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Overlooked for a century: Taxonomic status of *Camaena saturnia* (Gould, 1846) (Eupulmonata: Camaenidae)

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Abstract. *Camaena saturnia* (Gould, 1846) was described based on specimens obtained by F. Mason, a missionary and naturalist from Tavoy [Dawei, Tanintharyi Region] in Myanmar. Since this species description, only one more shell has been reported in literature, with the most recent record being a century ago. Thus, the generic assignment of this species remains doubtful and further investigation is required. The generic placement of this long-overlooked species is herein confirmed as *Camaena* and its geographical distribution discussed. The genital and radula morphology have been re-assessed and the type specimen figured herein for the first time. The unique morphological characters are a carinate shell with a widely opened umbilicus, a penis with a length nearly equal to that of the vagina, a retractor muscle attached near the penis, a flagellum longer than the epiphallus, and entirely longitudinal penial pilasters. It appears to be endemic to the southern part of the Tenasserim Range in Myanmar and Thailand. In addition, the recently described *C. ngocthachi* has identical shell characters and is synonymised with this species.

Key words. endemic, Tenasserim, systematics, synonym, Indochina

INTRODUCTION

The family Camaenidae is one of the most dominant families of pulmonate snails with respect to species diversity and biomass (Stanisic, 1998). The group is highly diversified into taxa that present many ecological characteristics, shell shapes and sizes, and has an especially high number of taxa (e.g., Pilsbry, 1891; Solem, 1959; Richardson, 1985; Stanisic, 1998). The land snail fauna in Indochina has been studied for over a hundred years, but most species have never been subjected to systematic revision. Additionally, most of the species were described without accompanying illustrations or demonstrations of the unique characters of the species. This may have important taxonomic consequences and prevent their correct identification, as proper identification requires examination of the type specimens (Páll-Gergely et al., 2020).

One such example is the group of large helicoid shells in the genus *Camaena* Albers, 1850, of which approximately 50 recognised species have radiated mainly from southern China to Southeast Asia and part of the Indian subcontinent (Pilsbry, 1891; Solem, 1959; Richardson, 1985; Schileyko, 2003; MolluscaBase Eds., 2021). Species currently included in this genus possess a large (shell width up to 70 mm) globose to depressed helicoid shell, either dextral or sinistral, and genitalia typical of camaenids without a dart apparatus or accessory vaginal organ (Pilsbry, 1891, 1892, 1894; Gude, 1914; Thiele, 1931; Zilch, 1960; Richardson, 1985; Schileyko, 2003). Recently, several studies applying an integrative taxonomic approach to the taxa found in southern China have revealed several cryptic species. These studies also emphasised that both shell and genitalia morphologies are useful characters for discriminating between species (Ai et al., 2016; Ding et al., 2016; Wang et al., 2020).

Helix saturnia Gould, 1846, was described based on a collection from Tavoy [Dawei, Tanintharyi Region, Myanmar] made by the missionary, Francis Mason (1799–1874) (Stewart, 1982; Mabberley, 1985). The original description was brief and lacked illustrations, which later led to conflicting opinions about its classification. Martens in Albers (1860) placed this species into *Helix* (*Phania*), then Pilsbry (1891) redescribed and transferred it to *Helix* (*Camaena*), while Godwin-Austen (1898) subsequently listed it as a member of the genus *Hemiplecta* Albers, 1850. Hanley & Theobald (1870: pl. 25 fig. 3) published the first illustration based on a single shell collected from Tenasserim [southern Myanmar]. Then, Gude (1914) examined the two specimen lots (the type and ex. Theobald collection) and agreed with Pilsbry's (1891) allocation by recognising it in its currently accepted generic position. Until now, these seemed to be the only two existing specimens for this species. Since Gude's (1914) work, this nominal species has been overlooked, and no new accounts or specimens have been published; it has even been considered as 'species inquirenda' in the MolluscaBase database (MolluscaBase

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Eds., 2021). Unexpectedly, specimens with similar morphology to the species in question were recently described under another name, *Camaena ngocthachi* Huber in Thach, 2020, from southern Thailand.

During an intensive study of large-sized land snail diversity in southern Thailand, we rediscovered the specimens identified as *Helix saturnia* Gould, 1846, that have allowed this systematic revision. In the present study, we clarify the taxonomic status of *C. ngocthachi* and confirm their systematic position for the first time based on the genitalia, radula, and protoconch. These results emphasise the effectiveness of including genital morphology in studies of the systematics and phylogeny of *Camaena*, and serve as a reminder that attention should be paid to the type specimen prior to nominating species based on shell morphology alone.

