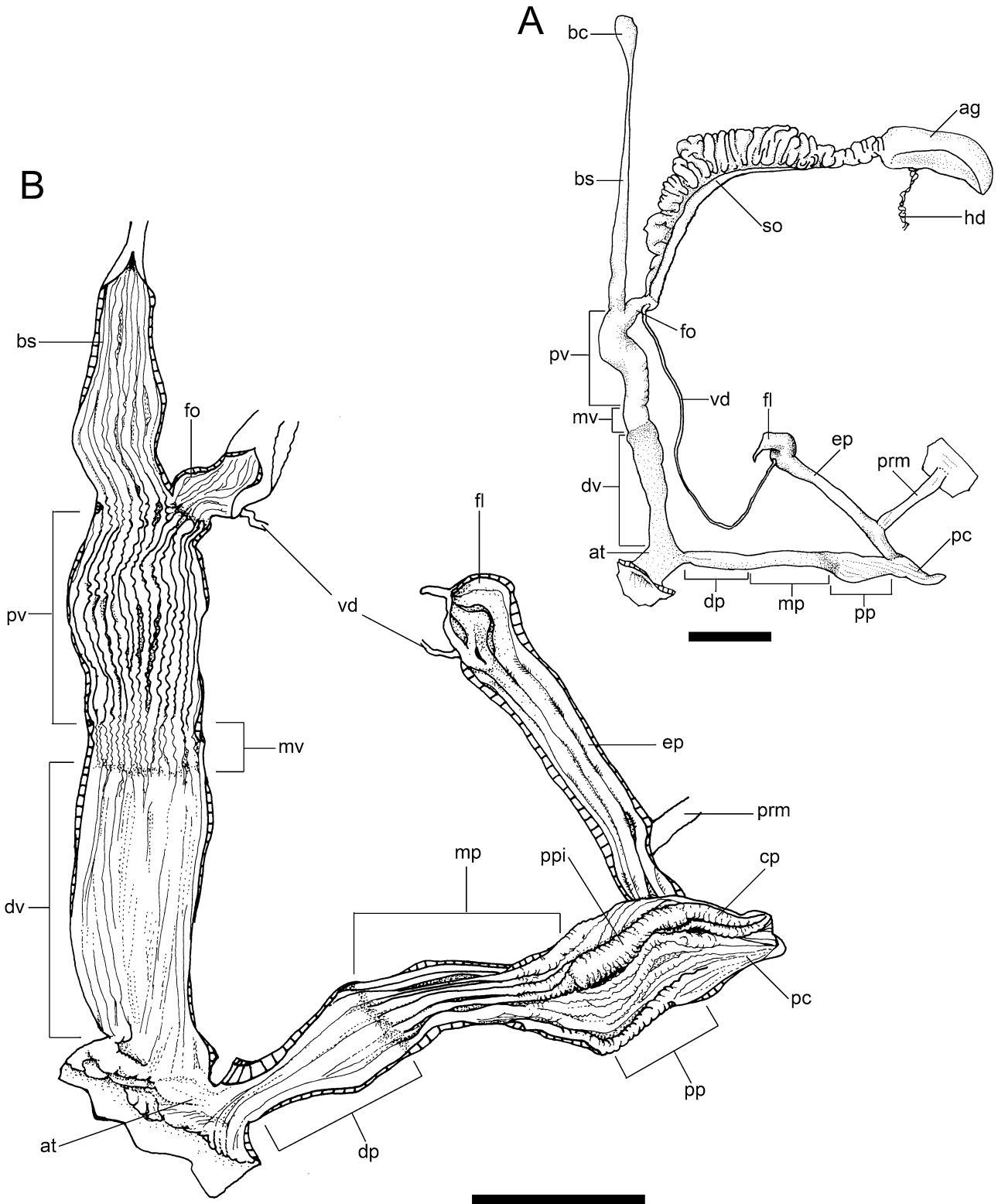
**Shell** (Fig. 33): Dextral, conical, thin, semi-translucent, medium sized to small. Apex obtuse. Whorls expanded. Periphery bluntly angulated. Base expanded. Pre-apertural constriction present only behind outer lip. Shell colour pale yellow with unevenly distributed white stripes. Periostracum thin. Surface even, with fine axial and spiral striae. Aperture diagonal ovate. Junction between outer lip and inferior lip roundly angulated. Peristome thin, expanded at inferior lip and outer lip. Inferior lip curved downward. Columellar lip subvertical, reflected. Umbilicus mostly covered by columellar lip, crevice-like. Junction between columellar lip and inferior lip obtusely angulated.

**Band or stain:** Polymorphism exists in this taxon. Although some individuals exhibit neither colour banding nor staining, others possess a light brown stain at the umbilicus and the apex. Band formula = 0 0 0 0 0 0 0 0; 1 0 0 0 0 0 7 0 (rare) (Fig. 2).

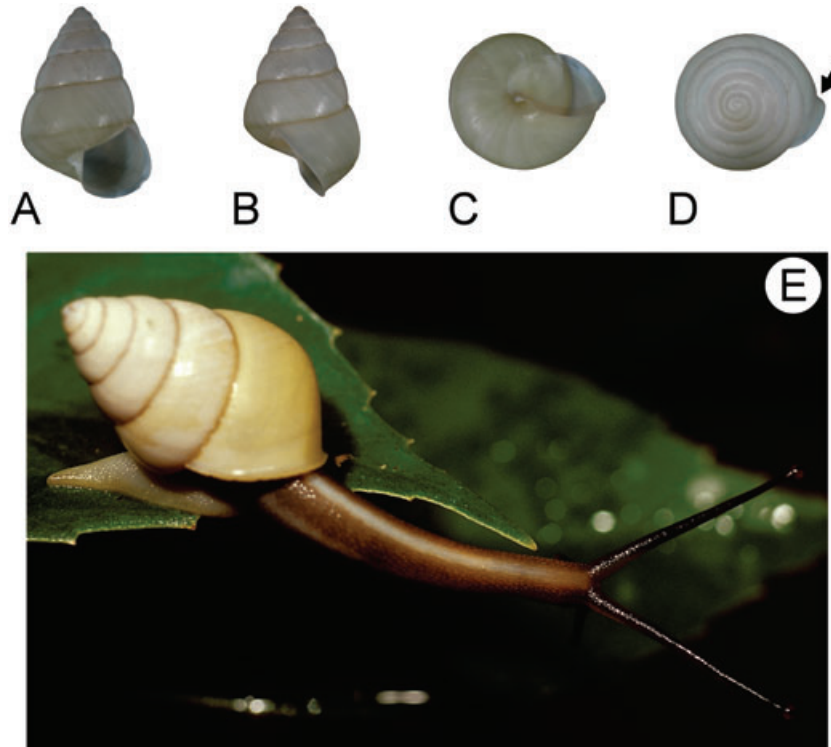
**Reproductive system** (Fig. 34): Bursa stalk short, two-thirds length of spermooviduct, tapering, not enlarged at base. Bursa copulatrix clavated. Proximal vagina short, swollen, with 16–19 folds; middle vagina very short, not particularly constricted, with 18–20 weak and wiggly folds inside; distal vagina long, nearly half length of vagina, same width as proximal vagina, constricted towards atrium, with low folds or fine wrinkles inside. Flagellum short, conical, swollen at base, with short, suddenly reduced and digitate tip. Epiphallus long, with four pilasters inside. Penial caecum moderate, conical, blunt, weakly furrowed on surface; cecal pilaster two in number; remaining inner walls of penial caecum contain six weak ridges. Proximal penis short, expanded, weakly furrowed externally, with one deep groove corresponding to principal pilaster internally; principal pilaster same length as penial caecum; middle penis constricted suddenly, regularly elongated, smooth externally, with six to eight strong pilasters; distal part short, with only weak folds or fine wrinkles inside. Spinules absent. Two individuals from the type locality were dissected.

