

## Three new species of *Satsuma* Adams, 1868 (Gastropoda, Camaenidae) from Taiwan

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*Satsuma hsuehshan* n. sp.; *Satsuma nivnu* n. sp.; *Satsuma sunlinksea* n. sp.

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# Three new species of *Satsuma* Adams, 1868 (Gastropoda, Camaenidae) from Taiwan

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## ABSTRACT

Three new species of the genus *Satsuma* Adams, 1868, *Satsuma hsuehsban* n. sp., *Satsuma nivnu* n. sp., and *Satsuma sunlinksea* n. sp. from western Taiwan are described. *Satsuma hsuehsban* n. sp. is characterized by a dextral shell, curved basal lip, and the presence of a penial pouch. *Satsuma nivnu* n. sp. is characterized by a dextral shell, whorl not descending behind aperture, curved basal lip, and the presence of a penial pouch. *Satsuma sunlinksea* n. sp. is characterized by a dextral shell, straight and slightly downward basal lip, and the absence of a penial pouch. The penial pouch is a newly discovered structure in the reproductive system of *Satsuma*. The three new species were collected in a mountainous, middle altitude mixed forest.

## RÉSUMÉ

*Trois nouvelles espèces de Satsuma Adams, 1868 (Pulmonata, Camaenidae) de Taïwan.*

Trois nouvelles espèces du genre *Satsuma* Adams, 1868, *Satsuma hsuehsban* n. sp., *Satsuma nivnu* n. sp., et *Satsuma sunlinksea* n. sp. sont décrites de l'ouest de Taïwan. *Satsuma hsuehsban* n. sp. se caractérise par une coquille dextre, une lèvre basale incurvée et la présence d'une poche péniale. *Satsuma nivnu* n. sp. se caractérise par une coquille dextre, un verticille ne descendant pas derrière l'ouverture, une lèvre basale incurvée et la présence d'une poche péniale. *Satsuma sunlinksea* n. sp. se caractérise par une coquille dextre, une lèvre basale droite et légèrement descendante, l'absence de poche péniale. La poche péniale est une structure nouvellement découverte sur le système reproducteur de *Satsuma*. Les trois nouvelles espèces ont été récoltées dans une forêt mixte montagneuse de moyenne altitude.

## KEY WORDS

Gastropoda,  
Pulmonata,  
Camaenidae,  
Taiwan,  
anatomy,  
new species.

## MOTS CLÉS

Gastropoda,  
Pulmonata,  
Camaenidae,  
Taïwan,  
anatomie,  
espèce nouvelle.

## INTRODUCTION

More than 100 species of the land snail genus *Satsuma* Adams, 1868 have been described from East Asia, including Taiwan, Japan, southern China, and the northern islands of the Philippines (Adams & Reeve 1850; Minato 1988; Schileyko 2004; Hsieh *et al.* 2013; Wang *et al.* 2014). *Satsuma* is characterized by a conical to global, yellow to dark brown shell, the presence of a penial caecum and an epiphallic flagellum in the male genitalia, and the absence of a dart sac, accessory sac and mucous glands in the female genitalia (Kuroda & Habe 1949; Schileyko 2004). The shape, size, colour, chirality and banding pattern of shells are prominently varied (Schileyko 2004; Hosono *et al.* 2010). Three ecological habits were observed for snails of the genus – strict terrestrial, arboreal and semi-arboreal (Wu *et al.* 2008). Owing to the extensive shell variability and ecological habits, three nominal genera, *Coniglobus* Pilsbry, 1906, *Luchuhadra* Kuroda & Habe, 1949 and *Pancala* Kuroda & Habe, 1949, have been treated as synonyms or subgeneric status under *Satsuma*, or as independent genera by different authors (Kuroda 1941; Minato 1988; Schileyko 2004; Hsieh *et al.* 2013). The *S. albida* (Adams, 1870) group from Taiwan and *S. largillierti* (Pfeiffer, 1849) group from the Ryukyu Islands are well-known groups of complete arboreal snails (Kameda *et al.* 2007; Wu *et al.* 2008; Hosono *et al.* 2010). The arboreal species of *Satsuma* usually have high conical and whitish shells (Kameda *et al.* 2007; Wu *et al.* 2008) and has been classified as a subgenus *Luchuhadra* (Kuroda & Habe 1949). *Coniglobus* was initially described as a subgenus of *Eulota* Hartmann, 1841 containing species found in Taiwan (Pilsbry & Hirase 1905-1906). It then included several *Satsuma* species with conical shells in Taiwan and the Ryukyu Islands, such as *S. mercatoria* (Pfeiffer, 1845) and *S. yaeyamensis* (Pilsbry, 1894) (Kuroda & Habe 1949). *Pancala* was named as a subgenus of *Camaena* Albers, 1850 for snails found in southern Taiwan. These snails are characterized by their yellowish shells and the absence of a penial caecum. The penial caecum is also called the penial appendix in some East Asian studies (e.g. Azuma 1995; Chang 1997). These generic names have been considered as synonyms of *Satsuma* based on morphological evidence (Schileyko 2004; Hsieh *et al.* 2013). The monophylies of these subgenera are not supported by molecular evidence (Hosono *et al.* 2010). Four Chinese species, previously classified as *Ganesella* Blanford, 1863 or *Bradybaena* Beck, 1837, were members of *Satsuma* by morphological and molecular characteristics (Wang *et al.* 2014).

Knowledge regarding the shell, genital morphology and molecular phylogenetics has been accumulated about the genus (Kameda *et al.* 2007; Wu *et al.* 2008; Hosono *et al.* 2010; Hsieh *et al.* 2013; Wu & Tsai 2014, 2015, 2016; Wu & Wu 2017a, b; Hwang & Wu 2018; Hwang *et al.* 2018; Zhang *et al.* 2020). Forty-eight valid species have been described from Taiwan; all of which are endemic to Taiwan and have confined distribution ranges (Wu *et al.* 2008; Hsieh *et al.* 2013). Due to the narrow distribution of the known *Satsuma* species and the complicated topography of Taiwan, more potentially undescribed species are expected to be discovered

there (Wu *et al.* 2007, 2008). In this article, we describe three new species of *Satsuma* from Taiwan. Species of morphological similarity are also compared based on shell morphology and genital anatomy.

## MATERIAL AND METHODS

Samples of the new species and additional species for comparisons were collected in Taiwan (Fig. 1; Table 1). Specimens were prepared using the Niku-nuku method (Fukuda *et al.* 2008). A portion of live adults were drowned in water overnight, then boiled briefly in hot water at 95°C. The soft bodies of the snails were fixed and preserved in 95% ethanol. Empty shells were cleaned, oven-dried and stored at room temperature. Reproductive systems were dissected under a stereomicroscope (Leica MZ7.5). Methods described by Kerney & Cameron (1979) were used to measure shell characteristics and to count the number of whorls, precise to 0.1 mm and 0.25 whorls, respectively. Measurements of genitalia were obtained from digital images using ImageJ 1.48k (Schneider *et al.* 2012). We followed Gómez's (2001) terminology in describing the reproductive system. All coordinate information is provided in the WGS84 EPSG:4326 coordinate system. A distribution map was created using the software Quantum GIS 3.24 (QGIS.org 2021) with topographic databases ASTER GDEM V2 released by NASA and METI (downloadable from <https://asterweb.jpl.nasa.gov>) and GADM 2.8 released by Global Administrative Areas (downloadable from <http://gadm.org/>). The type specimens are deposited in the National Museum of Natural Science, Taichung, Taiwan, Muséum national d'Histoire naturelle, Paris, France, and Biological Museum, University of Taipei, Taipei, Taiwan. Other voucher specimens are kept in the first author's laboratory, eventually to be deposited in a public museum.

## ABBREVIATIONS

### *Institutions*

MNHN	Muséum national d'Histoire naturelle, Paris;
NC	Nishinomiya Shell Museum, Nishinomiya (NCH for holotype collection, NCP for paratype collection);
NMNS	National Museum of Natural Science, Taichung;
SMF	Naturmuseum Senckenberg, Frankfurt am Main;
UTM	Biological Museum, Department of Earth and Life Sciences, University of Taipei, Taipei.