MATERIAL AND METHODS

Shells and living specimens were collected. Specimens were preserved in 70% (v/v) ethanol for anatomical examination, identified following Pilsbry (1891, 1894), and compared with existing authenticated specimens. For anatomical purposes, only one living specimen was collected and dissected under a stereomicroscope. Drawings were made to be representative of the species, with the aid of a camera lucida. The shell height and shell width of the adult shells were measured. The radula and embryonic shell were examined under scanning electron microscopy (SEM; JEOL, JSM-5410 LV). The radula teeth shape, radula formula, and embryonic shell sculpture were recorded.

Anatomical abbreviations. The following abbreviations are used as defined by Pilsbry (1892, 1894) and Solem (1992): ag, albumin gland; at, atrium; e, epiphallus; fl, flagellum; fo, free oviduct; gd, gametolytic duct; gs, gametolytic sac; hd, hermaphroditic duct; hg, hermaphroditic gland; ov, oviduct; p, penis; pp, penial pilaster; pr, penial retractor muscle; pv, penial verge; v, vagina; vd, vas deferens; vp, vaginal pilaster.

Institutional abbreviations.

CUMZ	Chulalongkorn University, Museum of Zoology, Bangkok
MNHN	Muséum National d'Histoire Naturelle, Paris
NHMUK	The Natural History Museum, London
SMF	Forschungsinstitut und Naturmuseum Senckenberg, Frankfurt, a.m.

SYSTEMATICS

Family Camaenidae Albers, 1850

Genus *Camaena* Albers, 1850

Type species. *Helix cicatricosa* Müller, 1774, by subsequent designation by Martens in Albers, 1860.

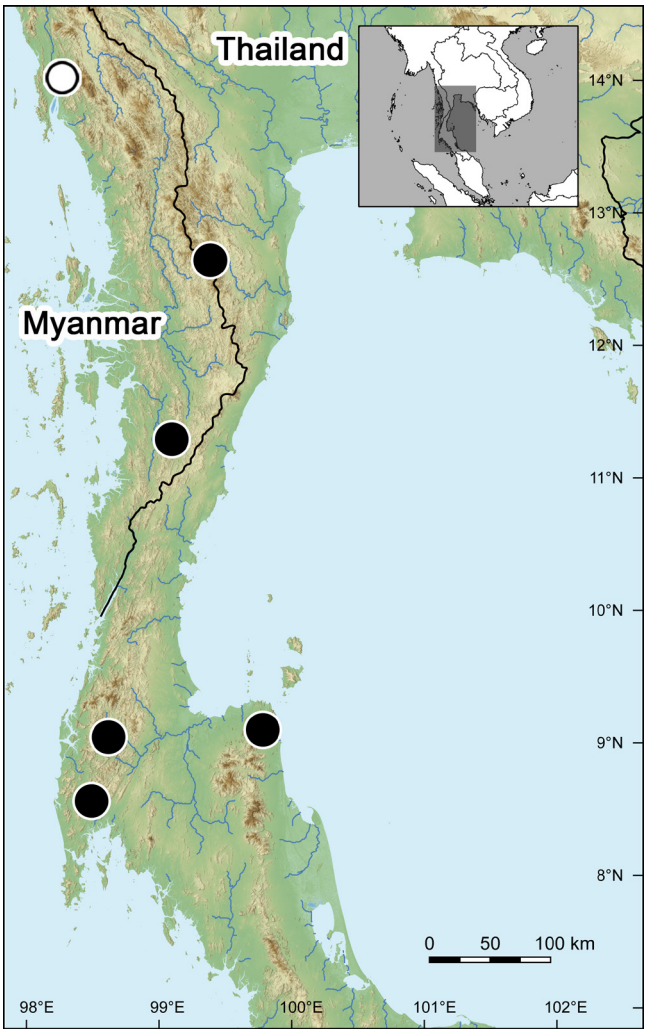

Fig. 1. Distribution range of *Camaena saturnia*. Open dot indicates the approximate type locality of the species, "Tavoy" [Dawei, Tanintharyi Region, Myanmar].

Diagnosis. Shell dextral or sinistral, large, solid, depressed to elevated globose in shape, widely perforated to sealed umbilicus, and surface smooth, malleated or wrinkled. Periostracum transparent; shell colour light brown to dark brown and/or encircled with brown spiral bands. Apex obtuse with large embryonic shell about 2 to 2½ whorls. Whorls 5 to 6; last whorl with angular periphery to well rounded. Aperture elliptical with thick or thin parietal callus. Peristome thickened, expanded, or reflected. Columella straight and thickened. Genitalia without vaginal accessory organs, penial verge present, and penis continuous with epiphallus and terminating with short to long flagellum.

Camaena saturnia (Gould, 1846)

(Figs. 1–3)

Helix saturnia Gould, 1846: 98, 99, type locality: Tavoy [Dawei, Tanintharyi Region, Myanmar]; 1862: 198; Pfeiffer, 1853: 250; 1859: 199, 300; Hanley & Theobald, 1870: 13, pl. 25 fig. 3; Johnson, 1964: 145.
Helix (*Phania*) *saturnia* – Martens in Albers, 1860: 157.
Helix (*Camaena*) *saturnia* – Pilsbry, 1891: 203, 204, pl. 60 fig. 5.
Camaena saturnia – Pilsbry, 1894: 104, pl. 60 fig. 5; Gude, 1914: 151, 152; Richardson, 1985: 77, 78.