#### *Distribution*

The species inhabits lowland (< 200 m) forest around the Taroko valley, Hualien County, eastern Taiwan. The animals were usually found at the Gekou area



**Figure 34.** Reproductive system of *Satsuma vallis* sp. nov. (paratype, TMMT 0664). A, whole genitalia; B, interior of genitalia. Scale bar = 5 mm. See text for abbreviations.



**Figure 35.** *Satsuma viridibasis* sp. nov. A–D, holotype (TMMT 0613, shell height = 22.4 mm). E, living specimen. Arrow indicates the pre-apertural constriction.

and Shenmigu valley of Taroko National Park (Fig. 1, Table 1).

#### Remarks

The perching distance from the ground is typically 2–5 m. Active individuals were also observed on low shrubs. Adults were found in summer (Fig. 33G).

*Satsuma vallis* is similar to *S. katipolensis* in shell dimensions, but it differs from the latter in having pre-apertural constriction, longer distal vagina, slender base of bursa stalk, shorter bursa stalk, more expanded proximal penis and lack of genital spinules.

#### *SATSUMA VIRIDIBASIS* SP. NOV. (FIGS 35, 36)

*Satsuma albida* (H. Adams). Chang *et al.*, 1996: 25–30, fig. 2 (genitalia) [non *albida*]

#### Material examined

*Type specimen:* Holotype: TMMT 0613 (from type locality, dry shell, tissue in alcohol). Total five paratypes: four paratypes from type locality: TMMT 0663 (dry shell, tissue in alcohol, dissected); BMNH 20060756, ANSP 413676, SMF 329385 (dry shell).

One paratype from Yangmingshan, Taipei: TMMT 0675 (dry shell, tissue in alcohol, dissected).

#### Type locality

Sikanshui, Xindian, Taipei County, northern Taiwan (Fig. 1, Table 1).

#### Diagnosis

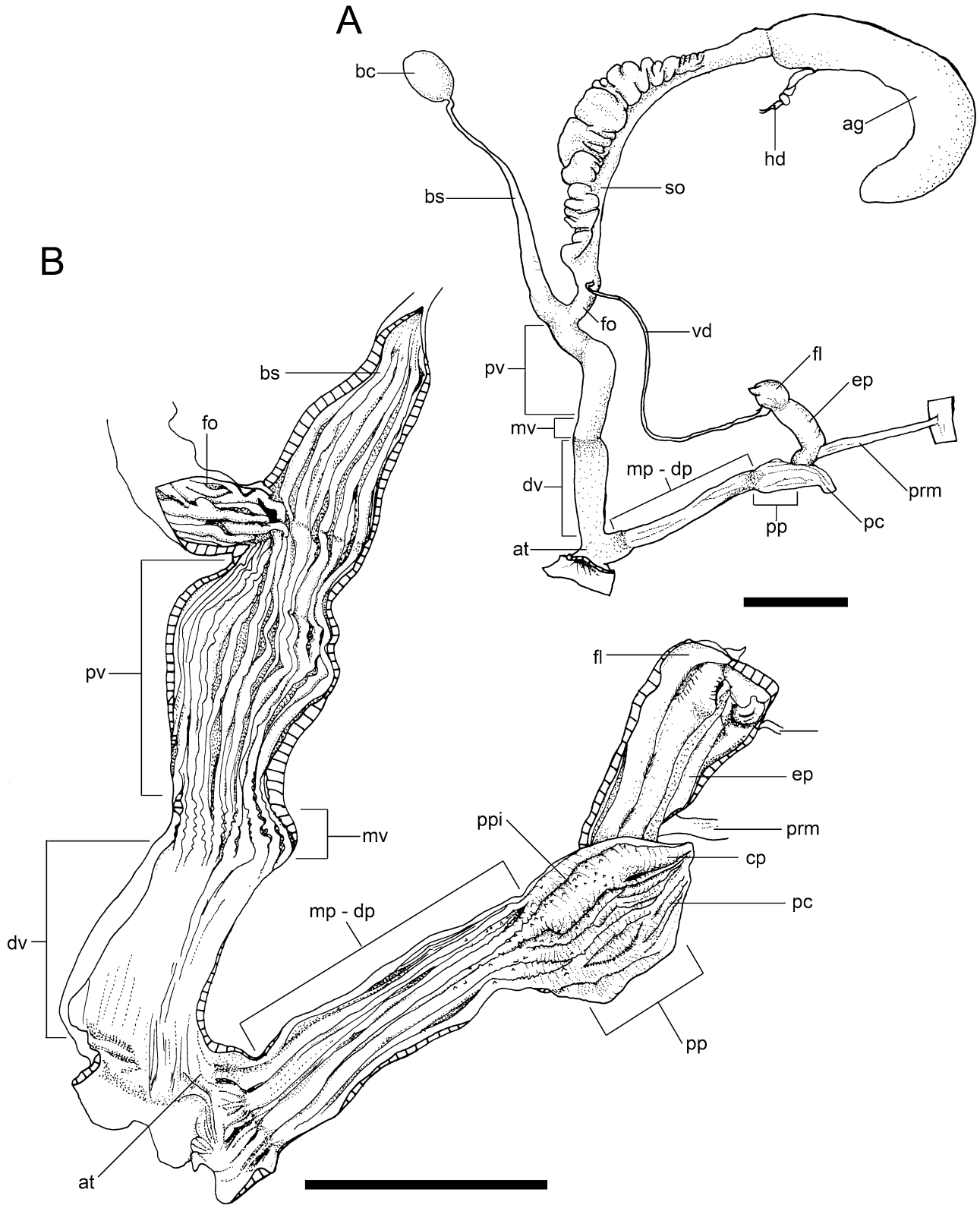
Shell and soft body yellowish without pedal stripe; colour of base greenish; pre-apertural constriction present behind outer lip; number of whorls more than six; bursa stalk shorter than spermooviduct; principal pilaster short; proximal penis short, apparently expanded.

#### Etymology

*L. viridis*: green; *L. basis*: base, referring to the green body whorl.

#### Description

*Shell* (Fig. 35): Dextral, conical, thin, medium sized. Apex obtuse. Whorls inflated. Periphery bluntly angulated, arc-like. Base inflated. Pre-apertural constriction behind outer lip only. Periostracum thin. Shell colour light yellow above periphery, light yellowish green to cyan below periphery. Surface smooth, with



**Figure 36.** Reproductive system of *Satsuma viridibasis* sp. nov. (paratype, TMMT 0675). A, whole genitalia; B, interior of genitalia. Scale bar = 5 mm. See text for abbreviations.



fine axial and spiral striae. Aperture subvertical, ovate. Junction between outer lip and inferior lip curved. Peristome thin, expanded at inferior lip and outer lip. Columellar lip vertical, reflected. Umbilicus mostly covered by columellar lip, crevice-like.

*Band or stain:* Band or stain is not present. Band formula = 0 0 0 0 0 0 0.

*Reproductive system* (Fig. 36): The reproductive system is similar to that of *S. vallis* with following exceptions: (1) the flagellum is shorter than that of *S. vallis*, (2) the epiphallus is short and has three pilasters inside, and (3) spinules are present. Three individuals from the type locality were dissected.

#### *Distribution*

The species was found in lowland (< 500 m) forest around the Taipei basin, northern Taiwan (Wulai, Sikanshui, Pinglin, Mt Yangmingshan and Mt. Xiangshan) although not in the western part of the basin (Fig. 1, Table 1).

#### *Remarks*

Found from 2 m to the canopy. Adult individuals were found in summer (Fig. 35E).

The present species is morphologically similar to *S. vallis* but with larger shell dimensions, greenish shell base, more diagonal aperture, more expanded base, presence of genital spinules and short epiphallus. The specimens dissected and figured by Chang *et al.* (1996: fig. 2) are actually this present species (see remarks in *S. albida*). The species is similar to *S. luteolella* in shell dimensions, but *S. viridibasis*

differs in having greenish shell base, pre-apertural constriction, shorter bursa stalk, short principal pilaster and more expanded proximal penis.

