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Trophobiosis between a new species of *Acropyga* (Hymenoptera, Formicidae) and new *Neochavesia* (Hemiptera, Xenococcidae) from Peru, and establishment of the *Acropyga smithii* species-group

John S. LaPolla[1], Scott A. Schneider[2]

1 *Department of Biological Sciences, Towson University, 8000 York Road, Towson, MD, 21252, USA* **2** *USDA, Agricultural Research Service, Henry A. Wallace Beltsville Agricultural Research Center, Systematic Entomology Laboratory, 10300 Baltimore Avenue, Beltsville, MD, 20705, USA*

Corresponding author: John S. LaPolla (jlapolla@towson.edu)

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Abstract

We describe a new pair of trophobiotic partners from the ant genus *Acropyga* and the root mealybug genus *Neochavesia*. A recent field study on *Acropyga* ants and associated root mealybugs, conducted in the Peruvian Amazon, led to the discovery of *Acropyga manuense* LaPolla & Schneider, **sp. nov.** and its root mealybug symbiont *Neochavesia podexuta* Schneider & LaPolla, **sp. nov.** The new root mealybug belongs to the family Xenococcidae, whose members are all obligate associates of *Acropyga* ants. Providing joint descriptions of new mutualist partners in the same article is a novel approach for this system, and it offers benefits to the ongoing study of mutualism and patterns of association among these symbiotic ants and scales. Here, we also begin to revise the species-group composition of *Acropyga* by establishing the *smithii* species-group, and we provide updated information to aid in identifying the new ant species and root mealybug species.

Keywords

Ants, Coccoidea, Coccomorpha, mutualism, root mealybug, taxonomy, symbiosis

Introduction

Efforts to understand the obligate symbiotic relationship between *Acropyga* Roger ants (Hymenoptera: Formicidae) and root mealybugs (Hemiptera: Rhizoecidae and Xenococcidae) hinge on an understanding of exactly which species associate with each other. Questions about fidelity and specificity among partnerships cannot be answered without detailed examination of species associations. However, given the cryptic nature of these mutualists (i.e., they are hypogeic, small, and difficult to identify), definitive associations are often difficult to confirm. Additionally, studies of each respective group are typically segregated by taxonomic discipline, and therefore, information about mutualistic partnerships can be disconnected both physically and temporally in the published record.

Schneider et al. (2022) recently detailed a protocol to confirm direct association between root mealybugs and *Acropyga* ants and reported on several new associations between partnered pairs from the Peruvian Amazon. As part of that field study, we discovered a new species of *Acropyga* associating with a new xenococcid root mealybug. All species in the family Xenococcidae, which is comprised of the Old World genera *Eumyrmococcus* Silvestri, 1926 and *Xenococcus* Silvestri, 1924 and the New World genus *Neochavesia* Williams & Granara de Willink, 1992, are obligatorily associated with *Acropyga*. Past experience has shown that when a new species of *Acropyga* is discovered, it is frequently associated with a new xenococcid as well. This is illustrated by the following (non-exhaustive) list of examples. In the Neotropics, LaPolla (2004) described two new species of *Acropyga* (*A. ayanganna* LaPolla and *A. stenotes* LaPolla) that were each associated with a new species of *Neochavesia* (*N. lapollai* Williams and *N. linealuma* Schneider & LaPolla, respectively). In the Old World, *Acropyga kinomurai* Terayama & Hashimoto was discovered associating with a new root mealybug species, *Xenococcus kinomurai* Williams & Terayama (Williams and Terayama 2000); *A. nipponensis* Terayama with *Eumyrmococcus nipponensis* Terayama (Terayama 1986); *A. pallida* (Donisthorpe) with *E. adornocapillus* (Schneider & LaPolla, 2011); and *A. paleartica* Menozzi with *E. corinthiacus* Williams (Williams 1993).