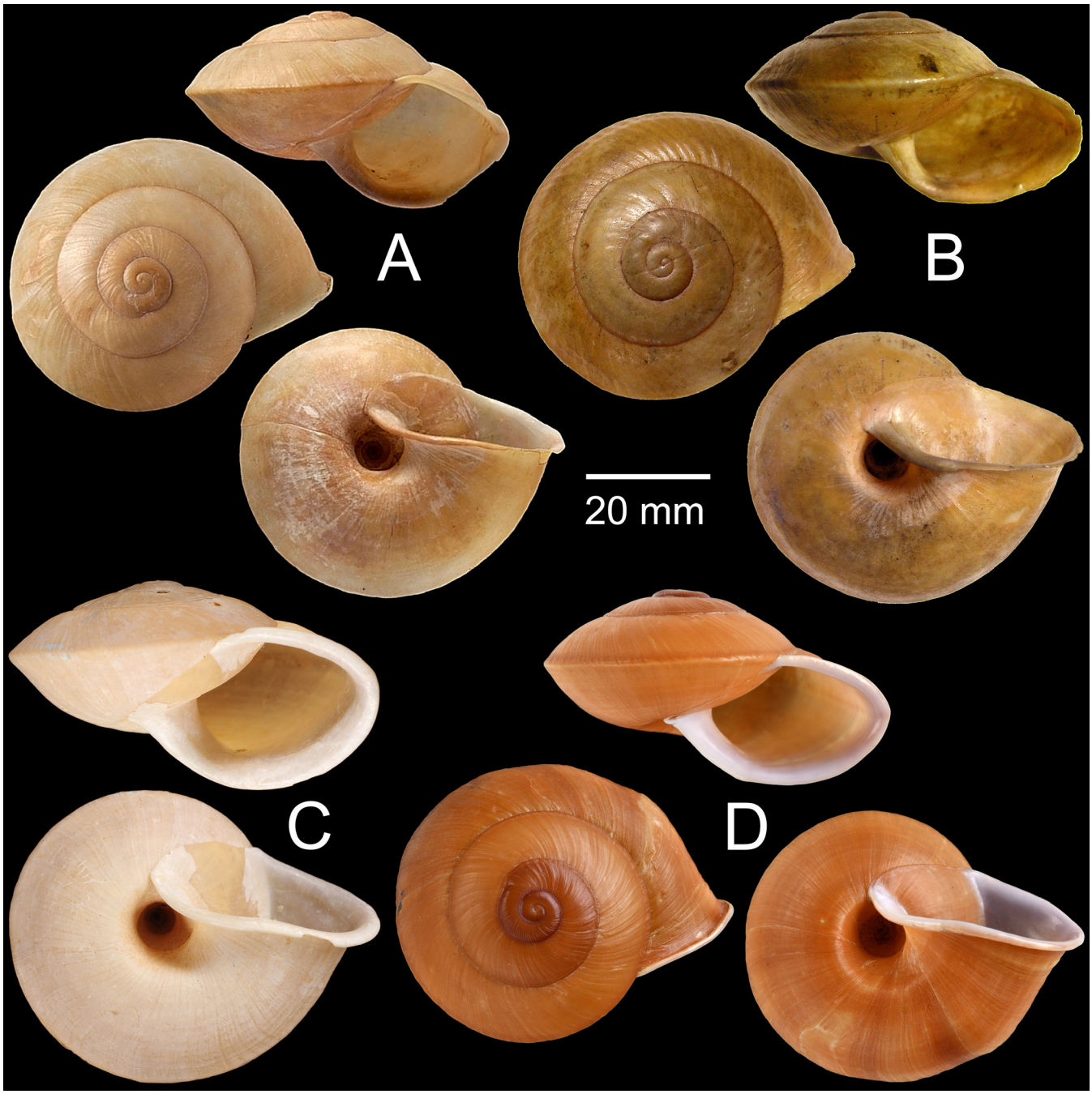

Fig. 2. Shell characteristics of *Camaena saturnia*. A, possible syntype NHMUK 20210010 ex. Cuming collection from Tavoy; B, specimen NHMUK 1888.12.4.2004 ex. Theobald collection from Tenasserim; C, holotype of *Camaena ngocthachi*, MNHN-IM-2000-35587; D, specimen CUMZ 7433 from Nakhon Sri Thammarat, Thailand.

Hemiplecta ? *saturnia* – Godwin-Austen, 1898: 73.

Camaena ngocthachi Huber in Thach, 2020: 86, figs. 932–934, type locality: suburb of Phang Nga city, Phang Nga Province, South Thailand. New synonym.