#### *SATSUMA PILSBRYI SP. NOV.* (FIGS 37, 38)

##### *Material examined*

*Type specimen:* Holotype: TMMT 0614 (from type locality, dry shell, tissue in alcohol, dissected). Nine paratypes: all from type locality, TMMT 0644, TMMT 0665–0670 (dry shell, tissue in alcohol); BMNH 20060766, ANSP 413684 (dry shell).

##### *Type locality*

Taiyuan, Taitung County, eastern Taiwan (Fig. 1, Table 1).

##### *Diagnosis*

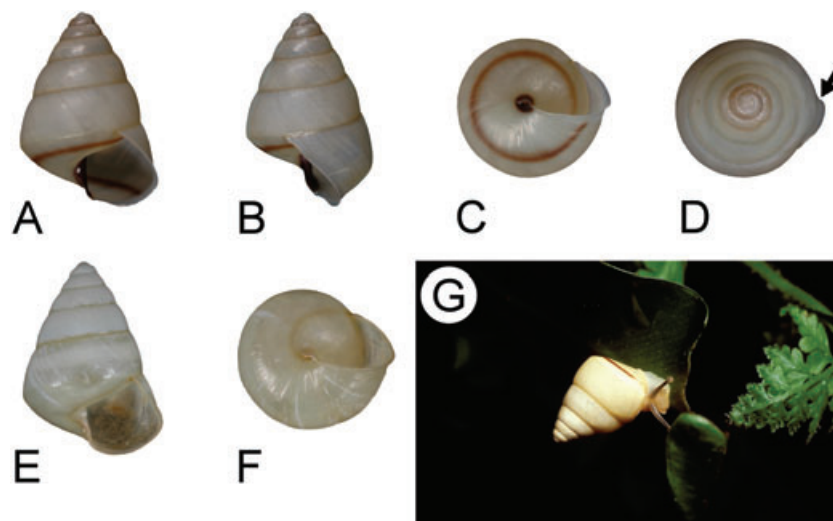
Shell and soft body yellowish without pedal stripe; shell conical with small diameter; pre-apertural constriction present behind outer lip; base of bursa stalk conical; principal pilaster short; proximal penis short, swollen.

##### *Etymology*

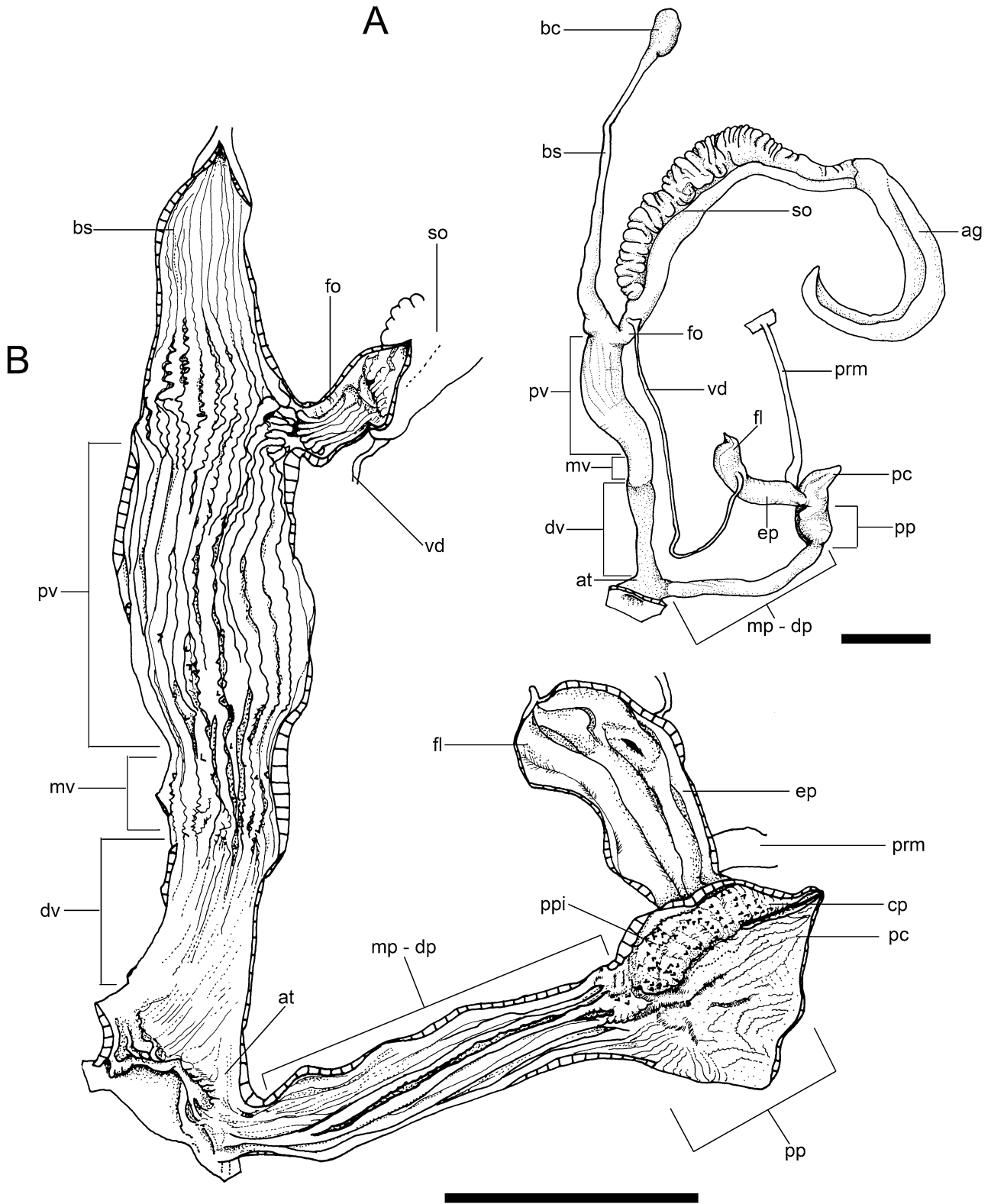
This species is named after the American malacologist Henry A. Pilsbry (1862–1957) who described two species of this group.

##### *Description*

*Shell* (Fig. 37): Dextral, conical, thin, medium sized to small. Apex obtuse. Whorls inflated. Periphery bluntly angulated, arc-like. Base expanded. Pre-apertural constriction behind outer lip only. Shell colour light yellow. Periostracum thin. Surface evenly



**Figure 37.** *Satsuma pilsbryi* sp. nov. A–D, holotype (TMMT 0614, shell height = 17.9 mm). E, F, paratype (TMMT 0644, shell height = 17.6 mm). G, living specimen. Arrow indicates the pre-apertural constriction.



**Figure 38.** Reproductive system of *Satsuma pilsbryi* sp. nov. (holotype, TMMT 0614). A, whole genitalia; B, interior of genitalia. Scale bar = 5 mm. See text for abbreviations.

smooth, with fine axial and spiral striae. Aperture diagonal, ovate. Junction between outer lip and inferior lip an angulated curve. Peristome thin, expanded at inferior lip and outer lip. Inferior lip curved downward. Columellar lip vertical, reflected. Umbilicus mostly covered by columellar lip, crevice-like. Junction between columellar lip and inferior lip obtusely angulated.

*Band or stain:* Polymorphism exists in this taxon. Some individuals lack colour band and stain, whilst some exhibit light red-brown apical spot, sub-peripheral band or umbilicus stain. Inferior and outer lips are colourless. Band formula = 0 0 0 0 0 0 0; 1 0 0 0 5 0 7 0.