### *Private collection*

Coll. HCC	the first author: Chung-Chi Hwang's laboratory, Kaohsiung.
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### *Shell*

AH	aperture height;
AW	aperture width;
SH	shell height;
SW	shell width;
W#	number of whorls

### *Genitalia*

ag	albumen gland;
at	atrium;

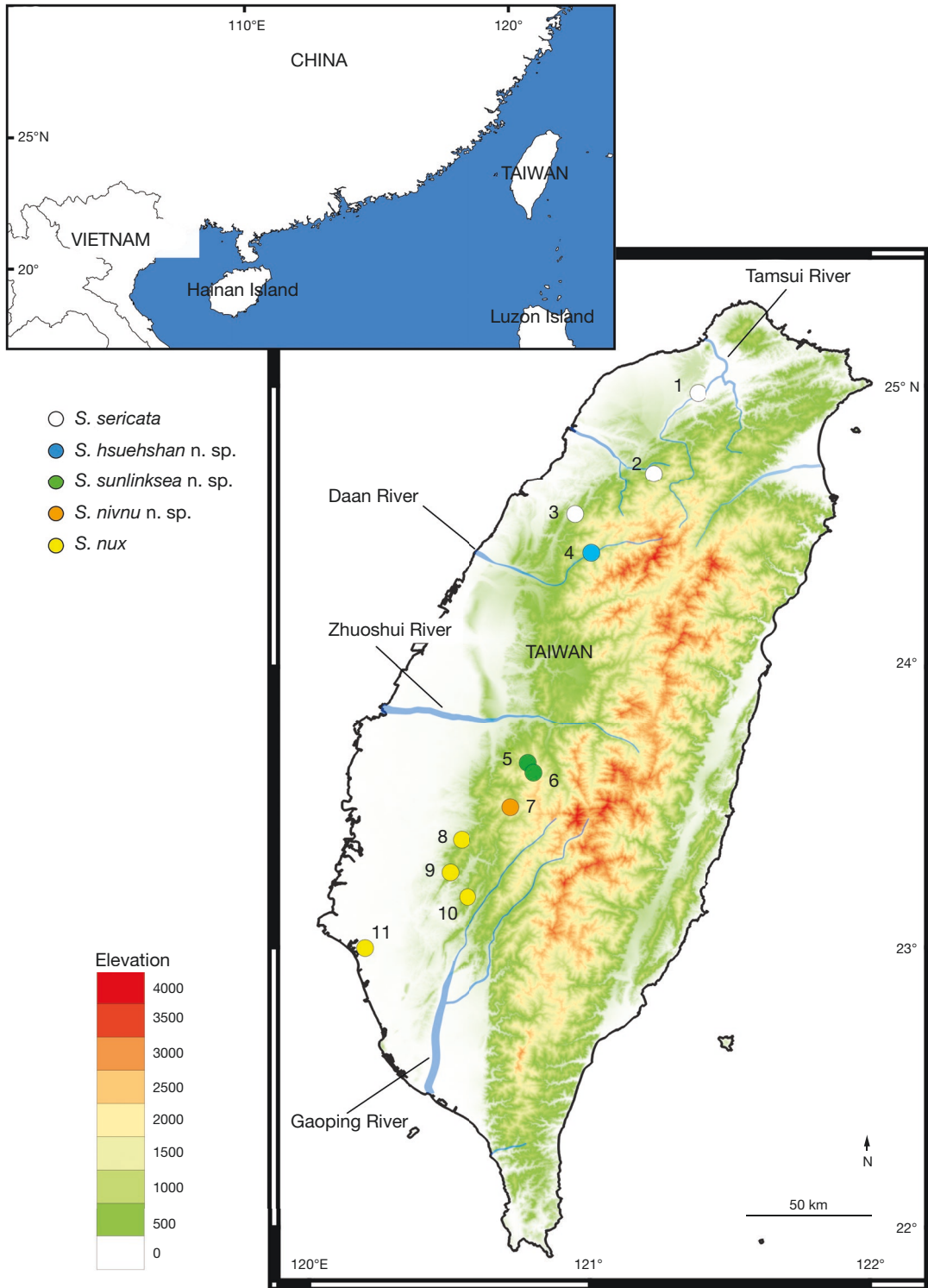


FIG. 1. — Sampling scheme for the snails of genus *Satsuma* Adams, 1868 used in this study. The numbered sampling sites are detailed in Table 1.

bc bursa copulatrix;  
 ep epiphallus;  
 fl flagellum;  
 fod free oviduct;  
 p penis;  
 pc penial caecum;  
 pd pedunculus of bursa copulatrix;

pp penial pouch;  
 rm retractor muscle;  
 sod spermooviduct;  
 v verge;  
 va vagina;  
 vd vas deferens.

TABLE 1. — List of *Satsuma* Adams, 1868 new species and examined samples used in this study. **Loc. #**, the numbered code for location corresponding to the map in Figure 1.

Species	Loc. #	Location	Coordinates	Alt. (m)	Voucher
<i>Satsuma sericata</i>	1	Sansykyaku, Taihoku = Shanjia, New Taipei City (type locality)	c. 24°58'26"N, 121°23'13"E	c. 100	holotype NCH-256, paratype NCP-245
	2	Frog Rock, Jianshih Township, Hsinchu County, Taiwan	24°41'12"N, 121°13'43"E	505	HCC-15562
	3	Sianshan trail, Shihtan Township, Miali County, Taiwan	24°32'28"N, 120°56'58"E	730	HCC-6921
<i>Satsuma hsuehshan</i> n. sp.	4	Hsuehjian, Simashian forest road, Taian Township, Miaoli County, Taiwan (type locality)	24°24'17"N, 121°0'25"E	1740	holotype NMNS-8676-001, paratype NMNS-8676-002-004, MNHN-IM-2022-13916, UTM-2023001
<i>Satsuma sunlinksea</i> n. sp.	5	Longfongsia, Lugu Township, Nantou County, Taiwan (type locality)	23°39'17"N, 120°46'53"E	1700	holotype NMNS-8676-010, paratype NMNS-8676-011-014, MNHN-IM-2022-13917, UTM-2023003
	6	Songlongyen, Sunlinksea, Lugu Township, Nantou County, Taiwan	23°37'12"N, 120°48'6"E	1720	paratype NMNS-8676-015
<i>Satsuma nivnu</i> n. sp.	7	Dadongshan forest trail, Shitz Village, Alishan Township, Jiayi County, Taiwan (type locality)	23°29'52"N, 120°43'11"E	1970	holotype NMNS-8676-005, paratype NMNS-8676-006-009, MNHN-IM-2022-13918, UTM-2023002
<i>Satsuma nux</i>	8	Jhongpu Township, Jiayi County, Taiwan	c. 23°22'55"N, 120°32'38"E	c. 300	HCC-1085
	9	Sianggong Temple, Dongshan District,, Tainan City, Taiwan	23°15'55"N, 120°30'12"E	800	HCC-14121a
	10	Mt. Jhuzhijian, Meiling, Nansi District, Tainan City, Taiwan	23°10'39"N, 120°33'58"E	1000	HCC-1925
	11	Taiwanfu, Formosa = Tainan City (type locality)	c. 22°59'49"N, 120°12'0"E	c. 10	lectotype SMF 8826

## SYSTEMATICS

### Family CAMAENIDAE Pilsbry, 1895

#### Genus *Satsuma* Adams, 1868

TYPE SPECIES. — *Helix japonica* Pfeiffer, 1847, by subsequent designation (Kuroda & Habe 1949: 54)

#### *Satsuma hsuehshan* n. sp.

雪山栗蝸

(Fig. 2)

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TYPE MATERIAL. — **Holotype.** Taiwan • Miaoli County, Taian Township, Simashian forest road, Hsuehjian; 24°24'17"N, 121°0'25"E; alt. 1740 m a.s.l.; 30.VIII.2020; SP Wu leg.; NMNS-8676-001; SH 23.7 mm, SW 27.0 mm.

**Paratypes.** Taiwan • 3 specimens; same data as holotype; NMNS-8676-002 • 5 specimens; from type locality; 27.VII.2021; SP Wu leg.; NMNS-8676-003-004, MNHN-IM-2022-13916 • 1 specimen; from type locality; 30.VIII.2022; SP Wu leg.; UTM-2023001 from type locality; 30.VIII.2022; SP Wu leg.

ETYMOLOGY. — The species is named for its distribution area, the Hsuehshan Range, treated as a simple noun in apposition.

TYPE LOCALITY. — Taiwan, Miaoli County, Taian Township, Simashian forest road, Hsuehjian; 24°24'17"N, 121°0'25"E; alt. 1740 m a.s.l.; middle altitude mixed forest.

DISTRIBUTION. — This species was found in type locality only.

DIAGNOSIS. — Shell dextral, conical, medium sized (SW < 35 mm); spiral striation absent above periphery; upper lip weakly sinuous or smoothly curved; columellar lip oblique, almost straight, joining curved basal lip in an angle; umbilicus partly open; penis with a muscular and bulging penial pouch; penial caecum conical and blunt; epiphallus swollen basally.