Material examined. Possible syntype NHMUK 20210010 ex. Cuming collection (1 shell; Fig. 2A) from Tavoy. NHMUK 1888.12.4.2004 ex. Theobald collection (1 shell; Fig. 2B) from Tenasserim. Holotype of *C. ngocthachi*, MNHN-IM-2000-35587 (Fig. 2C) from Suburb of Phang Nga City, Phang Nga Province, Thailand. Limestone outcrop at Phra (Buddha) Cave, Lenya National Park, Tanintharyi Township, Tanintharyi Region, Myanmar (11°13′46″N, 99°10′34″E): CUMZ 7434 (1 broken shell). Klong Laan, Suratthani Province, Thailand: CUMZ 2562 (1 shell; height 31.8 mm, width 53.5 mm). Pala-u waterfall, Phetchaburi Province, Thailand: CUMZ 2561 (2 intact + 1 broken shells; height 29.4 mm, width 52.0 mm, height 26.9 mm, width 51.4 mm), CUMZ 4152 (1 broken shell). Samet Chun Waterfall, Khanom District, Nakhon Sri Thammarat Province, Thailand (9°08′09.2″N, 99°50′53.2″E): CUMZ 7433 (1 ethanol preserved + 1 juvenile shell, height 25.3 mm, width 47.7 mm; Figs. 2D, 3A, B, D, E).

Shell. Shell dextral, relatively thin, and thick-lens-shaped (Fig. 2). Apex obtuse; embryonic shell rather large, about 2½ whorls, sculptured with regular parallel growth lines;