*Reproductive system* (Fig. 38): Bursa stalk short, four-fifths spermoviduct, tapering, swollen at base. Bursa copulatrix clavated. Proximal vagina muscular, swollen, smooth, with 14 pilasters internally; middle vagina short, constricted, thick-walled, with 17 weak and wiggly folds inside; distal vagina long, nearly one-third length of vagina, gradually constricted towards atrium, with low folds or fine wrinkles inside. Flagellum short and swollen at base, with apparently short and quickly tapering tip. Epiphallus short, with four pilasters inside. Penial caecum moderate, conical, blunt, smooth; cecal pilaster two in number; remaining inner walls of penial caecum contain several moderate ridges. Proximal penis short, swollen, smooth externally, with one deep groove on epiphallic side corresponding to principal pilaster internally; principal pilaster same length as penial caecum; middle penis constricted suddenly, regularly elongated, smooth externally, with seven to nine strong and smooth pilasters; distal penis short, only weak folds or fine wrinkles inside. Spinules present in vagina, penial caecum and proximal penis. Two individuals from the type locality were dissected.

#### *Distribution*

This species was found in lowland forest habitats around the Taiyuan valley, Taitung County, eastern Taiwan (Fig. 1, Table 1).

#### *Remarks*

The perching distance from ground is 2 m; also active on low shrubbery. Adults were found in summer (Fig. 37G).

The shell morphology of this species is similar to that of *S. vallis*, but it differs in dimensions and shell colour. The genital morphology of this species is fundamentally similar to that of *S. viridibasis* and *S. vallis* with the following exceptions: (1) the proximal vagina is stronger, (2) the base of the bursa stalk is conical and (3) the penial caecum and proximal penis

are strong, smooth and muscular. *Satsuma pilsbryi* is probably an intraspecific variation from southern populations of *S. vallis* and *S. viridibasis* in shell morphology. However, the well-defined geographical isolation and distinguishable reproductive system reveal it merits specific status.

## PHYLOGENY

### MOLECULAR DATA

A total of 484 (*S. lini*  $N = 4$ , for each of the remaining taxa  $N = 30$ ) individuals were successfully analysed in their CO1 sequences. Sequences of the 16S rRNA gene were analysed from 3–5 individuals from each of the species. Sequences of the ITS2 genes were analysed from one individual from each of the species. The ITS2 gene sequence of *Camaena longsonensis* was not available, which was difficult to amplify. Sequences were verified by forward and reverse comparisons and were deposited in GenBank (Table 3). Haplotypes of each species were monophyletic with high bootstrap support in a preliminary analysis using the neighbour-joining method (data not shown). Moreover, no haplotypes were shared between species. Therefore, only one haplotype was selected as a representative for each of the species and for the subsequent phylogenetic analyses. Two segments of 21 and 49 bp in the 16S sequences were excluded owing to highly variable and ambiguous alignment. A total of 1506 bp of aligned sequences were used in the following analyses containing 638 bp of CO1, 362 bp of 16S rRNA and 506 bp of ITS2.

The ILD test for congruence between datasets was marginally significant ( $P = 0.025$ ). Cunningham (1997) indicated that combining datasets with an ILD test  $P$  value of greater than 0.01 retained or improved phylogenetic accuracy. Therefore, the sequences of the three genes were combined for the subsequent analyses. The combined dataset provided higher bootstrap support and greater resolution than either dataset alone. Of the characters, 609 bp (40%) were variable, and 417 bp were parsimony informative. For the 23 species analysed, the heuristic searches resulted in two trees of equal maximum parsimony (MP) with a tree length of 1817 (CI = 0.53, RI = 0.59). All branches were sufficiently (> 50%) supported by bootstrap analysis except for the (*S. viridibasis*, *S. vallis*, *S. pilsbryi*) clade.

The general time-reversible model with a proportion of invariable sites and a gamma-shaped distribution of rates across sites (TvM + I + G) was determined as the best-fitting model for the combined sequences of the three genes using the hierarchical likelihood ratio test performed by the program Modeltest 3.7 (Posada & Crandall, 1998). The model was then adopted for the maximum-likelihood distance

**Table 3.** GenBank accession numbers of taxa

Species	GenBank accession number		
	COI	16S rRNA	ITS2
<i>Satsuma albida</i>	EF057384	EF057354	EF204853
<i>Satsuma insignis</i>	EF057382	EF057352	EF204863
<i>Satsuma mollicula</i>	EF057374	EF057363	EF204859
<b><i>Satsuma hagiomontis</i> sp. nov.</b>	EF057386	EF057356	EF204865
<b><i>Satsuma swinhoei</i> sp. nov.</b>	EF057385	EF057355	EF204866
<b><i>Satsuma lini</i> sp. nov.</b>	EF057383	EF057353	EF204864
<b><i>Satsuma phoenicis</i> sp. nov.</b>	EF057381	EF057350	EF204852
<b><i>Satsuma careocaecum</i> sp. nov.</b>	EF057380	EF057351	EF204851
<b><i>Satsuma polymorpha</i> sp. nov.</b>	EF057378	EF057357	EF204862
<b><i>Satsuma huberi</i> sp. nov.</b>	EF057375	EF057364	EF204858
<b><i>Satsuma auratibasis</i> sp. nov.</b>	EF057376	EF057365	EF204860
<b><i>Satsuma katipolensis</i> sp. nov.</b>	EF057377	EF057366	EF204854
<b><i>Satsuma luteolella</i> sp. nov.</b>	EF057373	EF057362	EF204856
<b><i>Satsuma kanoi</i> sp. nov.</b>	EF057372	EF057361	EF204861
<b><i>Satsuma viridibasis</i> sp. nov.</b>	EF057371	EF057358	EF204850
<b><i>Satsuma vallis</i> sp. nov.</b>	EF057369	EF057360	EF204855
<b><i>Satsuma pilsbryi</i> sp. nov.</b>	EF057370	EF057359	EF204857
<i>Satsuma nux</i>	EF057337	EF204778	EF204872
<i>Satsuma arisana takkiriensis</i>	EF204828	EF204791	EF204885
<i>Satsuma succincta</i>	EF204839	EF204802	EF204896
<i>Satsuma pekanensis</i>	EF204833	EF204796	EF204890
<i>Satsuma largillierti</i>	EF057387	EF057367	EF204904
<i>Satsuma myomphala</i>	EU131663	EU131664	EU131665
<i>Moellendorffia hiraseana</i>	EF204842	EF204805	EF204899
<i>Camaena longsonensis</i>	EF057379	EF057368	

setting for NJ analysis. The topology of the NJ tree was similar to the MP tree. *Satsuma myomphala* from Honshu, Japan, diverged from species in Ryukyu and Taiwan early. *Satsuma largillierti* from Okinawa Island formed a separate clade from this species complex and clustered with *S. pekanensis* and *S. succincta*. The phylogeny of *S. katipolensis* was not congruent in the MP and NJ trees. This species was clustered with *S. huberi* and *S. auratibasis* in the NJ tree, whereas it was closer to other species from eastern Taiwan in the MP tree but with low bootstrap value. The deep branches were not well resolved in the NJ tree where levels of bootstrap support were low. The 50% majority rule consensus tree (tree length 1817, CI = 0.53, RI = 0.59) of the two MP trees and the NJ tree was reconstructed by weighting each of the MP trees as 0.5 and the NJ tree as 1 (Fig. 39).

#### MORPHOLOGICAL DATA

The parsimonious analysis on 20 morphological characters (Table 4) resulted in 84 MP trees of 68 steps. The 50% majority rule consensus (Fig. 40) produced a tree of 70 steps (CI = 0.59, RI = 0.78, RC = 0.46) with

high bootstrap support for most branches. Bootstrap analysis showed sufficient support at deep branches and the clade (*mollicula*, *auratibasis*) only (Fig. 40). *Satsuma largillierti* from Okinawa Island formed a separate clade from this species complex and agreed with molecular phylogeny data. However, it was not clustered with *S. nux*. The 17 species of the *S. albida* species complex from Taiwan formed a monophyly. However, four species from west Taiwan, *insignis*, *lini*, *phoenicis* and *careocaecum*, could not be separated based on these characters. *Satsuma polymorpha* does not form an ancestral clade of species in west Taiwan. The clustering of sister species in this tree, e.g. (*huberi*, *katipolensis*) and (*mollicula*, *auratibasis*), agreed with the general impression but was incongruent with molecular phylogeny data (Fig. 39).