#### DESCRIPTION

Shell dextral, with conical spire, brown to dark brown with thin, red-brown peripheral band and umbilicus spot; thin and yellowish area visible immediately below suture and peripheral band. Apex acute. Whorls regularly increasing, slightly convex, mostly not descending behind aperture. Periphery almost round, very weakly angulated. Base of shell convex. Upper surface covered with small, dense, shortly elongate granules on apical 3.5 whorls, becoming loose, coarse, oblique axial ridges that are weak on base (Fig. 7A); spiral striation dense and weak on base of shell, absent above periphery. Aperture roundly lunate, pale brown inside. Peristome expanded; upper lip weakly sinuous or smoothly curved; columellar lip oblique, almost straight, joining curved basal lip in an angle in apertural view. Parietal callus absent to very thin. Umbilicus partly open, c. 1/3 covered by reflected columellar lip, with 2-3 clear creases.



FIG. 2. — Shell and reproductive system of *Satsuma hsehshan* n. sp.: **A**, shell of holotype (NMNS-8676-001); **B-D**, genitalia (paratype NMNS-8676-003), whole genitalia (**B**), male genitalia showing penial pouch (**C**), opened genitalia (**D**). Scale bars: 10 mm. Abbreviations: see Material and methods.

### Measurements

SH 20.3–23.7 mm, SW 24.6–27.0 mm, AH 11.6–12.9 mm, AW 14.3–16.4 mm, W# 6–6.25, protoconch 2.5 whorls, SH/SW 0.781–0.932 (n = 10).

### External morphology

Brown with irregular, small, dark brown spots and a distinct yellowish line running from head between tentacles to collar. Tentacles dark grey.

### Reproductive system

Bursa copulatrix oval to elongated oval. Pedunculus of bursa copulatrix as long as spermoviduct, 26.2–28.1 mm, slightly thickened basally, gradually slender toward bursa copulatrix. Free oviduct short, 4.5–5.2 mm. Vagina 9.7–10.1 mm in length, as thickened as penis, slender at middle, smooth externally, with 11–13 thin, dense, partly undulated internal pilasters. Atrium short, smooth to wrinkled inside. Penis elongate, 11.6–16.1 mm in length, smooth and slender externally; distal portion with a muscular, bulging penial pouch with smooth internal wall (Fig. 2C, D); slender at middle, becoming slightly thickened around verge, with 8–10 corrugated internal pilasters extending to penial caecum. Penial caecum conical, blunt, long, 2.4–3.3 mm. Verge narrow drop-shaped, extending along penial caecum with 2–4 stronger pilaster surrounding epiphallic pore. Epiphallus slender, as thick as middle penis, 6.5–8.5 mm in length, internally with 3 major and 1–2 minor pilasters along the entire length. Penis retractor muscle attached at basal 1/4 of epiphallus, becoming narrow distally. Flagellum 6.1–6.7 mm; swollen basally internally with thick swelling extending from epiphallic pilasters, opening into vas deferens at base; tapering toward tip, internally with 3–5 pilasters.

### REMARKS

This new species is similar to *S. sericata* (Kuroda, 1941) and *S. nux* (Möllendorff, 1888) in having a dextral and conical shell with similar sizes (Figs 3; 4). *Satsuma sericata*, however, has a horizontal basal lip with a weak fold (Fig. 3A), longer vagina, penis and epiphallus, shorter penial caecum than the new species, and the absence of a penial pouch (Fig. 3B, C; Ohara & Otani 2002: pl. 1, figs 14–16). *Satsuma nux* has a horizontal basal lip and latticed shell base (Fig. 4A). The genitalia of *S. nux* has been dissected in samples collected from four locations (Wu & Chang 1975). The four locations are distributed from Keelung in northernmost Taiwan to Tunghsu in southwestern Taiwan. The areas are inhabited by at least two other *Satsuma* species of similar shell shapes, based on the current understanding of Taiwanese *Satsuma* species (Hsieh *et al.* 2013). Because the location of the figured genitalia was not indicated clearly, it is inappropriate to compare directly with the description of Wu & Chang (1975). The newly dissected *S. nux* in the present study were collected from three locations (loc. # 8–10, Fig. 1; Table 1) close to its type locality, Taiwanfu (Tainan City nowadays), and have the same shell morphology as the lectotype of *S. nux*. The genitalia of *S. nux* (Fig. 4B–E) has a shorter penial caecum, a shorter

verge extending along penial caecum, a stronger protrusion on the radix of flagellum than the new species, and the absence of a penial pouch. The interior of the epiphallus of *S. nux* is smooth or has four weak pilasters between the penial caecum and retractor muscle, becoming six strong pilasters when approaching the insertion of the vas deferens. In contrast, the new species has three major pilasters along the entire length of the epiphallus. Sexually mature adults of this new species were collected in July 2021. Four individuals collected in August 2020 have expanded perisomes, but their genitalia are not fully matured.

### *Satsuma nivnu* n. sp.

妮芙努栗蝸

(Fig. 5)

urn:lsid:zoobank.org:act:EFF743A3-16B4-4648-BC40-D405E43840B5

**TYPE MATERIAL.** — **Holotype.** Taiwan • Jiayi County, Alishan Township, Shitz Village, Dadongshan forest trail; 23°29'52"N, 120°43'11"E; alt. 1970 m a.s.l.; 14.VIII.2020; S. P. Wu leg.; NMNS-8676-005; SH 31.8 mm, SW 39.4 mm.

**Paratypes.** Taiwan • 6 specimens; same data as holotype; NMNS-8676-006 • 2 specimens; from type locality; VIII.2014; C. F. Lin leg.; NMNS-8676-007, MNHN-IM-2022-13918 • 2 specimens; from type locality; 9.VIII.2022; S. P. Wu leg.; NMNS-8676-008-009 • 1 specimen; from type locality; 26.VIII.2020; S. P. Wu leg.; UTM-2023002 • 1 specimen; from type locality; 26.VIII.2020; S. P. Wu leg.

**ETYMOLOGY.** — Nivnu, treated as a simple noun in apposition, is the goddess of creation and agriculture in the mythology of the indigenous Tsou race.

**TYPE LOCALITY.** — Taiwan, Jiayi County, Alishan Township, Shitz Village, Dadongshan forest trail; 23°29'52"N, 120°43'11"E; alt. 1970 m a.s.l.

**DISTRIBUTION.** — This species was found in type locality, Alishan National Forest Recreation Area, and Tefuya Ancient Trail.

**DIAGNOSIS.** — Shell dextral, conical, medium to large sized (SW > 35 mm); spiral striation weakly malleated above and below periphery; whorl not descending behind aperture; upper lip smoothly curved; columellar lip oblique, almost straight; basal lip curved; umbilicus partly open; penis with a muscular and bulging penial pouch; penial caecum conical and short; epiphallus swollen basally.

### DESCRIPTION

Shell dextral, with conical spire, brown to dark brown with red-brown peripheral band and umbilicus spot; thin and pale brown area visible immediately below suture and peripheral band. Apex acute. Whorls regularly increasing, slightly convex, not descending behind aperture. Periphery almost round, very weakly angulated. Base of shell convex. Surface covered with small, dense, elongate, axial granules on apical 3.5 whorls, becoming loose, coarse, continuous, oblique axial ridges that are weak on base (Fig. 7B); spiral striation wavy and loose on base of shell, becoming weakly malleated above and below periphery. Aperture roundly lunate, light purplish inside. Peristome expanded; outer lip smoothly curved; columellar lip oblique, almost straight, joining curved basal lip in an angle.