In the above examples, each ant and root mealybug species were described separately from their mutualist partner. Historically, descriptions of new trophobiotic root mealybugs tend to lag behind the descriptions of their mutualist ants, sometimes by many decades. Thus, researchers have had to spend significant effort compiling and reconciling information about species associations scattered across the literature (see Williams 1998; Johnson et al. 2001; LaPolla 2004; Schneider and LaPolla 2011). By combining the methodology outlined in Schneider et al. (2022) with descriptive taxonomy, we aim to present a clearer picture of trophobiotic associations between *Acropyga* and root mealybugs going forward and to keep critical ecological data together in the published record when possible. Here, we describe the trophobiotic association between a new species of *Acropyga* with a new species of *Neochavesia* from Peru.

Materials and methods

Root mealybug specimens

Specimens were preserved in 95–100% ethanol and stored at –80C prior to preparation and subsequently mounted on glass slides in Canada balsam. Morphological terminology for *Neochavesia* conforms to usage from Williams (2004) and Schneider and LaPolla (2011). Measurements were made on a Zeiss Axio Imager.M2 (Carl Zeiss Microscopy, LLC, White Plains, NY, USA) microscope with the aid of an AxioCam and AxioVision software. Slide-mounted specimens were examined under phase contrast and differential interference contrast (**DIC**) microscopy.

Ant specimens

Specimens were preserved in 95–100% ethanol and stored at –80C prior to preparation. Specimens were later point mounted for morphological examination. Ants were measured using a KM33-R micrometer on a Leica MZ16 dissecting microscope to the nearest 0.001 mm. Images were taken with a 10× lens attachment using a Canon EOS 6D Mark II camera with a MP-E 65mm manual focus macro lens on a Macropod Pro 3D and Micro Kit System (Macroscopic Solutions, East Hartford, CT, USA). Images were focus stacked using Zerene Stacker ver. 1.04 software. Morphological terminology used for *Acropyga* description conforms to usage from LaPolla (2004) and LaPolla et al. (2017).

Ant measurements and indices are defined as:

EL (Eye Length): In full-face view, maximum anteroposterior length of the compound eye.

PFL (Profemur Length): Length of profemur in lateral view.

HL (Head Length): In full-face view, length from a line drawn across the posterior margin of the head to a line drawn across the anterior margin of the clypeus.

HW (Head Width): In full-face view, maximum width of the head between the lateral margins, excluding the compound eyes.

ML (Mesosoma Length): In lateral view, maximum length from the point at which the pronotum meets the cervical shield to the posterior basal angle of the metapleuron.

PW (Pronotum Width): In dorsal view, maximum width of the pronotum.

SL (Scape Length): In a view perpendicular to the long axis of the scape, maximum length of the scape, excluding the condyle.

CI (Cephalic Index): (HW/HL) × 100.

REL (Relative Eye Length Index): (EL/HL) × 100.

SI (Scape Index): (SL/HW) × 100.

Specimen depositories

Type depositories are abbreviated as follows:

UNMSM Museo de Historia Natural, Universidad Nacional Mayor de San Marcos, Lima, Peru.

USNM Smithsonian National Museum of Natural History, Coccomorpha collection at USDA Agricultural Research Service, Beltsville, Maryland, USA.

USNM Smithsonian National Museum of Natural History, Washington, D.C., USA. (ant specimens)

Results

Establishment of the *Acropyga smithii* species-group

Diagnosis of *Acropyga smithii* species-group

New World species; workers with 8 antennal segments and 4 mandibular teeth (one exception occasionally seen in *A. oreithauma* where a much smaller tooth is found between the 3rd and basal teeth); males with penial sclerites elongated with distal tips that bend towards gonopods; anterior portion of the ventral margin of the penial sclerites dentate.