The cladograms based on molecular and morphological data (Figs 39, 40) presented three major clades from Taiwanese species, as judged by the topology, branch lengths and geographical distribution: an 'east clade' (*S. vallis*, *S. pilsbryi*, *S. viridibasis*, *S. kanoi*, *S. luteolella*, *S. mollicula*, *S. katipolensis*, *S. huberi* and *S. auratibasis*), a 'west clade' (*S. albida*, *S. swinhoei*, *S. hagiomontis*, *S. insignis*, *S. lini*, *S. careocaecum* and *S.*



**Table 4.** Data matrix for phylogenetic analysis of *Satsuma albida* species complex. See text for character coding and further explanation

	1	2	3	4	5	6	7	8	9	0	1	1	1	1	1	1	1	1	1	1	2	
<i>S. albida</i>	2	1	1	1	1	1	0	0	1	1	2	1	0	0	0	1	0	0	0	0	0	2
<i>S. hagiomontis</i>	1	1	1	1	1	0	1	0	1	1	1	1	0	0/1	0	2	1	0	0	0	1	1
<i>S. swinhoei</i>	1/2	1	1	1	1	0/1	1	0	1	1	1	0	0	0	0	1	0	0	0	0	2	1
<i>S. insignis</i>	2	1	1	1	1	0	0	0	1	1	2	0	0	0	0	1	1	0	0	0	1	1
<i>S. lini</i>	2	1	1	1	1	1	0	0	1	1	?	?	?	?	?	?	?	?	?	?	?	?
<i>S. phoenicis</i>	2	1	1	1	1	1	0	0	1	1	2	0	0	0	0	1	1	1	1	1	2	1
<i>S. careocaezum</i>	2	1	1	1	1	0/1	0	0	1	1	2	0	0	0	0	0	0	0	0	0	0	0
<i>S. polymorpha</i>	1	1	1	1	1	0/1	0	0	1	1	2	1	0	0/1	0	1	1	0	0	0	2	1
<i>S. mollicula</i>	3	3	3	0	0	1	1	0	2	0	2	1	1	1	1	2	1	1	2	1	1	1
<i>S. huberi</i>	3	1/2	1/2	0	0	1	0	0	2	0	1	0	0	1	1	2	1	1	1	1	2	1
<i>S. auratibasis</i>	3	2	3	0	0	1	0	0	2	0	2	1	1	1	1	2	1	1	2	1	1	1
<i>S. katipolensis</i>	3	2	2	0	0	1	0	0	2	0	1	1	0	1	1	2	1	1	1	1	2	1
<i>S. luteolella</i>	3	2	2	0	0	1	0	0	2	0	2	0	0	1	1	2	1	1	2	1	1	1
<i>S. kanoi</i>	3	2	2	0	1	1	0	1	2	0	1	0	0	1	1	2	1	1	2	1	1	1
<i>S. vallis</i>	3	2	2	0	1	1	0	0	2	0	2	0	1	0	1	2	0	1	1	1	1	1
<i>S. viridibasis</i>	3	2	4	0	1	1	0	0	2	0	2	0	1	1	1	2	0	1	1	1	2	1
<i>S. pilsbryi</i>	3	2	2	0	1	1	0	0	2	0	2	1	0	1	1	2	0	1	1	1	2	1
<i>S. nux</i>	0	0	0	0	0	0	0	1	0	0	0	1	1	0	1	2	0	0	0	0	0	0
<i>S. largillierii</i>	1	2	2	0	0	0	0	1	0	0	?	1	?	?	0	1	1	0	?	?	2	1
<i>Camaena</i>	0	0	0	0	0	0	0	1	0	0	0	1	2	0	0	0	0	0	0	0	0	0

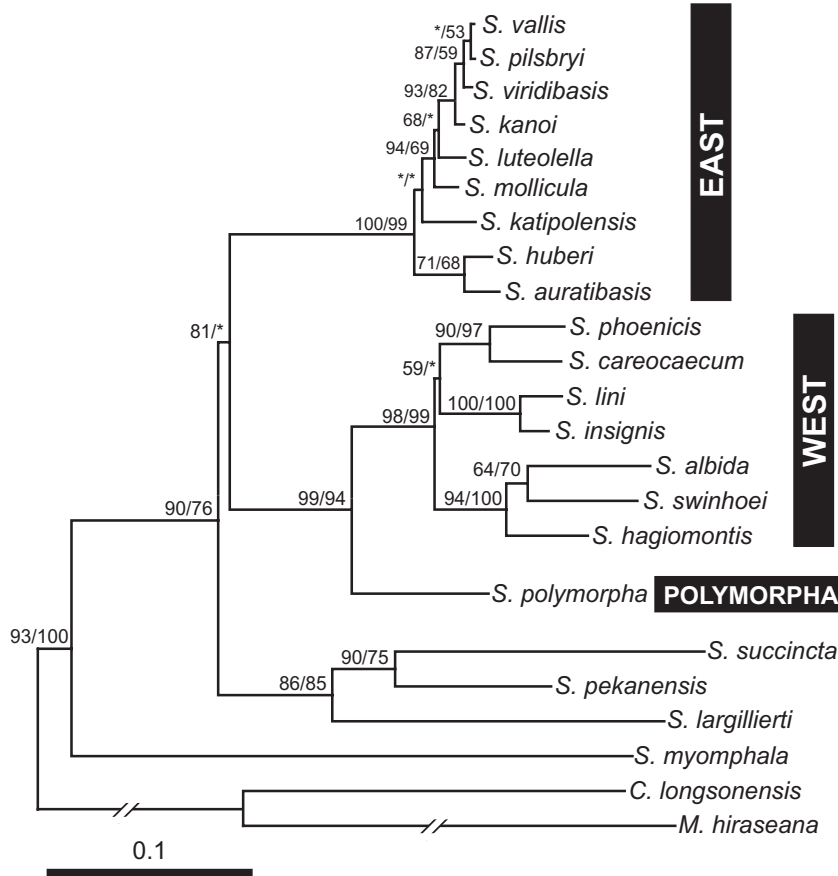
*phoenicis*) and the 'polymorpha clade' (*S. polymorpha*). High genetic diversity was observed amongst the different clades, with sufficient statistical support using molecular data as shown by the branch length in Figure 39. Nevertheless, genetic divergence among each of the clades was different. Taxa of the east clade were estimated to have lower genetic distances between each other compared with species of the west clade. The polymorpha clade is a sister taxon of the west clade containing only one species, although the morphological phylogeny (Fig. 40) did not agree with the separate status of this clade. This species is unique in having highly polymorphic banding patterns and the most widespread geographical distribution in eastern and northern Taiwan with low genetic divergences (data not shown).

## DISCUSSION

This study represents the first comparative studies of *S. albida* and its allied species using conchological, anatomical and molecular characteristics. Taxonomical decisions, which were inconclusive in the past based on morphological characters only (Kuroda, 1941; Kuroda, 1958; Sinagawa, 1980; Chang *et al.*, 1996), were made accordingly and included the erection of 14 new species, raising the taxonomic status of two subspecies and the correction of previous identi-

fication. Raising two previous subspecies of *S. albida*, *S. insignis* and *S. mollicula*, to full species was suggested as they belonged to different clades on the phylogenetic tree in addition to morphological characters. Morphological evidence demonstrated that the reproductive system of '*S. albida*' figured by Chang *et al.* (1996) was in fact that of *S. viridibasis* sp. nov. based on similarities in their anatomical morphology and close geographical distribution.