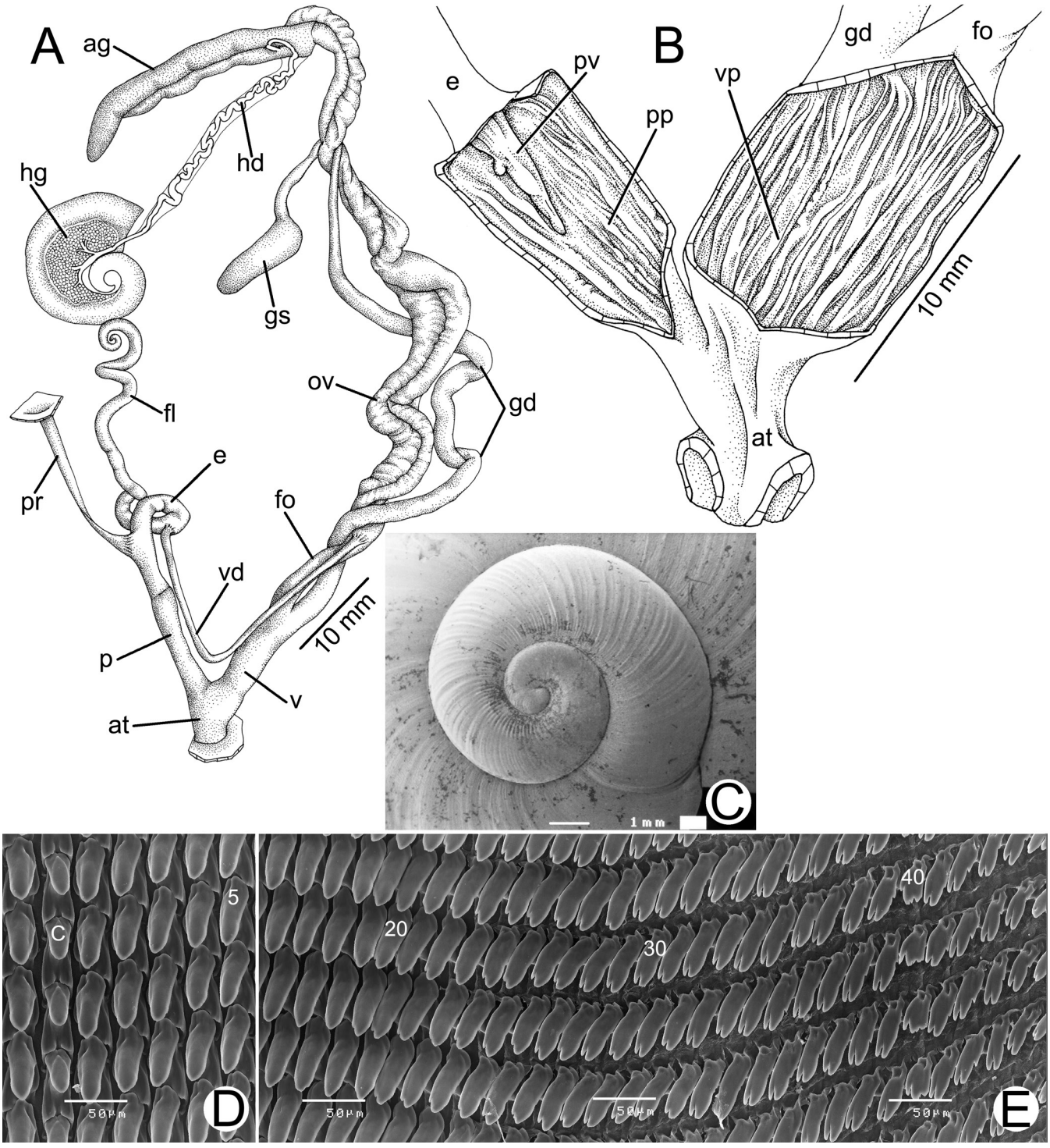

Fig. 3. *Camaena saturnia*. A, B, genitalia of specimen CUMZ 7433. A, whole genitalia; B, internal sculpture of penis and vagina. C, protoconch sculpture, specimen CUMZ 7433. D, E, radular morphology of specimen CUMZ 7433. D, central teeth with the first to fifth lateral teeth; E, lateral teeth with the tricuspid marginal teeth transition and outer marginal teeth. Central tooth indicated by 'C'; numbers indicate the order of lateral and marginal teeth.

following whorls nearly smooth-surfaced with fine and regular growth lines, and tiny nodules spread on last whorl. Shell reddish-brown to dark brown in colour; periostracum thin and transparent. Whorls 5 to 6 increasing regularly. Spire dome-shaped to little elevated; suture very wide and shallow to little impressed. Last whorl large and angular with strong peripheral keel. Aperture wide, rhomboid-shaped, whitish inside, and connected by thin whitish to transparent parietal callus. Peristome white to brownish, little thickened, and widely expanded. Columella dilated, whitish, and slightly curved. Umbilicus perforated and widely opened.

Genitalia. Atrium (at) short. Penis (p) somewhat slender and long. Epiphallus (e) relatively short and folded. Penial retractor muscle (pr) long and attached near penis. Flagellum (fl) very long, nearly equivalent to length of penis and epiphallus, and coiled terminally. Vas deferens (vd) narrow tube passing forward from free oviduct and