Included species:

A. fuhrmanni (Forel, 1914)

A. manuense LaPolla & Schneider, sp. nov.

A. oreithauma LaPolla, Williams & Fan, 2017

A. smithii Forel, 1893

Diagnosis and remarks

LaPolla (2004) created nine informal species-groups within *Acropyga* to replace the old subgenera that had previously been recognized within the genus. Those species-groups were largely based on a phylogenetic analysis of male genitalic characters. The most speciose of the New World groups is the *decedens* species-group, with 12 species included by LaPolla (2004) and a thirteenth species (*A. oreithauma* LaPolla, Williams & Fan, 2017) implied to be included by LaPolla et al. (2017), since they considered it a possible sister species to *A. fuhrmanni* (Forel, 1914).

The prior inclusion of *A. fuhrmanni*, *A. oreithauma* and *A. smithii* Forel, 1893 within the *decedens* species-group is challenged by the discovery of a new species, *Acropyga manuense* LaPolla & Schneider sp. nov., along with additional male specimens of *A. fuhrmanni* and *A. smithii* collected from Peru. Evidence drawn from the morphology of males and workers suggests that these four species form a clade within the New World *Acropyga* that is separate from the *decedens* species-group. The penial sclerites of *A. fuhrmanni*, *A. manuense*,

and *A. smithii* share key diagnostic similarities (Figs 1–3). Unfortunately, the male of *A. oreithauma* remains unknown. In all three species the penial sclerites are elongated with distal tips that bend towards the gonopods. These are quite different than the expanded distal tips observed in most of the *decedens* species-group members (the species with such penial sclerites were called the *goeldii* complex by LaPolla (2004) within the *decedens* species-group). The anterior portion of the ventral margin of the penial sclerites also has dentate edges. The workers of *A. fuhrmanni*, *A. manuense*, *A. oreithauma* and *A. smithii* all have 8 antennal segments (occasionally *A. smithii* workers will have as few as 7 segments but this is rarely seen in specimens in collections) and mandibles with 4 mandibular teeth (occasionally a much smaller tooth is found between the 3rd and basal teeth in *A. oreithauma*).

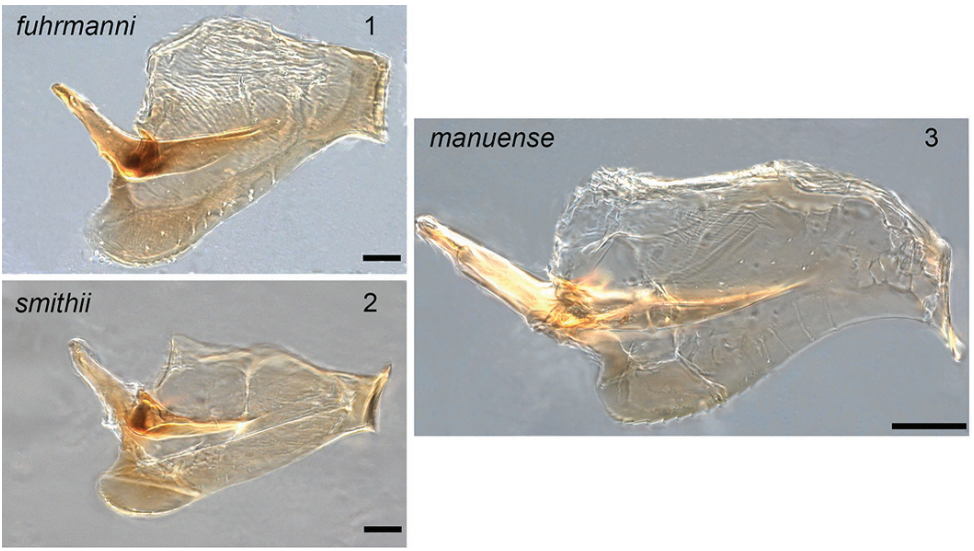
Molecular-based work has suggested that at least *A. fuhrmanni* and *A. smithii* are separated from the *decedens* species-group (Blaimer et al. 2016) and a more recent molecular phylogeny (J. LaPolla, unpub. data) of all described New World *Acropyga* confirms that *A. fuhrmanni*, *A. manuense*, *A. oreithauma* and *A. smithii* comprise a separate clade in alignment with the morphological assessment provided above. Therefore, morphological evidence from both males and workers, combined with molecular results, support the establishment of the *Acropyga smithii* species-group. A revision of the other *Acropyga* species-groups will follow pending publication of molecular phylogenetic results and morphological reassessment.