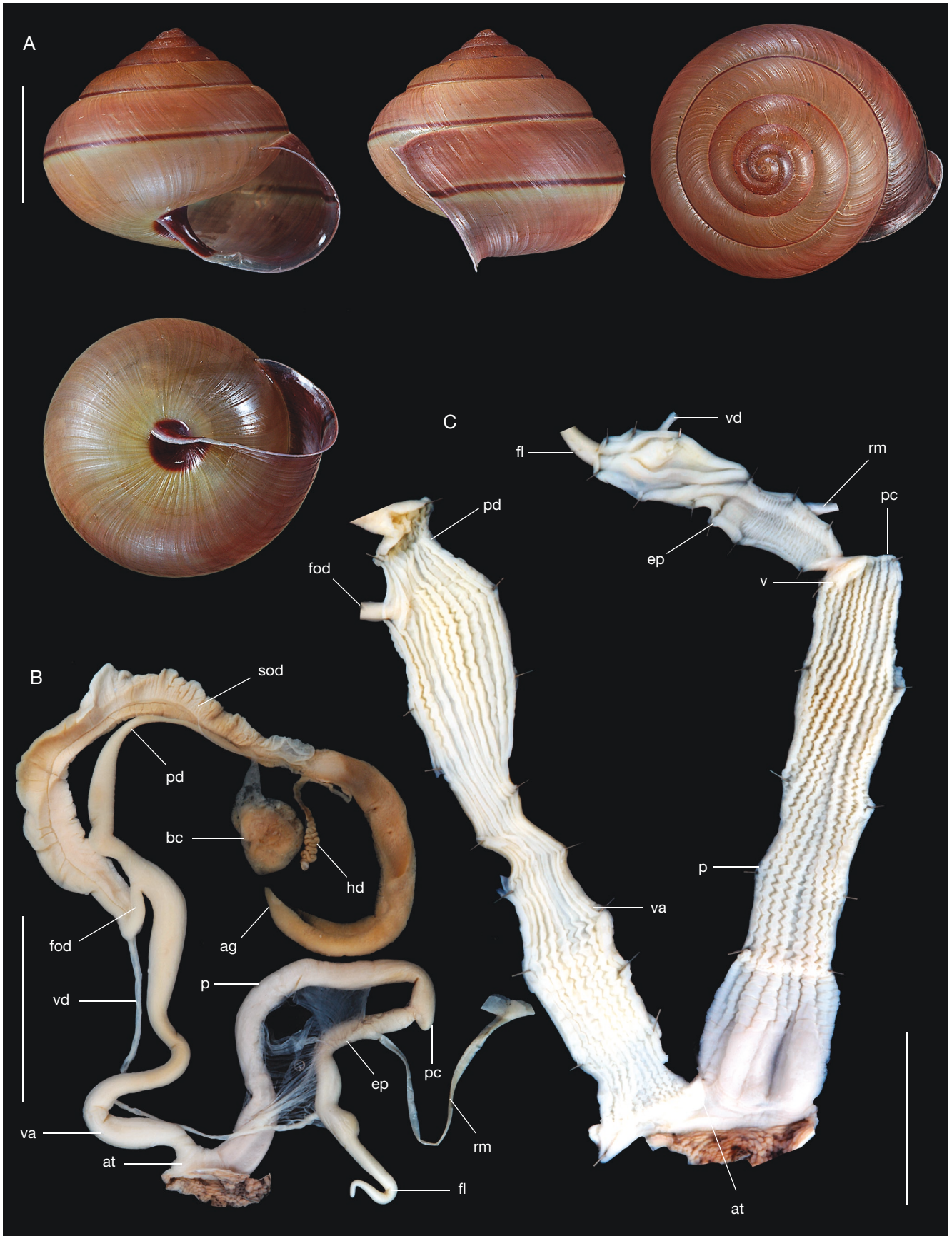


FIG. 3. — Shell and reproductive system of *Satsuma sericata* (Kuroda, 1941): **A**, shell (HCC-15562a); **B**, whole genitalia (HCC-6921); **C**, opened genitalia (HCC-6921). Scale bars: 10 mm. Abbreviations: see Material and methods.

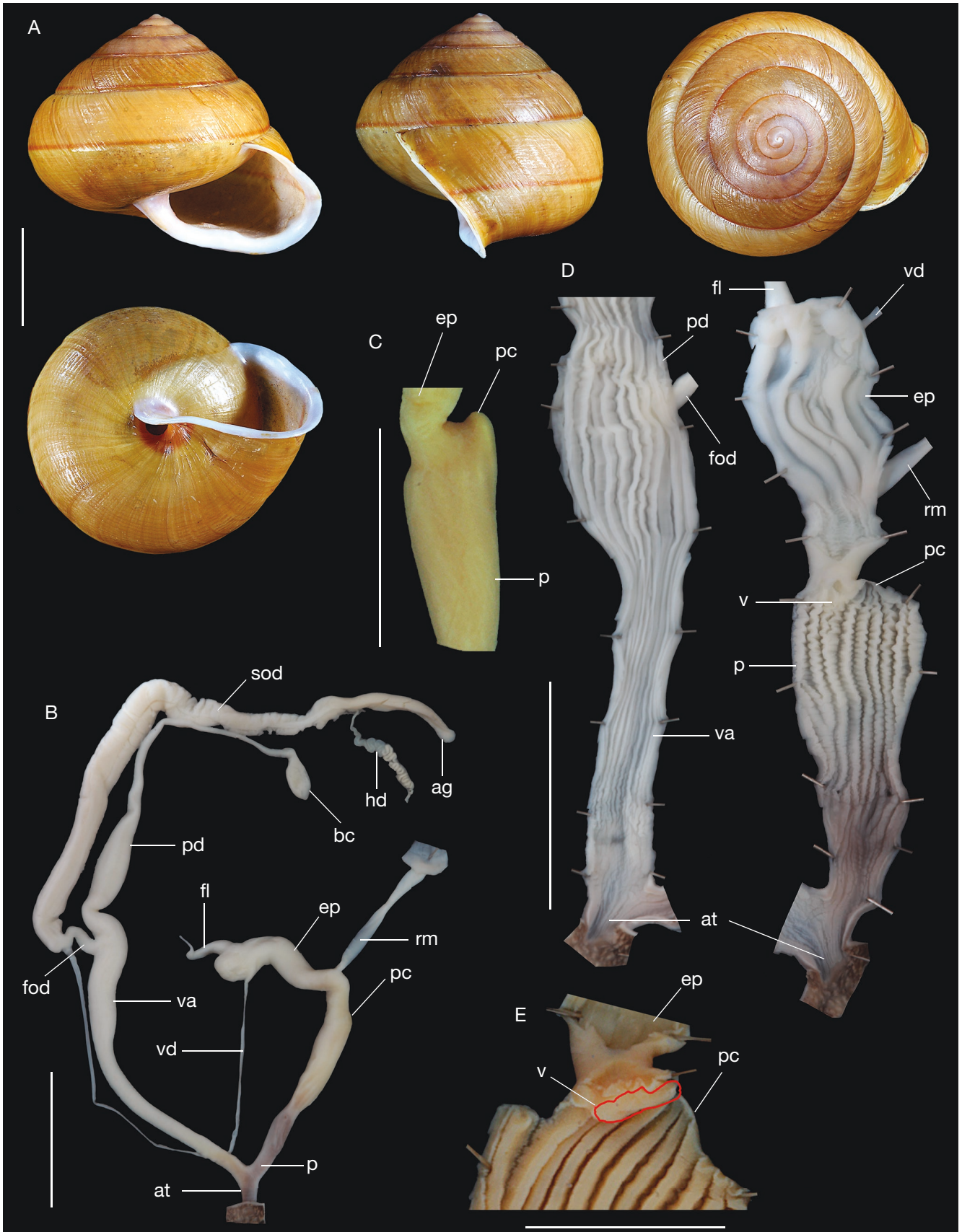


FIG. 4. — Shell and reproductive system of *Satsuma nux* (Möllendorff, 1888): **A**, shell (HCC-1925); **B**, whole genitalia (HCC-14121a); **C**, male genitalia showing penial caecum (HCC-1925); **D**, opened genitalia (HCC-14121a); **E**, opened male genitalia showing verge (**red outlined**, HCC-1925). Scale bars: 10 mm, unless otherwise noted. Abbreviations: see Material and methods.



FIG. 5. — Shell and reproductive system of *Satsuma nivnu* n. sp.: **A**, shell of holotype (NMNS-8676-005); **B**, **C**, genitalia (paratype NMNS-8676-006): whole genitalia (**B**), opened genitalia (**C**); **D**, living animal. Scale bars: 10 mm. Abbreviations: see Material and methods.

Parietal callus absent. Umbilicus partly open, *c.* 1/5 covered by reflected columellar lip, with 2-3 clear creases.

#### Measurements

SH 28.9-32.9 mm, SW 36.3-42.6 mm, AH 17.5-20.3 mm, AW 23.0-26.8 mm, W# 6.25-6.75, protoconch 2.5 whorls, SH/SW 0.726-0.822 (n = 12).

#### External morphology (Fig. 5D)

Brown with irregular, small, dark brown spots and a distinct yellowish line running from head between tentacles to collar. Tentacles dark grey.