The general morphology of the reproductive system, e.g. the presence of flagellum and penial caecum, in the *S. albida* species complex agrees with the known structures of other *Satsuma* species (Kuroda & Habe, 1949; Habe, 1955; Minato, 1976; Chang, 1992). However, an exception was observed in *S. careocaezum*, which showed a lack of the penial caecum. The presence/absence of the penial caecum (= penial appendix) was considered as a diagnostic character to distinguish related camaenid (sub-)genera. That is, *Satsuma* (including subgenus *Satsuma s.s.*, *Luchuhadra* and *Coniglobus* Pilsbry & Hirase, 1906 [1905]) presented a penial caecum of variable size, whereas *Pancala* Kuroda & Habe, 1949 and *Camaena* Albers, 1850 and *Camaena* (*Miyakoia*) Minato, 1980 showed a lack of penial caecum (Kuroda & Habe, 1949; Minato, 1980; Chang, 1992). Therefore, *Pancala* and *Miyakoia* were assigned as subgenera of *Camaena* (Kuroda & Habe, 1949; Minato, 1980). The species of *Camaena*



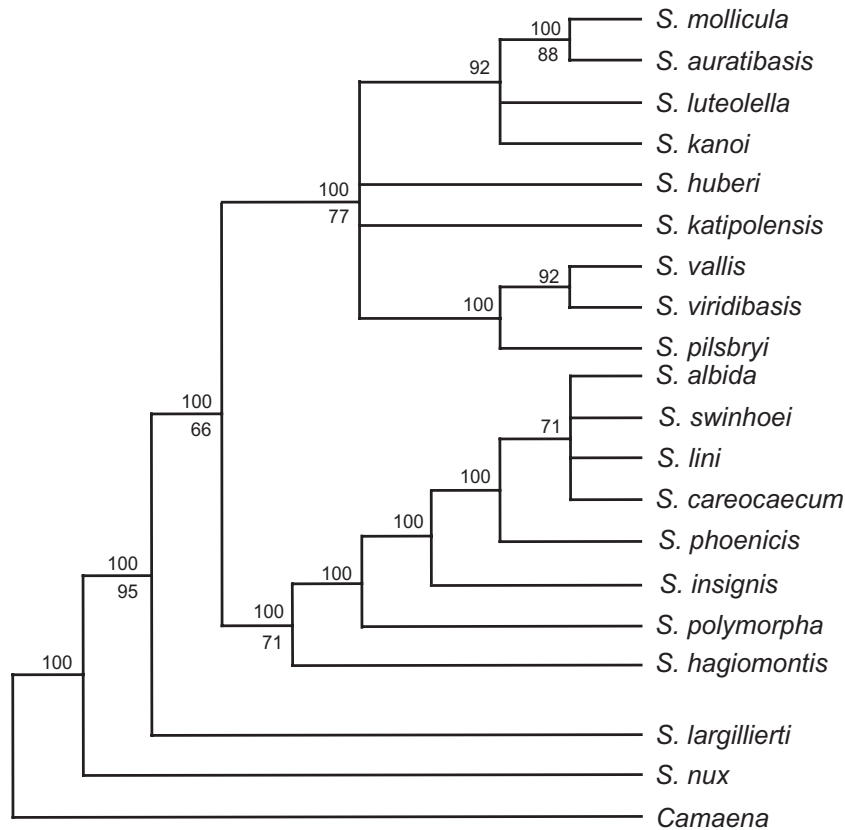
**Figure 39.** The phylogenetic relationships of the *Satsuma albida* species complex from Taiwan based on the tree reconstructed by the maximum-parsimonious method on a combined dataset of the partial CO1, 16S rRNA and complete ITS2 genes. East, West and Polymorpha indicate the three major clades of the group in Taiwan. Numbers beside the nodes refer to the percentage bootstrap support of 1000 replicates based on the maximum-parsimonious method (left) and the neighbour-joining tree (right). An asterisk indicates bootstrap value of less than 50%.

showed an elongated and conic penial verge at the insertion of the epiphallus into the penis instead of a protruding penial caecum (Pilsbry, 1895; Sinagawa, 1979; Hwang, 1995). The species of the genus *Pancala*, *Satsuma succincta*, *S. nux paiwanis* and *S. longkiauwensis* Wu, Lin & Hwang, 2007 showed a weak and hemispherical verge only, neither conical nor elongated as a penial caecum (unpublished data).

The lack of a penial caecum observed in *S. careocaecum* is unique not only in this species complex but also in the genus *Satsuma*. No verge or similar structure was observed in this species; instead, there is only a constrictive tubule between the epiphallus and the penis. With regard to development, the lack of a penial caecum in *S. careocaecum* may be considered as a pedomorphosis as all of the subadult specimens dissected in the present study showed the same absence (see the immature genitalia of a juvenile *S. lini*, Fig. 12). Anatomical evidence showed that characters of the male genitalia

are better in distinguishing between species than female genitalia, which agrees with Kameda, Kawakita & Kato (2007). The characters of the flagellum, and portions at the insertion of the epiphallus, which include the penial caecum, proximal penis, internal pilasters and verge, are useful in taxonomy at the specific level. Due to the lack of internal morphology of genitalia for most *Satsuma* species, the phylogenetic relationship based on morphological characters presented in here is tentative. A complete phylogenetic analysis is required to clarify their evolutionary significance.

Spinules of the genitalia were observed mainly in species of the east clade, except *S. vallis* which does not bear any spinules. The reverse was observed in the other two clades, members of which usually do not have spinules in the genitalia. Spinules were born in genitalia of some individuals of *S. hagiomontis*, *S. swinhoei* and *S. polymorpha* from Shenmihu. Occasionally, female and male genitalia of the same indi-



**Figure 40.** Fifty per cent majority rule consensus tree of 84 maximum-parsimonious trees based on 20 morphological characters of the *Satsuma albida* species complex from Taiwan. Tree length: 70, CI: 0.59, RI: 0.78, RC: 0.46. Numbers above the branches are the percentage of the consensus tree, and those below are the bootstrap percentage of 1000 replicates. Bootstrap values of less than 50% were omitted.

vidual do not have spinules simultaneously. Penial armatures were observed in some *Westraltrachia* and related genera in Australia (Solem, 1984), which showed a hardened edge on the principal pilaster. Hooked penial armatures were observed in several species of the family Streptaxidae (Verdcourt, 2000). However, a similar structure was not reported in *Satsuma* and other East Asian camaenids partly because of few reports on interior genitalia. The function and phylogenetic significance of such penial armature in the *S. albida* group remain unknown. It was suggested to function partly as stimulator or hold-fast surface during copulation (Gómez, 2001). However, Solem (1984) doubted that the armatures may be seasonally variable.

Three clades of distinct genetic characters were found among the Taiwanese arboreal species (Fig. 39), which agreed partly with the morphological phylogeny based on characters of the shell, soft body and reproductive system (Fig. 40). The species of the east clade uniformly have more conical and yellowish shells, a yellowish soft body and stout male genitalia. The species of the west and polymorpha clades have

less conical and white shells, white/grey soft body with dark grey stripes on the foot and slender male genitalia.

The nine species clustered in the east clade have conspicuous morphological differences in the shell and reproductive system. Furthermore, no common haplotypes derived from mtDNA CO1 and 16S rRNA gene sequences were shared between each of these species. Therefore, no gene flow is revealed between the species and no sign of hybridization. However, these species share short genetic distances (uncorrected proportional distance = 0.006–0.052). Species within this clade are considered to have arisen only recently with prompt divergence that may have been caused by geographical barriers and rapid speciation via significant morphological shifts to aspects of body form and reproductive system in east Taiwan.