New species descriptions

Hymenoptera Linnaeus, 1758
Formicidae Latreille, 1809

***Acropyga manuense* LaPolla & Schneider, sp. nov.**
https://zoobank.org/1C9F0061-5D0F-49B6-A003-3D71BB9AC4E4
Figs 4–6 (worker), 7–8 (queen), 3 and 9–12 (male)

Description. *Worker* (*N = 10*). Uniformly yellow; covered in a dense layer of pubescence including lateral portions of pronotum and mesopleuron; scattered erect setae across body. Head slightly longer than wide (CI: 90–99); posterior margin slightly concave medially; posterolateral corners rounded with ca. 6 erect setae found along margin; eyes small with uneven pigmentation (REL: 6–11); 8-segmented, incrassate antennae; scapes short of posterior margin by about ¼ to ½ length of pedicel (SI: 71–83); scapes with dense layer of pubescence and scattered erect setae across its length. Clypeus narrow (width in holotype = 0.113 mm) and medially convex. Mandibles with 4 distinct teeth; apical teeth are the longest; teeth 2 and 3 are about equal in size and basal tooth is slightly smaller than teeth 2 and 3; a slight diastema exists between tooth 3 and the basal teeth. In lateral view, mesosoma profile of pronotum steeply rising toward mesonotum (ca. 45° angle if a line is drawn parallel to mesosomal venter). Posterior portion of pronotum and remainder of mesosomal notum with scattered erect setae of varying heights. Highest portion of mesonotum slightly higher than propodeum. Metanotal area dis-