#### Reproductive system

Bursa copulatrix oval. Pedunculus of bursa copulatrix as long as spermoviduct, 33.7-43.5 mm, thickened basally, gradually slender toward bursa copulatrix. Free oviduct short, 9.7-11 mm. Vagina slender, 22.1-25 mm in length, as thickened as penis, smooth externally, with 13-15 thin internal pilasters. Atrium short, coarsely wrinkled inside. Penis elongate, 21.6-28.7 mm in length; slender shortly near atrium with smooth interior, becoming bulging penial pouch (Fig. 5B) with 6-11 smooth and muscular internal pilasters; apparently thickened near epiphallus, twice the thickness of distal portion, furrowed and striped externally corresponding to 16-18 strong, straight, corrugated pilasters internally. Penial caecum conical, short, 2.1-2.7 mm. Verge extending along penial caecum, fusiform, with smooth surface. Epiphallus slender, 8.3-13.9 mm in length, internally with 2 major and 2-3 minor pilasters. Penis retractor muscle attached at basal 1/10-1/5 of epiphallus. Flagellum 6.7-7.8 mm; swollen basally, internally with thick swelling extending from epiphallallic pilasters, opening into vas deferens at base; tapering toward tip, internally with 3-5 pilasters.

#### REMARKS

The new species is similar to *S. arisana* (Kuroda, 1941), *S. tani* (Kuroda, 1941), and *S. longkiauensis* Wu, Lin & Hwang, 2007 in Taiwan, *S. myomphala* (Martens, 1865) in Japan, and *S. mercatoria* in Okinawa Island in having a large shell that is wider than 40 mm. *Satsuma arisana*, *S. myomphala*, and *S. tani* have the umbilicus completely covered by a reflected columellar lip. The former two species have been dissected for their genitalia (Azuma 1995; Chang 1997) which lack a penial pouch near the atrium and a basally swollen flagellum. *Satsuma longkiauensis* has a lower shell (SH/SW = 0.718 vs 0.726-0.822 in *S. nivnu* n. sp.), lighter shell colour, a more covered umbilicus, an unapparent penial caecum, and a short, truncated oval penial verge that is not extended along penial caecum (Wu *et al.* 2007). *Satsuma mercatoria* has a lower shell, lighter shell colour, descending behind aperture, weaker spiral striations on the base of the shell, and the absence of a penial pouch (Azuma 1995). The new species is similar to *S. hsuehsan* n. sp. in having conical spire and a penial pouch. *Satsuma hsuehsan* n. sp. has a smaller shell (maximum SW = 27.0 mm), denser spiral striation on base of shell, a stronger penial pouch than the present new species.

### *Satsuma sunlinksea* n. sp.

杉林溪栗蝸  
(Fig. 6)

urn:lsid:zoobank.org:act:C33584AB-0830-4929-84DC-27A1204300BD

*Satsuma* sp. 7 – Hosono *et al.* 2010: suppl. fig. S1, suppl. data 2.

TYPE MATERIAL. — **Holotype.** Taiwan • Nantou County, Lugu Township, Longfongzia; 23°39'17"N, 120°46'53"E; alt. 1700 m a.s.l.; 28.IX.2019; S. P. Wu leg.; NMNS-8676-010; SH 27.0 mm, SW 32.9 mm.

**Paratypes.** Taiwan • 2 specimens; from type locality; 22.VII.2022; S. P. Wu leg.; NMNS-8676-011, MNHN-IM-2022-13917 • 1 specimen; from type locality; 1.VIII.2010; S. P. Wu leg.; NMNS-8676-012 • 2 specimens; from type locality; 28.VII.2011; S. P. Wu leg.; NMNS-8676-013, UTM-2023003 • 6 specimens; from type locality; 3.IX.2019; S. P. Wu leg.; NMNS-8676-014 • 1 specimen; Nantou County, Lugu Township, Sunlinksea, Songlongyen; 23°37'12"N, 120°48'6"E; alt. 1720 m a.s.l.; 24.IV.2019; S. P. Wu leg.; NMNS-8676-015.

ETYMOLOGY. — The species is named for its type locality, where is close to the Sunlinksea Vacation Resorts; treated as a simple noun in apposition.

TYPE LOCALITY. — Taiwan, Nantou County, Lugu Township, Longfongzia; 23°39'17"N, 120°46'53"E; alt. 1700 m a.s.l.

DISTRIBUTION. — This species was found in type locality and Sunlinksea, 4 km apart.

DIAGNOSIS. — Shell dextral, conical, medium sized (SW < 35 mm); spiral striation, fine above periphery, weakly malleated immediately below periphery; periphery roundly angulated; upper lip weakly sinuated; columellar lip oblique, almost straight; basal lip straight and slightly downward; umbilicus partly open; penis with a muscular expansion distally, penial pouch absent; penial caecum conical and short; epiphallus swollen basally.

#### DESCRIPTION

Shell dextral, with conical spire, brown to dark brown with red-brown peripheral band and umbilicus spot; thin and yellowish area visible immediately below suture and peripheral band. Apex acute. Whorls regularly increasing, slightly convex, not descending behind aperture. Periphery almost round, very weakly angulated. Base of shell convex. Surface covered with small, dense, elongate, axial granules on apical four whorls, becoming loose, coarse, continuous, oblique axial ridges that are weak on base (Fig. 7C); spiral striation fine above periphery, weakly malleated immediately below periphery, clear and loose on base of shell. Aperture roundly lunate, light purplish inside. Peristome expanded; upper lip weakly sinuated; columellar lip oblique, almost straight, joining straight and slightly downward basal lip in an angle. Parietal callus thin. Umbilicus partly open, *c.* 1/2 covered by reflected columellar lip.

#### Measurements

SH 23.0-27.9 mm, SW 26.4-36.3 mm, AH 12.1-16.1 mm, AW 16.8-21.8 mm, W# 5.75-6.5, protoconch 2.5 whorls, SH/SW 0.800-0.894 (n = 13).

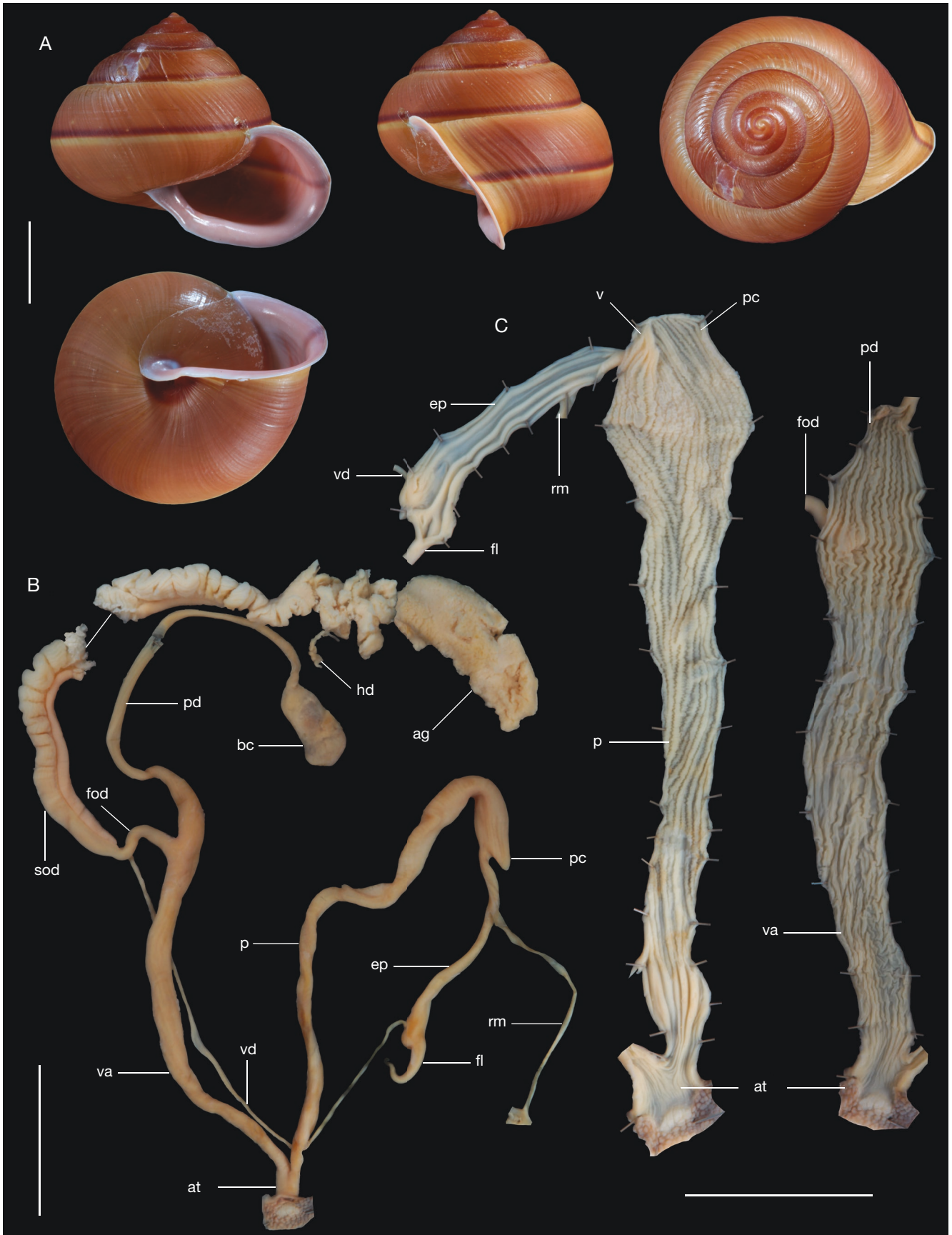


FIG. 6. — Shell and reproductive system of *Satsuma sunlinksea* n. sp.: **A**, shell of holotype (NMNS-8676-010); **B**, **C**, genitalia (paratype NMNS-8676-012): whole genitalia (**B**), opened genitalia (**C**). Scale bars 10 mm. Abbreviations: see Material and methods.