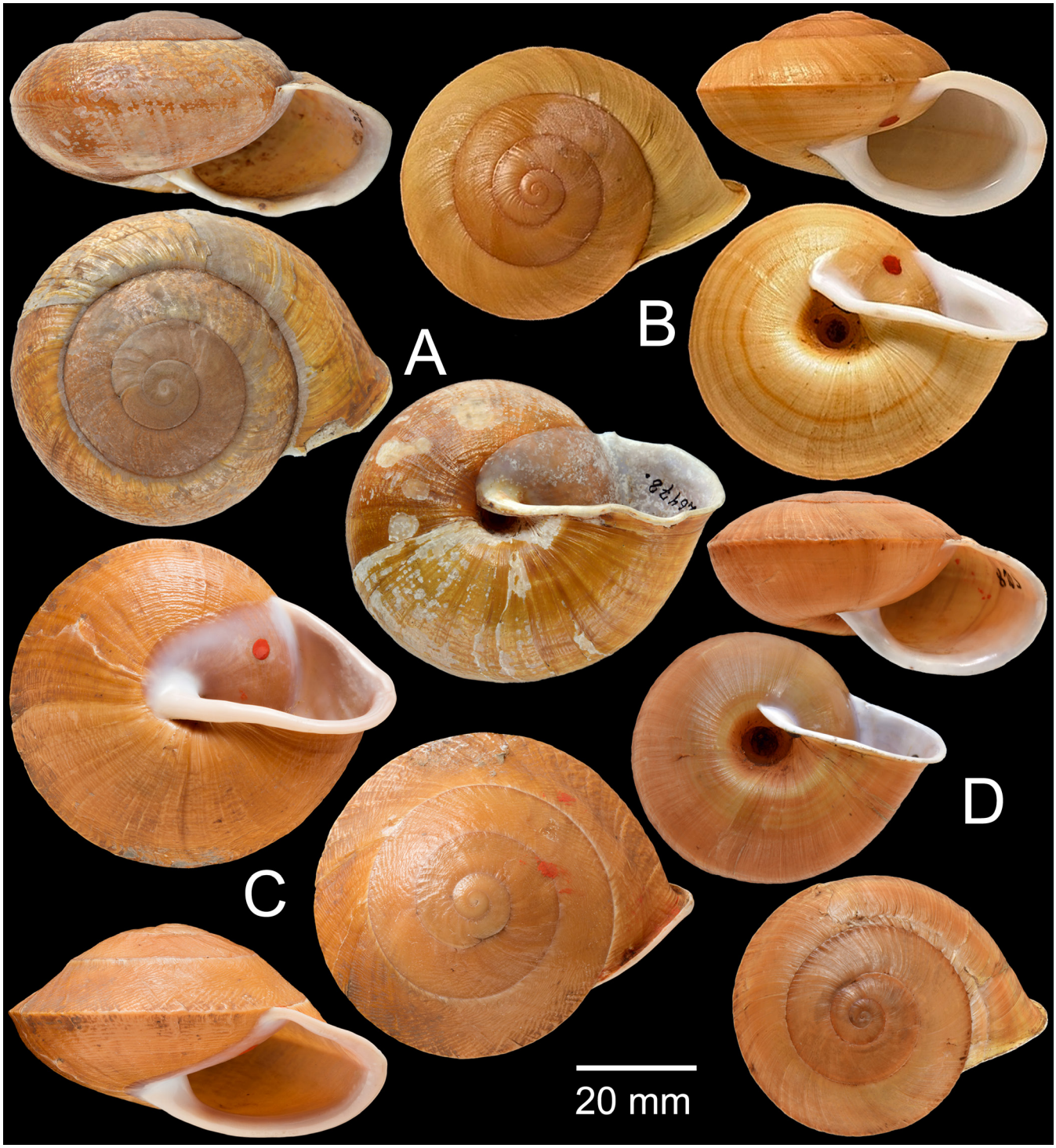

Fig. 4. Shell characteristics for further comparison. A, *Camaena ochthoplax* (Benson, 1860), specimen SMF 26478/1 from Naga Burge; B, *Camaena pachychila* (Smith, 1893), syntype NHMUK 1893.2.26.2.3 from Annam; C, *Camaena vanbuensis* Smith, 1896, syntype NHMUK 1896.1.25.1 from Vanbu, Tonkin; D, *Camaena suprafusca* Möllendorff, 1898, lectotype SMF 8105/1 from Boloven, Annam.

joining at junction of epiphallus and flagellum (Fig. 3A). Internal wall of penis corrugated and exhibiting series of thin longitudinal penial pilasters (pp), which form fringe around penial verge. Penial verge (pv) long-conical-shaped, and with nearly smooth surface (Fig. 3B).

Vagina (v) cylindrical, shorter than penis, and held in position by a series of muscle filaments arising from foot floor (Fig. 3A). Gametolytic duct (gd) very long, similar diameter as vagina, then tapering to a narrow and long tube, and connected to swollen and elliptical gametolytic sac (gs). Free oviduct (fo) very short. Oviduct (ov) not enlarged. Albumen gland (ag) slightly enlarged and tongue shaped. Hermaphroditic duct (hd) twisted, curved, and connected to alveoli hermaphroditic gland (hg). Internally, vagina possesses irregular longitudinal vaginal pilasters (vp) that exhibit a series of swollen and smooth ridges. Vaginal pilasters are apparently uniform throughout entire vaginal chamber (Fig. 3B).

Radula. Radula arranged in a nearly straight row with about 137 teeth with the formula 68-(21-22)-1-(21-22)-68. Central tooth unicuspid with obtuse cusp (Fig. 3D). Lateral teeth unicuspid, oblique-shaped, and with obtuse cusp (Fig. 3D, E). Marginal teeth starting around teeth no. 21 to 22. Inner marginal teeth bicuspid; ectocone large with dull cusp; endocone very small, located near the tip and with pointed cusp (Fig. 3E). Outer marginal teeth small and tricuspid; endocone and mesocone with rather large and pointed cusps; ectocone very small and located at base of the teeth (Fig. 3E).

Distribution. The historical record of this species is known only from the type locality "Tavoy" and the broad geographical area of "Tenasserim" (Hanley & Theobald, 1870; Pilsbry, 1891; Gude, 1914). Both records are currently located in the Tanintharyi Region, southern Myanmar (Fig. 1). A recent study collected records from several localities along the east coast of the Tenasserim Range in Petchaburi, Suratthani, Phang Nga and Nakhon Sri Thammarat Provinces, Thailand. The southern limit of the distribution of the species is possibly in Phang Nga Province.

Remarks. Although *C. saturnia* has a wide distribution, ranging from Myanmar to Thailand, its populations are low in density and quite rare. In this study, only four heavily worn shells and one live specimen were collected from the non-limestone areas examined. The live snail was found among leaf litter with decaying leaves and rotten logs in primary forest. Gradually increasing deforestation is probably the main reason for the restricted habitats and population decline of this species.

The nominal species *Camaena ngocthachi* was recently described from southern Thailand based on one holotype now deposited in the MNHN collection and two paratypes housed in the author's personal collection. The holotype MNHN-IM-2000-35587 (Fig. 2C) is a worn specimen showing no informative character differences from the syntype of *C. saturnia* (Fig. 2A) and other specimens from nearby areas (Fig. 2B, D). Therefore, we do not hesitate to synonymise *Camaena ngocthachi* as a junior subjective synonym of *C. saturnia*.