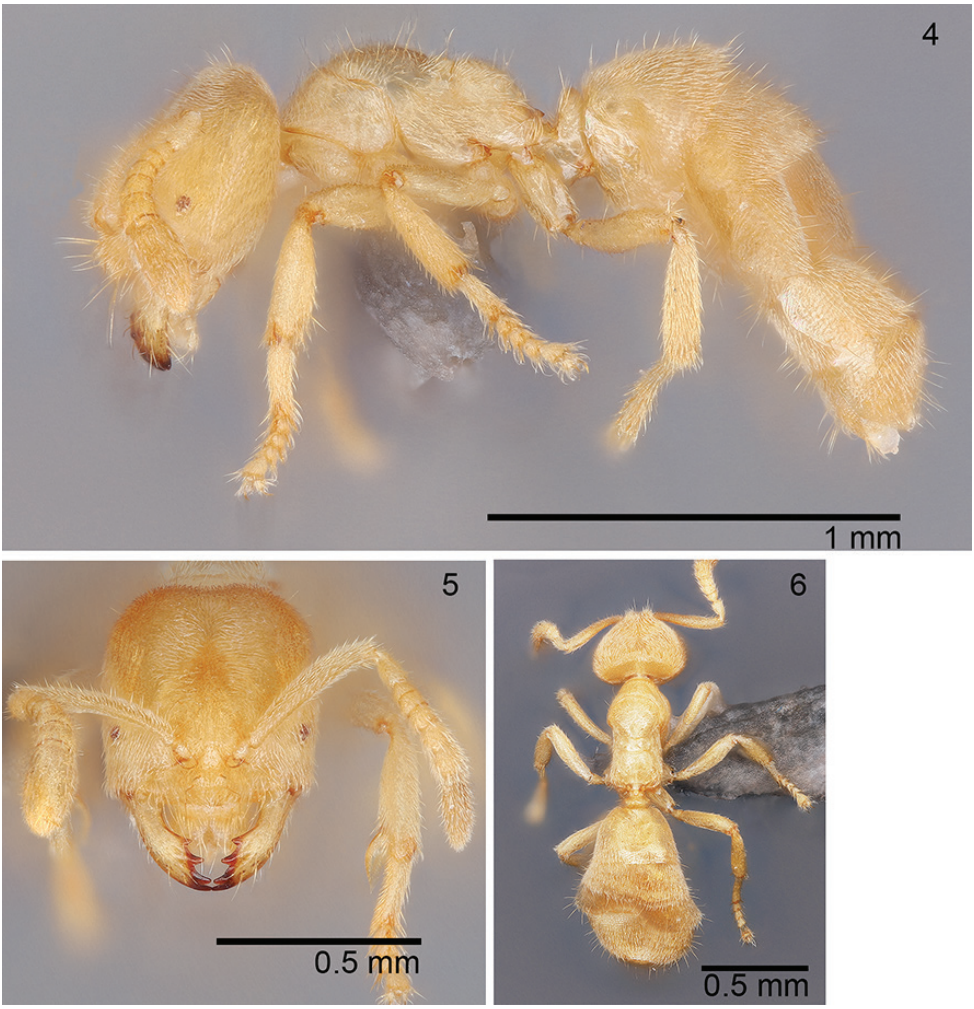


Figures 1–3. Dissected penial sclerites of various species in ectal view. Scale bar: *fuhrmanni* and *smithii* = 0.03 mm; *manuense* = 0.05 mm.

tinct with length in holotype = 0.061 mm. Dorsal face of propodeum flat with length in holotype = 0.122 mm; declivitous face steep (ca. 75° angle). Petiole thick and erect with rounded apex; last ¼ of petiole surpasses the most dorsal portion of the propodeal spiracle. Gaster typical of *Acropyga* with thick layer of pubescence and scattered erect setae. Measurements (*N* = 8). HW: 0.432–0.489; HL: 0.46–0.531; EL: 0.031–0.057; ML: 0.467–0.583; PW: 0.277–0.329; PFL: 0.326–0.413; HL+ML: 0.927–1.09.

***Queen* (*N* = *4*).** As in worker with modifications expected for caste and with the following differences: CI: 95–100; SI: 78–87; REL: 26–32. Measurements (*N* =3). HW: 0.524–0.59; HL:0.55–0.59; EL: 0.147–0.188; ML: 0.844–1.03; PW: 0.531–0.606; PFL: 0.428–0.454; HL+ML: 1.4–1.62.

***Male* (*N* = *4*).** Head yellowish-brown, excluding mandibles and funicular segments which are yellow; remainder of body yellow. Head about as long as wide (CI: 99–108); posterior margin slightly rounded; medially with three prominent ocelli just anterior to posterior margin; posterolateral corners rounded with an indistinct angle and 2–3 erect setae. Compound eyes large, surpassing head margin in full-frontal view (REL: 34–40). 9-segmented incrassate antennae; scapes surpass posterior margin by about length of antennal pedicel (SI: 93–97); scapes covered with dense pubescence and widely scattered short erect setae. Clypeus medially convex (clypeal width in paratype USNMENT01130437 = 0.08 mm long); mandible with three teeth, large apical tooth and two smaller teeth at the basal angle; on some mandibles the two smaller teeth appear to have fused at the basal angle rendering the mandible 2-toothed. Mesosoma covered with dense pubescence and scattered short erect setae on mesoscutum and mesoscutellum. Pronotum small and collar-like with overarching large, rounded mesonotum. Mesoscutellum slightly higher than mesos-