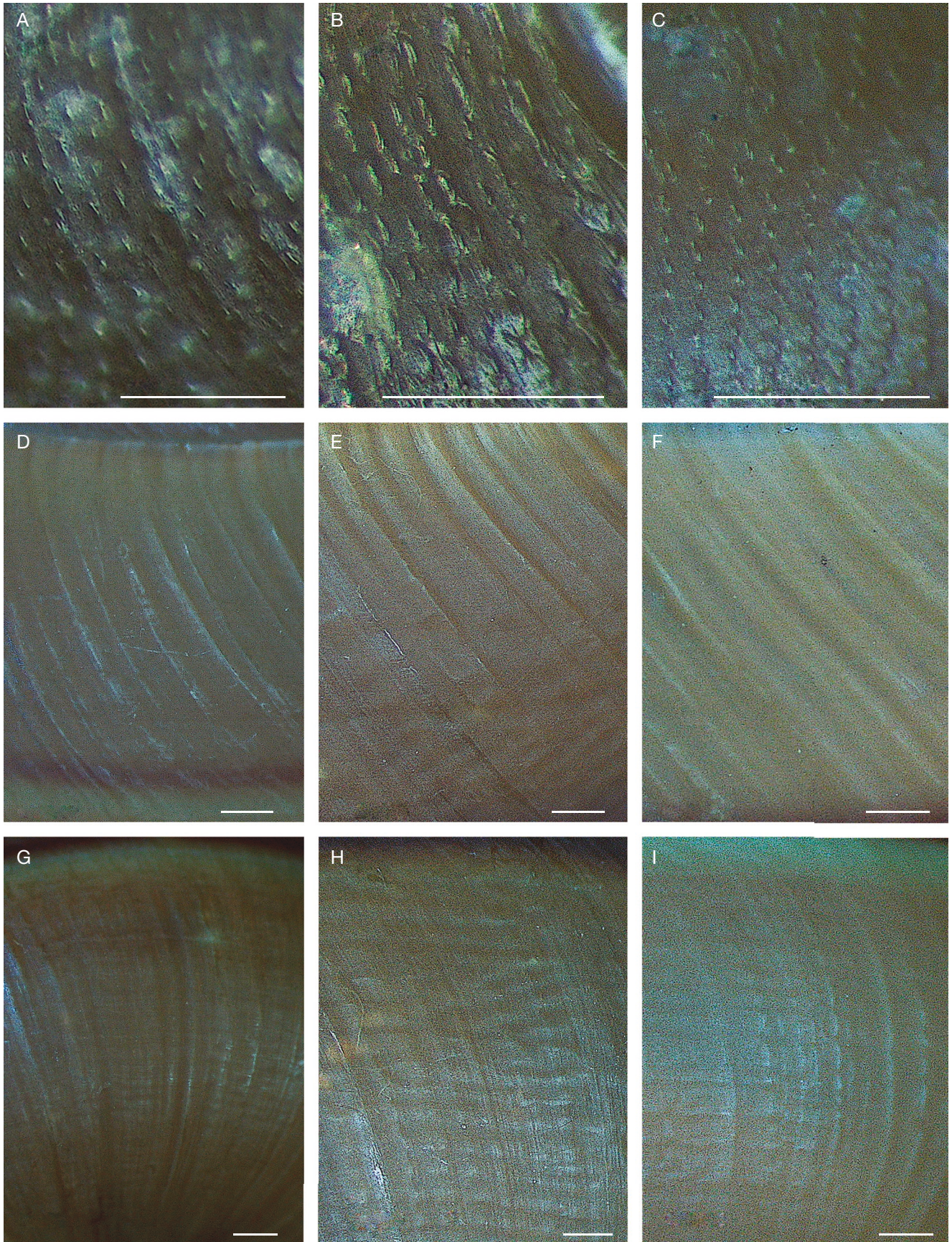


FIG. 7. — Shell sculptures on the 3rd whorl (A, B, C); surface of the last whorl (D, E, F); shell base (G, H, I): A, D, G, *Satsuma hsuehshan* n. sp.; B, E, H, *Satsuma nivnu* n. sp.; C, F, I, *Satsuma sunlinksea* n. sp. Scale bars: A-C, 0.5 mm; D-I, 1 mm.

*External morphology*

Brown with irregular, small, dark brown spots and a distinct yellowish line running from head between tentacles to collar. Tentacles dark grey.

*Reproductive system*

Bursa copulatrix elongated oval. Pedunculus of bursa copulatrix as long as spermoviduct, 30.7-32.4 mm, thickened and expanded basally, gradually slender toward bursa copulatrix. Free oviduct short, 3.5-5.3 mm. Vagina 24.9-29.1 mm, thick, becoming slender towards atrium, smooth externally, with 9-11 thin internal pilasters. Atrium short, coarsely wrinkled inside. Penis elongated, 35.4-41.7 mm in length, 1.4 times as long as vagina; slender basally, continued with an expanded portion having 6-8 smooth and muscular internal pilasters, penial pouch absent; thickened near epiphallus, twice the thickness of basal portion, smooth externally, with strong, corrugated longitudinal pilasters internally, numbered 7 at distal portion, gradually becoming 23 around penial verge. Penial caecum conical, short, 1.7-2.4 mm. Verge low conical, elongated, formed by six pilasters, extending along penial caecum. Epiphallus slender, 11.3-14.0 mm in length, internally with 3 major and 2 minor pilasters along the entire length. Penis retractor muscle attached at basal  $\frac{1}{3}$ - $\frac{1}{5}$  of epiphallus. Flagellum 7.1-7.5 mm; swollen basally, internally with thick

swelling extending from epiphallic pilasters, opening into vas deferense at base; tapering toward tip, internally with 3-4 pilasters.

## REMARKS

*Satsuma sunlinksea* n. sp. is similar to *S. nivnu* n. sp. and *S. nux* (Fig. 4A) in the shape of the shell. *Satsuma nivnu* n. sp. differs from *S. sunlinksea* n. sp. in having a larger shell, greater number of whorls, smoothly curved outer and basal lips, malleated upper surface above periphery, distinct penial pouch, and shorter penis relative to shell height. *Satsuma nux* differs from the new species in having a malleated surface above the periphery, latticed shell base, less covered umbilicus ( $\frac{1}{3}$ ), a horizontal basal lip, and smaller shell sizes (23.6 × 29.0 mm, lectotype SMF 8826, photographed in Zilch 1966, plate 5, fig. 24). The genitalia of *S. nux* (Fig. 4B-E) shows a shorter penial caecum, fewer penial pilasters (7-11), more epiphallic pilasters (4-6), and a stronger protrusion on the radix of the flagellum than *S. sunlinksea* n. sp. The gene sequences of these species have been examined for the evolution of chirality (Hoso *et al.* 2010: supplementary fig. S1, *Satsuma* sp. 7). The phylogenetic tree shows its sister species is an undescribed species (Hoso *et al.* 2010: supplementary fig. S1, *Satsuma* sp. 3) collected from Tengchih, a mountainous area in Kaohsiung City, rather than *S. nux*.