The west clade comprises seven species showing high genetic divergence between the taxa (uncorrected proportional distance = 0.032–0.15) although their shell morphologies are similar to each other. Long branch lengths on the phylogenetic tree imply that these species may have diverged a long time ago.

Furthermore, the seven species do not share haplotypes from the molecular survey. All taxa have a distinctive reproductive system that suggests reproductive isolation is well established among species of the west clade. Most species from this clade are confined to a narrow geographical range and altitude limitation, and are dependent on primary broadleaf forest. Thus, species formation of this early clade arisen is considered to have resulted from dispersal or vicariance events through a long evolutionary process (Avice, 2000). The fixed genetic structure and habitat limitation is probably derived from habitat fractures caused by the repetitive expansion and retreat of the forests during glacial periods of the past million years on Taiwan (Lin, 1970; Chai, 1972; Teng, 1990). The similarity in shell morphology is probable due to similar selective forces on ecology,

*Satsuma polymorpha*, despite being the most widespread species in eastern and northern Taiwan and having distinctly divergent banding pattern, does not diverge into different species between populations. Eastern populations of *S. polymorpha* are distributed over a wide geographical range of mid-altitude forests (south Yilan to Taitung) with high polymorphism in banding pattern, whereas northern populations (north Yilan and Taipei, Taoyuan, Hsinchu and Miaoli) do not display such polymorphism, i.e. all shells exhibit a whitish colour as seen in *S. albida*. However, a similar genetic structure and haplotypes are shared between populations (data not shown). Reasons for the asymmetric evolution in the morphological and genetic variability of *S. polymorpha* from the eastern and northern populations remain uncertain. The molecular phylogenetic relationship suggests that *S. polymorpha* arose at the same time as the west clade, but no further divergence to species level as seen in the west clade has taken place.

The *Luchuhadra* species in the Ryukyu Islands formed a separate clade with other ground-dwelling *Satsuma* in Taiwan showing that the major clades of these arboreal species evolved independently after the divergence from their common ancestor. This disagrees with the suggestion of assigning the arboreal *S. albida* group to *Luchuhadra* (Kuroda & Habe, 1949; Habe, 1955; Minato, 1976). Further phylogenetic investigations are required for a better resolution of the evolutionary history of the genus *Satsuma*, including its nominal subgenera *Coniglobus* and *Luchuhadra*, and its allies from East Asia. Therefore, no generic determinations are proposed herein and the genus *Satsuma* (including species in *Satsuma s.s.*, *Luchuhadra* and *Coniglobus*) is suggested to be applied tentatively to these arboreal snails.

Despite the controversies mentioned in the Introduction on the systematics of these arboreal snails, we consider that these three clades of Taiwanese

arboreal camaenids have arisen from their common ancestor through the evolutionary process of speciation in their areas of distribution. The pyramidal shell, pale coloration, highly polymorphic banding patterns and stains should be adaptive consequences of the arboreal process from their dark-coloured, depressed-conical and less polymorphic *Satsuma*-like ground ancestor. Similar selective forces on arboreal ecology during the adaptive evolution are considered to have maintained the phenotypic coincidence of the three groups. Morphological similarities of these arboreal camaenid snails illustrate apomorphy of these taxa as compared with their ground-dwelling ancestor. Therefore, the three groups show similar colour pattern and shell morphology but are located in different clades. The use of shell morphology and coloration may not be appropriate for taxonomy of this group of animals. Anatomical study of the reproductive system and molecular analysis provide should be used to clarify a group of organisms such as these.

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#### REFERENCES

- Adams A. 1868. On the species of Helicidae found in Japan. *Annals and Magazine of Natural History, Series 4* 1: 459–472.  
 Adams H. 1866. Descriptions of fifteen new species land and freshwater shells from Formosa, collected by Robert



- Swinhoe, Esq., Consul at Taiwan in that island. *Proceedings of the Zoological Society of London* **1866**: 316–319.
- Adams H. 1870.** Descriptions of ten new species of land and freshwater shells collected by Robert Swinhoe, Esq., in China and Formosa. *Proceedings of the Zoological Society of London* **1870**: 377–380.
- Albers JC. 1850.** *Die Heliceen, nach natürlicher Verwandtschaft systematisch geordnet*. Berlin: Verlag von Th. Chr. Fr. Enslin.
- Avise JC. 2000.** *Phylogeography: the history and formation of species*. London: Harvard University Press.
- Azuma M. 1995.** *Colored illustrations of the land snails of Japan*. Osaka: Hoikusha.
- Baker HB. 1963.** Type land snails in the Academy of Natural Sciences of Philadelphia. Part II. Land Pulmonata, exclusive of North America and Mexico. *Proceedings of the Academy of Natural Sciences of Philadelphia* **115**: 191–259.
- Blandford WT. 1863.** On Indian species of land shells belonging to the genus *Helix* Linn. and *Nanina* Gray. *Annals and Magazine of Natural History, Series 3* **11**: 81–91.
- Chai BHT. 1972.** Structure and tectonic evolution of Taiwan. *American Journal of Science* **272**: 389–422.
- Chang KM. 1984.** Catalogue of land snails from Taiwan. *Pei-Yo* **9**: 2–41.
- Chang KM. 1989.** Anatomy of *Coniglobus nux paiwanis* (Kuroda) and *Coniglobus pekanensis* (Rolle) from south Taiwan (Pulmonata: Camaenidae). *Bulletin of Malacology* **14**: 1–8.
- Chang KM. 1992.** Dwarf type of *Camaena batanica pancala* (Schmacker and Boettger) from South Cape, Taiwan and its allied species (Pulmonata: Camaenidae). *Bulletin of Malacology* **17**: 11–20.
- Chang KM, Chang HW, Hwang CC. 1996.** Anatomy on *Satsuma albida* (H. Adams, 1870) from Taiwan (Pulmonata: Camaenidae). *Bulletin of Malacology* **20**: 25–30.
- Chang WC. 1985.** *Distribution and ecology of land snails of Kenting National Park*. Pingtung: Kenting National Park Administration Office.
- Clench WJ, Turner RD. 1962.** *New names introduced by H. A. Pilsbry in the Mollusca and Crustacea*. Philadelphia, PA: Academy of Natural Sciences of Philadelphia.
- Cunningham CW. 1997.** Can three incongruence tests predict when data should be combined? *Molecular Biology and Evolution* **14**: 733–740.
- Felsenstein J. 1985.** Confidence limits on phylogenies: an approach using the bootstrap. *Evolution* **39**: 783–791.
- Folmer O, Black M, Hoeh W, Lutz R, Vrijenhoek R. 1994.** DNA primers for amplification of mitochondria cytochrome c oxidase subunit I from diverse metazoan invertebrates. *Molecular Marine Biology and Biotechnology* **3**: 294–299.
- Gómez BJ. 2001.** Structure and functioning of the reproductive system. In: Baker GM, ed. *The biology of terrestrial molluscs*. Wallingford, UK: CABI Publishing, 307–330.
- Habe T. 1955.** Anatomical studies of Japanese land snails (3). *Venus* **18**: 221–234.
- Hall TA. 1999.** BioEdit: a user-friendly biological sequence alignment editor and analysis program for Windows 95/98/NT. *Nucleic Acids Symposium Series* **41**: 95–98.
- Hsieh BC, Hwang CC, Wu SP. 2006.** *Landsnails of Taiwan*. Taipei: Forestry Bureau Council of Agriculture, Executive Yuan.
- Hwang CC. 1995.** Analysis of mitochondrial DNA phylogeny of *Camaena* (Pulmonata: Camaenidae). Master dissertation of National Sun Yat-sen University, Taiwan.
- Jones JS, Leith BH, Rawlings P. 1977.** Polymorphism in *Cepaea*: a problem with too many solutions? *Annual Review of Ecology and Systematics* **8**: 109–143.
- Kameda Y, Kawakita A, Kato M. 2007.** Cryptic genetic divergence and associated morphological differentiation in the arboreal land snail *Satsuma (Luchuhadra) largillierti* (Camaenidae) endemic to the Ryukyu Archipelago, Japan. *Molecular Phylogenetics and Evolution* **45**: 519–533.
- Kerney MP, Cameron RAD. 1979.** *Land snails of Britain & North-west Europe*. London: HarperCollins.
- Kuroda T. 1941.** A catalogue of molluscan shells from Taiwan (Formosa), with description of new species. *Memoirs of the Faculty of Science and Agriculture Taihoku Imperial University* **12**: 65–216.
- Kuroda T. 1958.** Land shell fauna of Japan (4). *Venus* **20**: 132–158.
- Kuroda T. 1960.** *A catalogue of molluscan fauna of the Okinawa Islands*. Okinawa: Ryukyu University.
- Kuroda T, Habe S. 1949.** *Helicacea*. Tokyo: Sanmeisha.
- Lai KY. 1981.** Study on morphology and ecology of the land snail *Pancala batanica pancala*. *Bulletin of Malacology* **8**: 1–10.
- Lai KY. 1990.** *World of landsnails*. Taipei: Taiwan Museum.
- Lin CC. 1970.** *The Quaternary period of Taiwan*. Taipei: Bibliography of Taiwan.
- Martens KE. 1865.** Neue Landschnecken aus Ostasien. *Monatsbericht der Königlich-Preussischen Akademie der Wissenschaften zu Berlin* **1865**: 51–55.
- Mickevich MF, Farris JS. 1981.** The implications of congruence in *Menidia*. *Systematic Zoology* **30**: 351–370.
- Minato H. 1976.** Genital studies of the Japanese land snails – VII. The genitalia of *Satsuma amanoi* Kuroda, 1960 and *S. tanegashimae* (Pilsbry, 1901). *Venus* **35**: 83–86.
- Minato H. 1980.** Land shells fauna of Miyako Islands, the southern Ryukyu, Japan. *Venus* **39**: 83–99.
- Moellendorff OF. 1882.** Diagnoses specierum novarum Chinae meridionalis. *Jahrbuch der Deutschen Malakozoologischen Gesellschaft* **9**: 179–188.
- Moellendorff OF. 1884.** Materialien zur Fauna von China. *Jahrbuch der Deutschen Malakozoologischen Gesellschaft* **11**: 307–390.
- Morlet L. 1891.** Diagnoses Molluscorum novorum, in Indo-Chinâ collectorum. *Journal de Conchyliologie, Paris* **39**: 25–28.
- Müller OF. 1774.** *Vermium Terrestrium et Fluviatilium, seu Animalium Infusoriorum, Helminthicorum et Testaceorum, non Marinorum, Succincta Historia*. Havniae & Lipsiae: Heineck & Faber.
- Ohara K, Otani Y. 2002.** Catalogue of the Dr. Tokubei Kuroda shell collection deposited in the Nishinomiya Shell Museum. Part 1 Non-marine Gastropoda. *Bulletin of the Nishinomiya Shell Museum* **1**: 1–139.