Pilsbry (1891) stated that *C. saturnia* has a similar shell to *C. ochthoplax* (Benson, 1860). For comparison, *C. saturnia* has a smaller shell size (width about 51 mm) with a strong peripheral keel on the last whorl, widely opened umbilicus, nearly smooth shell surface, and a very shallow suture. In contrast, *C. ochthoplax* (Fig. 4A) has a larger shell (width about 68 mm), a rounded last whorl, rimate umbilicus, shell surface with strong growth lines and rough with malleations, and impressed suture. Gude (1914) also noted that *C. saturnia* is similar to *C. vanbuensis* Smith, 1896. However, the recently examined type specimen clearly shows no similarity between them. *Camaena saturnia* has a thinner and smaller shell, a widely opened umbilicus, and nearly smooth or thin growth lines of the shell surface. On the other hand, *C. vanbuensis* (Fig. 4C) has a relatively larger and thicker shell, nearly closed umbilicus, and shell surface with strong malleated surface.

The other two umbilicate species, *C. pachychila* (Smith, 1893) and *C. suprafusca* Möllendorff, 1898, also closely resemble *C. saturnia*. However, *C. pachychila* (Fig. 4B) from Vietnam is distinct in having narrow brownish spiral bands on the periphery and below the periphery surrounding the umbilicus and more convex whorls. In contrast, *C. suprafusca* (Fig. 4D) from Laos has a wide-angled peripheral keel, dome-shaped spire, last whorl inflated below the periphery, and reddish-brown spiral bands on the periphery and below the periphery surrounding the umbilicus (for further comparison, see Inkhavilay et al., 2019: fig. 47e). However, *C. suprafusca* has been treated as a junior synonym of *C. pachychilus* without clear evidence (Páll-Gergely et al., 2020). The molecular phylogenies of the umbilicate group (Wang et al., 2020) and sinistral group (Ai et al., 2016; Ding et al., 2016) clearly indicate that the traditional morphological-based classification using shell and genitalia characters is effective and able to differentiate species. In addition, field observation and a genetic study both revealed that *Camaena* species tend to be locally endemic and are restricted to primary forest, which may play an important role in their isolation (Ding et al., 2016; Wang et al., 2020). Therefore, the opinion of Páll-Gergely et al. (2020) is still provisional; we treat *C. suprafusca* as a distinct species and await further data from genitalia anatomy and molecular studies.

DISCUSSION

Camaena is a diverse genus of land snails that are endemic from eastern India to southern China and Indochina (Pilsbry, 1892; Gude, 1914; Zilch, 1960; Richardson, 1985; Schileyko, 2003). The species from the Philippines and the Greater Sunda Islands have been recognised as distinct genera (see Schileyko, 2003, 2004; MolluscaBase Eds., 2021). In this study, the reproductive anatomy of *C. saturnia* is described for the first time, and our findings confirm its generic status. Up to now, genital morphology has been studied in 15 species (Table 1), and the described characters generally correspond with those of the type species, *C. cicatricosa*. The male genitalia have many more variable characters than those of the females and are generally helpful characteristics for traditional classification. For example, the genus *Satsuma* Adams, 1868, differs from *Camaena* by having a penial caecum and lacking a penial verge, while *Camaena* possesses a conical penial verge and lacks a penial caecum (Schileyko, 2003, 2004; Wang et al., 2014). However, the function of the penial verge and caecum is currently unknown, and it most likely reflects sexual selection, where reproductive isolation is strongly associated with reproductive morphology, especially in the stylommatophorans (Gómez, 2001; Kameda et al., 2007; Baur, 2010).

Within the genus *Camaena*, the general genital morphology among species is relatively similar, except for the terminal part of the penis, including the attachment of the retractor muscle and length of the epiphallus and flagellum; these features are taxonomically informative at the species level (Table 1). For example, *C. saturnia* has a similar shell form (dextral, umbilicate, and strong keel) to four recently

Table 1. Comparison of all known genital anatomy of *Camaena* species and some shell characters. ? = no data; D = dextral; e = epiphallus; fl = flagellum; go = genital orifice; p = penis; pr = penial retractor muscle; pv = penial verge; S = sinistral; v = vagina.