KEY TO THE DEXTRAL SPECIES OF *SATSUMA* ADAMS, 1868 IN TAIWAN

- 1 Shell high conic; shell height > shell width ..... 2
- Shell depressed conic; shell height < shell width ..... 3
- 2 Shell white or yellowish golden; with/without polymorphic bands .....  
..... *S. albida* species complex (see Wu *et al.* 2008)
- Shell brown; with a peripheral band ..... *S. sphaeroconus* (Pfeiffer, 1866)
- 3 Shell colour yellow ..... *S. bacca* (Pfeiffer, 1866)
- Shell colour light brown to dark brown ..... 4
- 4 Umbilicus totally covered by reflexed columellar lip ..... 5
- Umbilicus partly open to completely open ..... 6
- 5 Shell large-sized, shell width > 50 mm ..... *S. arisana* (Kuroda, 1941)
- Shell medium-sized, shell width < 45 mm ..... *S. tani* (Kuroda, 1941)
- 6 Shell width > 35 mm ..... 7
- Shell width < 35 mm ..... 10
- 7 Upper lip clearly sinuous; fold on basal lip present ..... *S. bairdi* (H. Adams, 1866)
- Upper lip smoothly curved; fold on basal lip absent ..... 8
- 8 Spire lower; shell height/shell width < 0.7 ..... *S. takahashii* (Kuroda, 1941)
- Spire higher; shell height/shell width > 0.7 ..... 9
- 9 Umbilicus completely open; penial caecum weak ..... *S. longkiauensis* Wu, Lin & Hwang, 2007
- Umbilicus partly open; penial caecum low conical ..... *S. nivnu* n. sp.
- 10 Periphery angulate to carinate ..... 11
- Periphery round, at most roundly angulate ..... 16
- 11 Umbilicus not covered by reflexed columellar lip ..... *Satsuma mellea* (Pfeiffer, 1866)
- Umbilicus partly covered by reflexed columellar lip ..... 12

- 12 Periphery sharply carinate; surface immediately below periphery concave; basal lip flat ..... *Satsuma friesiana* (Möllendorff, 1884) + syn. *Coniglobus carinatus* Chang, 1990  
 — Periphery bluntly carinate; surface immediately below periphery convex; basal lip smoothly curved ..... 13
- 13 Periphery angulate in front; whorls flat to weakly convex ..... 14  
 — Periphery round in front; whorls convex ..... 15
- 14 Whorls flat; base convex; axial striae dense ..... *S. succincta succincta* (H. Adams, 1866)  
 — Whorls convex; base less convex; axial striae loose ..... *S. paiwanis* (Kuroda, 1941)
- 15 Spire higher; shell height/width ratio = 0.79; peristome very thick; whorls less convex ..... *S. succincta rubrotincta* (Kuroda, 1941)  
 — Spire lower; shell height/width ratio = 0.69; peristome not particularly thickened; whorls convex ..... *S. succincta amblytropis* (Pilsbry, 1901)
- 16 Umbilicus close ..... *S. takkiriensis* (Kuroda, 1941)  
 — Umbilicus partly covered ..... 17
- 17 Basal lip curved ..... *S. litus* (Chang & Tada, 2000)  
 — Basal lip flat ..... 18
- 18 Upper surface roughly and loosely ridged; outer lip sinuate ..... 19  
 — Upper surface finely and densely ridged; outer lip smoothly curved ..... 20
- 19 Basal lip horizontal, straight; surface above periphery malleated ..... *S. nux* (Möllendorff, 1888)  
 — Basal lip straightly downwrds; surface above periphery not malleated ..... *S. sunlinksea* n. sp.
- 20 Spire high, shell height/shell width > 0.8 ..... 21  
 — Spire low, shell height/shell width < 0.75 ..... 22
- 21 Upper lip smoothly curved; basal lip horizontal with a weak fold; penial pouch absent ..... *S. sericata* (Kuroda, 1941)  
 — Upper lip sinuous; basal lip oblique without a fold; penial pouch present ..... *S. hsuehshan* n. sp.
- 22 Tooth on basal lip apparent; flagellum hooked on tip, tapering ..... *S. chengi* Wu & Tsai, 2015  
 — Tooth on basal lip inapparent; flagellum spirally tapering ..... 23
- 23 Distinguished by molecular characters only; shell larger; shell colour paler; penis shorter; distributed around Chipen, southeastern Taiwan ..... *S. mii* Wu & Wu, 2017  
 — Distinguished by molecular characters only; shell smaller; shell colour darker; penis longer; distributed around Antong, eastern Taiwan ..... *S. paradoxa* Wu & Tsai, 2016

## DISCUSSION

Three new species of dextral *Satsuma* were described based on shell and genital characteristics in this study. There are 51 known *Satsuma* (sub-)species in Taiwan currently. All of them are endemic. The high biodiversity of the genus on the island may be explained by a variety of hypotheses. Allopatric speciation (Kameda *et al.* 2007), arboreal behavior (Wu *et al.* 2008), and prey-predator coevolution and chirality (Hoso *et al.* 2010) have been proposed to explain the diversification of *Satsuma*. Taiwan Island is a young landmass uplifted above seawater about 5-6 million years ago by the tectonic collision between the Eurasian plate and the Philippine Sea plate (Huang *et al.* 2006). In spite of its geologically young age, Taiwan Island has a high diversity of habitats and prolific vegetation because of its 1) great variability of topography from sea level to 3952 m a.s.l.; 2) complex climate system driven by the interaction between the warm Kuroshio current and the cold South China Sea western boundary current;

and 3) repeated connections with the Asian mainland during the Pleistocene epoch. Each of these features contributes to the diversification of land snails in this island (Chou & Tang 2016; Hwang *et al.* 2021). A paleoisland hypothesis has been applied to explain the diversification of the genus *Formosana* Boettger, 1877 (family Clausiliidae Gray, 1855) in Taiwan (Hwang *et al.* 2022). Phylogenetic analyses with molecular and morphological characters have been used to explore the diversification of a portion of Taiwanese *Satsuma* (Wu *et al.* 2008; Hoso *et al.* 2010; Wang *et al.* 2014; Wu *et al.* 2019). Phylogenetic analyses with a complete sampling scheme will elucidate the evolutionary history of the genus in East Asia.

Among the known *Satsuma* in Taiwan, *S. nux* is morphologically and geographically close to *S. sunlinksea* n. sp. The type locality of *Satsuma nux*, “Taiwanfu, Formosa” (Möllendorff 1888; Fig. 1; Table 1), is the area presently between the coast and downtown Tainan City. Molecular phylogeny based on COI sequences (Wu *et al.* 2019) indicates that *Satsuma nux* (STW group of Wu *et al.* 2019) is distributed in southwest-



ern Taiwan, including lowland, < 900 m, of Nantou County (Zhongliao, Lugu, and Xitou), Yunlin County (Huben), Chiayi County (Zhongpu), and Tainan County (Guanziling, Dongshan). Among these known locations of *S. nux*, Xitou (alt. 900 m) is geographically closest to the type locality of *S. sunlinksea* n. sp., Sunlinksea (alt. 1600 m), by 2.5 km apart. *Satsuma sunlinksea* n. sp. is apparently a species inhabiting middle elevations in central Taiwan. A similar situation is also observed in *S. hsuehshan* n. sp. and morphologically similar species *S. sericata*. *Satsuma sericata* has been recorded from Sansykyaku, Taihoku (type locality, nowadays Shanjia, New Taipei City; Fig. 1; Table 1), Tentana, Sintiku-syu (nowadays Jianshih, Hsinchu County), and Pakari, Sintiku-syu (nowadays Baguali, Miali County) (Kuroda 1941), Beipu, Hsinchu County (Wu *et al.* 2019), and Shihtan, Miali County (this study). All the locations are at lower altitude (< 800 m), whereas *S. hsuehshan* n. sp. is recorded at 1740 m. Altitudinal differences and resulting ecological factors, and geological history may play roles in the speciation of these species.

In our study, we found that the genital system of the two new species, *S. hsuehshan* n. sp. and *S. nivnu* n. sp., is presented with a penial pouch. To our knowledge, our study is the first record that described the presentation of a penial pouch in genus *Satsuma*. As dissection of the genital system has not routinely been performed in studies describing species of *Satsuma*, we cannot rule out the possibility that some other *Satsuma* species may also have a penial pouch not yet described. A thicker, muscular segment in the distal portion of the penis, which is immediately connected with the atrium or is separated from the atrium a little, has been observed in many species of *Satsuma*, such as *S. sericata* (Fig. 3B, C), *S. jinlunensis* Hwang, Okubo & Tada, 2017 and *Satsuma albida* species complex (Wu *et al.* 2008; Hwang *et al.* 2018). They never form pouches. Additionally, the penial pouch of *S. nivnu* n. sp. is weaker than that of *S. hsuehshan* n. sp., suggesting a transition from a thick and muscular segment to a penial pouch. The evolutionary significance of the distal penis and the function of the penial pouch in *Satsuma* remains questionable, and this may be clarified through more comprehensive phylogenetic analyses.