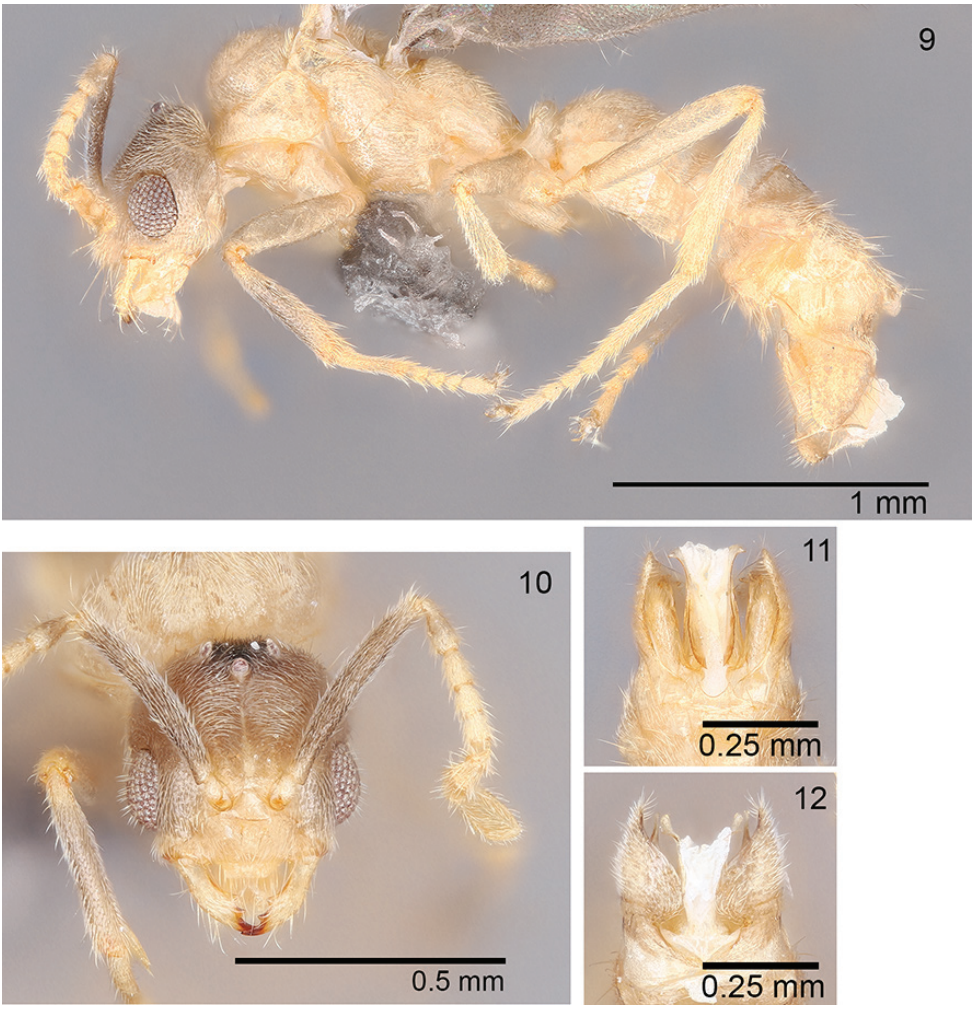
Figures 4–6. *Acropyga manuense* sp. nov., worker USNMENT01130435 (holotype) **4** lateral view **5** full-face view **6** dorsal view.

cutellum in lateral view. Propodeum lower than mesonotum with no separation into dorsal and declivitous faces; propodeum flat (paratype USNMENT01130437 = 0.212 mm long) with a slight slope toward petiole. Petiole thick and erect just surpassing the lowest portion of the propodeum in lateral view. Gaster typical of male *Acropyga* with thick layer of pubescence and scattered erect setae. Gonopods in lateral view tapered to a rounded apex (paratype USNMENT01130437 gonopod length = 0.216 mm long); in dorsal view gonopods medially expanded. Cuspi tubular (paratype USNMENT01130437 = 0.094 mm long); where cuspi meet digiti several peg-like teeth span the surface; several setae extend off of cuspi apex as well; digiti tubular before a distinct right angle bending ventrally where they meet the cuspi; ventral facing portion of digiti taper toward apex becoming

Figures 7, 8. *Acropyga manuense* sp. nov., queen USNMENT01130436 **7** lateral view **8** full-face view.

needle-like (paratype USNMENT01130437 = 0.108 mm long); apex of digiti visible beyond ventral margin of gonopod in lateral view. Penial sclerites elongate (Fig. 3); ventral margin curves from apex through rounded posterior region; along rounded section of penial sclerites margin dentate; apodeme located medially on anterior end of penial sclerites; apex of penial sclerites bend toward gonopods. Measurements (*N* =3). HW: 0.389–0.399; HL: 0.36–0.4; EL: 0.128–0.155; ML: 0.663–0.692; PW: 0.465–0.494; PFL: 0.412–0.451; HL+ML: 1.04–1.08.