- Palumbi SR. 1996.** What can molecular genetics contribute to marine biogeography. An urchin's tale. *Journal of Experimental Marine Biology and Ecology* **203**: 75–92.
- Pfeiffer L. 1849.** Nachträge zu L. Pfeiffer Monographia Heliceorum. *Zeitschrift für Malakozoologie* **6**: 66–79.
- Pfeiffer L. 1866 [1865].** Descriptions of thirteen new species of land-shells from Formosa, in the collection of the late Hugh Cuming, collected by Mr. Robert Swinhoe, vice-consul of that island. *Proceedings of the Zoological Society of London*, pp. 828–831.
- Pfeiffer L. 1876.** *Monographiae heliceorum viventium*, vol. 9. Lipsiae: F. A. Brockhaus.
- Pilsbry HA. 1895.** *Manual of Conchology*, 2nd series (Helicidae vol. 7), vol. 9. Philadelphia, PA: Academy of Natural Sciences of Philadelphia.
- Pilsbry HA. 1905.** Notes on *Moellendorffia* and *Stegodera*. *Nautilus* **19**: 63–67.
- Pilsbry HA, Hirase Y. 1906 [1905].** Catalogue of the land and fresh-water Mollusca of Taiwan (Formosa). *Proceedings of the Academy of Natural Sciences of Philadelphia* **57**: 720–752.
- Pilsbry HA, Hirase Y. 1909 [1908].** New land mollusca of the Japanese empire. *Proceedings of the Academy of Natural Sciences of Philadelphia* **60**: 586–599.
- Posada D, Crandall KA. 1998.** Modeltest: testing the model of DNA substitution. *Bioinformatics* **14**: 817–818.
- Richardson L. 1985.** Camaenidae: catalog of species. *Tryonia* **12**: 1–479.
- Rolle H. 1911.** Diagnosen neuer Arten. *Nachrichtsblatt der Deutschen Malakozoologischen Gesellschaft* **43**: 30–32.
- Saitou N, Nei M. 1987.** The neighbor-joining method: a new method for reconstructing phylogenetic trees. *Molecular Biology and Evolution* **4**: 406–425.
- Schmacker B, Boettger O. 1891.** Neue Materialien zur Charakteristik und geographischen Verbreitung chinesischer und japanischer Binnenmollusken II. *Nachrichtsblatt der Deutschen Malakozoologischen Gesellschaft* **23**: 145–194.
- Sinagawa K. 1979.** Anatomy of *Camaena cicatricosa*, *Pancala bacca* and *Pancala batanica pancala*. *Kainakama* **13**: 4–7.
- Sinagawa K. 1980.** On the reproduction system of two camaenids (Pulmonata: Camaenidae) from Taiwan. *Kainakama* **13**: 6–8.
- Solem A. 1984.** Camaenid land snails from western and central Australia (Mollusca: Pulmonata: Camaenidae). IV. Taxa from the Kimberley, *Westraltrachia* Iredale, 1933 and related genera. *Records of the Western Australian Museum Supplement* **17**: 427–705.
- Swinhoe R. 1864.** Notes on the Island of Formosa. *Journal of the Royal Geographical Society of London* **34**: 6–18.
- Swofford DL. 2003.** PAUP\*. *Phylogenetic analysis using parsimony (\*and other methods)*, version 4. Sunderland, MA: Sinauer Associates.
- Teng LS. 1990.** Geotectonic evolution of late Cenozoic arc-continent collision in Taiwan. *Tectonophysics* **183**: 57–76.
- Thompson JD, Gibson TJ, Plewniak F, Jeanmougin F, Higgins DG. 1997.** The ClustalX windows interface: flexible strategies for multiple sequence alignment aided by quality analysis tools. *Nucleic Acids Research* **25**: 4876–4882.
- Truett GE, Heeger P, Mynatt RL, Truett AA, Walker JA, Warman JL. 2000.** Preparation of PCR Quality Mouse Genomic DNA with Hot Sodium Hydroxide and Tris (HotSHOT). *BioTechniques* **29**: 52–54.
- Tryon GW. 1887.** *Manual of conchology*, 2nd series, (Helicidae vol. 1), vol. 3. Philadelphia, PA: Academy of Natural Sciences of Philadelphia.
- Verdcourt B. 2000.** The penial armature of three species of east African Streptaxidae (Gastropoda, Stylommatophora). *Folia Malacologica* **8**: 215–221.
- Wade CM, Mordan P. 2000.** Evolution within the gastropod molluscs: using the ribosomal RNA gene cluster as an indicator of relationships. *Journal of Molluscan Studies* **66**: 565–570.
- Wu SP, Lin YS, Hwang CC. 2007.** A new *Satsuma* species (Pulmonata: Camaenidae) endemic to Taiwan. *Zootaxa* **1608**: 59–68.
- Wu SP, Wu WL. 1998.** The distribution of camaenidae in Taiwan. *Bulletin of Malacology* **22**: 43–48.