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### REFERENCES

- ADAMS A. & REEVE L. 1850. — Mollusca, Part III., in ADAMS A. (ed.), *The Zoology of the Voyage of H.M.S. Samarang; Under the Command of Captain Sir Edward Belcher, C.B., F.R.A.S., F.G.S., During the Years 1843-1846*. London, Reeve, Benham & Reeve: 1-87.
- AZUMA M. 1995. — *Colored Illustrations of the Land Snails of Japan*. Osaka, Hoikusha, xvi + 343 p.
- CHANG K.-M. 1997. — Anatomy of *Coniglobus arisanus* (Kuroda) from Taiwan (Pulmonata: Camaenidae). *Bulletin of Malacology* 21: 41-48.
- CHOU C.-H. & TANG H.-Y. 2016. — Conservation of biodiversity in Taiwan. *Botanica Orientalis: Journal of Plant Science* 10: 1-5. <https://doi.org/10.3126/botor.v10i0.21016>
- FUKUDA H., HAGA T. & TATARA Y. 2008. — Niku-nuki: a useful method for anatomical and DNA studies on shell-bearing molluscs. *Zoosymposia* 1 (2): 15-38. <https://doi.org/10.11646/zoosymposia.1.1.5>
- GÓMEZ B. J. 2001. — Structure and functioning of the reproductive system, in BAKER G. M. (ed.), *The Biology of Terrestrial Molluscs*. Oxon, UK, CABI Publishing: 307-330.
- HOSO M., KAMEDA Y., WU S.-P., ASAMI T., KATO M. & HORI M. 2010. — A speciation gene for left-right reversal in snails results in anti-predator adaptation. *Nature Communications* 1: 133. <https://doi.org/10.1038/ncomms1133>
- HSIEH B.-C., WU S.-P. & TSAI C.-L. 2013. — *Land Snails of Taiwan, 3rd ed.* Taipei, Forestry Bureau, Council of Agriculture, Executive Yuan, Taiwan, 381 p.
- HUANG C.-Y., YUAN P. B. & TSAO S.-J. 2006. — Temporal and spatial records of active arc-continent collision in Taiwan: A synthesis. *Geological Society of America Bulletin* 118 (3-4): 274-288. <https://doi.org/10.1130/B25527.1>
- HWANG C.-C. & WU S.-P. 2018. — Two new species of *Satsuma* A. Adams, 1868 from Taiwan (Pulmonata, Camaenidae). *ZooKeys* 795: 115-126. <https://doi.org/10.3897/zookeys.795.28958>
- HWANG C.-C., OKUBO K. & TADA A. 2018. — *Satsuma jinlunensis*—a new species from Taiwan (Stylommatophora: Camaenidae). *Molluscan Research* 38 (1): 50-55. [Published online: 2017] <https://doi.org/10.1080/13235818.2017.1358340>
- HWANG C.-C., ZHOU W.-C., GER M.-J., GUO Y., QIAN Z.-X., WANG Y.-C., TSAI C.-L. & WU S.-P. 2021. — Biogeography of land snail genus *Acusta* (Gastropoda: Camaenidae): Diversification on East Asian islands. *Molecular Phylogenetics and Evolution* 155: 106999. <https://doi.org/10.1016/j.ympev.2020.106999>
- HWANG C.-C., GER M.-J. & WU S.-P. 2022. — Within-island diversification in the land snail genus *Formosana* (Gastropoda, Clausiliidae) in Taiwan. *Zoologica Scripta* 51 (5): 562-588. <https://doi.org/10.1111/zsc.12557>
- 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 (2): 519-533. <https://doi.org/10.1016/j.ympev.2007.03.021>
- KERNEY M. P. & CAMERON R. A. D. 1979. — *Land Snails of Britain & North-west Europe*. London, HarperCollins, 288 p.
- 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. & HABE T. 1949. — *Helicacea*. Tokyo, Sanmeisha. v + 129 p.
- MINATO H. 1988. — *A Systematic and Bibliographic List of the Japanese Land Snails*. Shirahama, Japan, Nihon Rikusan Kairui Sou-mokuroku Kanko-kai: x + 294 p.
- MÖLLENDORFF O. F. VON 1888. — Mittheilungen aus dem Gebiete der Malakozoologie. Diagnoses specierum novarum sinensium. *Nachrichtsblatt der Deutschen Malakozoologischen Gesellschaft* 20 (3/4): 38-44.

- 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.
- PILSBRY H. A. & HIRASE Y. 1905-1906. — Catalogue of the land and fresh-water Mollusca of Taiwan (Formosa). *Proceedings of the Academy of Natural Sciences of Philadelphia* 57: 720-752. <https://www.jstor.org/stable/4063050>
- QGIS.ORG 2021. — QGIS Geographic Information System. QGIS Association. <http://www.qgis.org>
- SCHILEYKO A. A. 2004. — Treatise on recent terrestrial pulmonate molluscs, Part 12: Bradybaenidae, Monadeniidae, Xanthonychidae, Epiphragmophoridae, Helminthoglyptidae, Elonidae, Humboldtianidae, Sphincterochilidae, Cochlicellidae. *Ruthenica, supplement* 2: 1627-1763.
- SCHNEIDER C. A., RASBAND W. S. & ELICEIRI K. W. 2012. — NIH Image to Image]: 25 years of image analysis. *Nature Methods* 9 (7): 671-675.
- WANG P., XIAO Q., ZHOU W.-C. & HWANG C.-C. 2014. — Revision of three camaenid and one bradybaenid species (Gastropoda, Stylommatophora) from China based on morphological and molecular data, with description of a new bradybaenid subspecies from Inner Mongolia, China. *ZooKeys* 372: 1-16. <https://doi.org/10.3897/zookeys.372.6581>
- WU S.-P. & TSAI C.-L. 2014. — A new sinistral *Satsuma* land snail (Pulmonata: Camaenidae) endemic to Taiwan. *Bulletin of Malacology* 37: 61-72.
- WU S.-P. & TSAI C.-L. 2015. — A new endemic dextral *Satsuma* land snail (Pulmonata: Camaenidae) from Taiwan. *Bulletin of Malacology* 38: 41-48.
- WU S.-P. & TSAI C.-L. 2016. — A new dextral species land snail of genus *Satsuma* (Pulmonata: Camaenidae) endemic to Taiwan. *Bulletin of Malacology* 39: 47-58.
- WU S.-P. & WU C.-C. 2017a. — A new and endemic sinistral *Satsuma* land snail (Pulmonata: Camaenidae) from South Taiwan. *Bulletin of Malacology* 40: 27-42.
- WU S.-P. & WU C.-C. 2017b. — A new dextral land snail of genus *Satsuma* (Pulmonata: Camaenidae) endemic to Taiwan. *Bulletin of Malacology* 40: 13-26.
- WU S.-P., LIN Y.-S. & HWANG C.-C. 2007. — A new *Satsuma* species (Pulmonata: Camaenidae) endemic to Taiwan. *Zootaxa* 1608 (1): 59-68. <https://doi.org/10.11646/zootaxa.1608.1.8>
- WU S.-P., HWANG C.-C. & LIN Y.-S. 2008. — Systematic revision of the arboreal snail *Satsuma albida* species complex (Mollusca: Camaenidae) with descriptions of 14 new species from Taiwan. *Zoological Journal of the Linnean Society* 154 (3): 437-493. <https://doi.org/10.1111/j.1096-3642.2008.00415.x>
- WU S.-P., TSAI C.-L. & HWANG C.-C. 2019. — Population genetic structure of the endemic land snail *Satsuma nux* (Pulmonata: Camaenidae) from Taiwan with preliminary phylogenetic study of its akin species. *Bulletin of Malacology* 42: 43-58.
- WU W.-K. & CHANG K.-M. 1975. — Anatomy of the land snail *Ganesella* (*Coniglobus*) *nux* (Moellendorff). *Bulletin of Malacology* 2: 107-111.
- ZHANG L.-J., ZHU Y. & LYU Z.-T. 2020. — A new sinistral species of the land-snail genus *Satsuma* (Pulmonata: Camaenidae) from China. *Molluscan Research* 40 (1): 93-100. <https://doi.org/10.1080/13235818.2019.1644721>
- ZILCH A. 1966. — Die Typen und Typoide des Natur-Museums Senckenberg, 34: Mollusca, Camaenidae (4). *Archiv für Molluskenkunde* 95 (3/4): 197-223.

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