Species	Shell coiling / umbilicus	Penis (p) and vagina (v) length	Attachment of penial retractor muscle (pr)	Flagellum (fl) and epiphallus (e) length	Inner penial wall sculpture	References
C. cicatricosa (Müller, 1774)	S / rimate	p shorter than v	middle	nearly equal length	entirely with longitudinal pilasters	Solem, 1992; Schileyko, 2003; Ai et al., 2016, Ding et al., 2016
C. connectens (Dautzenberg & Fischer, 1906)	S / rimate	nearly equal length	middle	fl longer than e	longitudinal pilaster near go; transverse pilasters near pv	Ding et al., 2016
C. detianensis Zhou & Lin in Ai et al., 2016	S / rimate	p shorter than v	close to p	nearly equal length	entirely with longitudinal pilasters	Ai et al., 2016
C. funingensis Zhou, Wang & Lin in Wang et al., 2020	D / umbilicate	p longer than v	middle	fl shorter than e	entirely with longitudinal pilasters	Wang et al., 2020
C. gaolongensis Zhou, Wang & Lin in Wang et al., 2020	D / umbilicate	p longer than v	close to p	nearly equal length	entirely with longitudinal pilasters	Wang et al., 2020
C. hahni (Mabille, 1887)	S / umbilicate	nearly equal length	middle	fl shorter than e	longitudinal pilaster near go; transverse pilasters near pv	Ai et al., 2016
C. inflata (Möllendorff, 1885)	S / rimate	nearly equal length	close to fl	fl shorter than e	longitudinal pilaster near go; transverse pilasters near pv	Ding et al., 2016
C. lingyunensis Zhou & Lin in Ai et al., 2016	S / umbilicate	p shorter than v	close to fl	nearly equal length	longitudinal pilaster near go; transverse pilasters near pv	Ai et al., 2016
C. maguanensis Zhou, Wang & Hu in Wang et al., 2020	D / umbilicate	nearly equal length	middle	nearly equal length	entirely with longitudinal pilasters	Wang et al., 2020
C. obtecta (Fischer, 1898)	S / imperforate	p shorter than v	close to fl	nearly equal length	entirely with transverse pilasters	Ding et al., 2016
C. platyodon (Pfeiffer, 1846)	D / imperforate	nearly equal length	close to fl	fl shorter than e	entirely with longitudinal pilasters	Pilsbry, 1892
C. poyuensis Zhou, Wang & Ding in Ding et al., 2016	S / imperforate	nearly equal length	middle	nearly equal length	longitudinal pilaster near go; transverse pilasters near pv	Ding et al., 2016
C. rugata Möllendorff, 1899	D / imperforate	nearly equal length	close to p	fl shorter than e	?	Wiegmann, 1900
C. saturnia (Gould, 1846)	D / umbilicate	nearly equal length	close to p	fl longer than e	entirely with longitudinal pilasters	This study
C. xanthoderma (Möllendorff, 1882)	D / imperforate	p shorter than v	middle	fl longer than e	entirely with longitudinal pilasters	Pilsbry, 1894
C. yulinensis Zhou, Wang & Hu in Wang et al., 2020	D / umbilicate	p longer than v	close to p	nearly equal length	entirely with longitudinal pilasters	Wang et al., 2020

described species, *C. maguanensis*, *C. funingensis*, *C. gaolongensis*, and *C. yulinensis*. The distinction from these species is that the flagellum of *C. saturnia* is longer than the epiphallus, while the other four species have a flagellum nearly equal in length to or shorter than the epiphallus (Table 1). *Camaena gaolongensis* and *C. yulinensis* both exhibit similar shell and genitalia morphologies. However, they differ from each other in the internal wall sculpture of the penis: *C. gaolongensis* has strong pilasters with curved shapes near the genital orifice, and the penial verge is open at the base; while *C. yulinensis* has thin and smooth surface pilasters, and the penial verge is opened at the tip (Table 1). This indicates that accurate species recognition can be based on the internal (micro)sculpture of the penial chamber (Gómez, 2001; Seki et al., 2008; Baur, 2010).

Among the stylommatophoran species, penial morphology is highly variable and plays an important role in physical isolation during interspecific copulation, as the epiphallus and flagellum form the spermatophore during copulation (Gómez, 2001; Baur, 2010). In addition, the spermatophore has a species-specific shape and surface structure that is taxonomically significant (Baur, 1998, 2010) and clearly distinguishes closely related species such as in the confamilial genus *Amphidromus* Albers, 1850 (Sutcharit & Panha, 2006; Schilthuizen & Looijestijn, 2009). However, a description of the spermatophore has never been reported for *Camaena*.

A conclusive phylogenetic relationship of the genus *Camaena* has never been published, except for species from southern China and North Vietnam (Ai et al., 2016; Ding et al., 2016; Wang et al., 2020). The genus *Camaena* contains primarily dextral species, but at least eight sinistral species are also included and have been systematically studied. The phylogenetic results by Ai et al. (2016) and Wang et al. (2020) revealed the monophyly of sinistral species but without strong support. This suggests the unique evolutionary history of the lineage, where all the sinistral species are derived from a single sinistral ancestor. This evolutionary pattern is also evident in other low-spired snails, such as *Euhadra* Pilsbry, 1890 (Camaenidae; Ueshima & Asami, 2003; Davision et al., 2005), and *Hemiplecta* (Ariophantidae; Sutcharit et al., 2021). The evolution of sinistrality in *Camaena* is in contrast to that of the monophyletic genus *Satsuma*, where the sinistrality is polyphyletic, showing multiple sinistral lineages, and where the multi-locus phylogeny strongly supports the assumption of independent origin of multiple sinistral ancestors (Hoso et al., 2010; Zhang et al., 2020).

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