Material examined. ***Holotype*:** Peru • worker; Madre de Dios, Las Cruces, Manu Paradise Lodge, nest behind lodge, in soil around small rotting branches; 13.055°S, 71.544°W; 31.v.2019; J.S. LaPolla and S.A. Schneider leg.; USNMENT01130435 (UNMSM). ***Paratypes*:** Peru • same data as holotype; 9 paratype workers: USN-



Figures 9–12. *Acropyga manuense* sp. nov., male USNMENT01130437 **9** lateral view **10** full-face view **11** ventral view of genitalia **12** dorsal view of genitalia.

MENT01130438 (USNM), USNMENT01130439 (USNM), USNMENT01130450 (USNM), USNMENT01130451 (USNM), USNMENT01130452 (USNM), USNMENT01130453 (USNM), USNMENT01130454 (USNM), USNMENT01130465 (USNM), USNMENT01130483 (USNM); paratype queens: USNMENT01130436 (USNM), USNMENT01130467 (USNM), USNMENT01130468 (USNM), USNMENT01130480 (USNM); paratype males: USNMENT01130437 (USNM), USNMENT01130466 (USNM), USNMENT01130481 (USNM), USNMENT01130482 (USNM).

Etymology. The epithet is a noun in apposition, referring to its type location near Manu National Park, Peru.

Remarks. The workers of *A. manuense* are similar in overall appearance to both *A. fuhrmanni* and *A. smithii* with all three possessing 8 antennal segments (although *A. smithii* workers can occasionally be found with as few as 7 segments) and 4 mandibular teeth. One of the most obvious ways *A. manuense* workers differ from both *A. fuhrmanni* and *A. smithii* workers is in mesosomal pubescence. In *A. manuense* workers possess thick pubescence that extends down the lateral portions of the pronotum and onto the mesopleuron. In *A. fuhrmanni* and *A. smithii* pubescence is very sparse to lacking on the lateral portions of the pronotum and the mesopleuron.

Several measurements will also allow for separation of the three species. The smallest of the three species is *A. smithii* with a head width and length less than 0.4 mm, whereas both *A. fuhrmanni* and *A. manuense* have head widths and lengths greater than 0.4 mm. The scape length in *A. smithii* is less than 0.27 mm, while it is greater than 0.3 mm in both *A. fuhrmanni* and *A. manuense*. The small size of *A. smithii* makes it fairly easy to distinguish from both *A. fuhrmanni* and *A. manuense*. Workers of *A. fuhrmanni* and *A. manuense* possesses different eye sizes with a relative eye length index between 12–15 in *A. fuhrmanni* and between 6–11 in *A. manuense* (Fig. 13). The cephalic index is also instructive with *A. fuhrmanni* generally having a value over 100 with *A. manuense* less than 100.

The most striking differences between *A. fuhrmanni*, *A. smithii* and *A. manuense* are found in males. The mandibles of the three species' males differ in the number and size of teeth, with *A. manuense* possessing three distinct equally sized teeth. Both *A. fuhrmanni* and *A. smithii* only have two teeth: a prominent apical tooth and a much smaller tooth at the basal angle. There are several genitalic differences between the three species such as each possessing uniquely shaped penial sclerites (Figs 1–3). The digitus is very distinctive within *A. manuense*, being ventrally directed, elongated and coming to a prominent point (Figs 9, 11). The elongated, pointed structure of the digitus is unique among all *Acropyga* species.

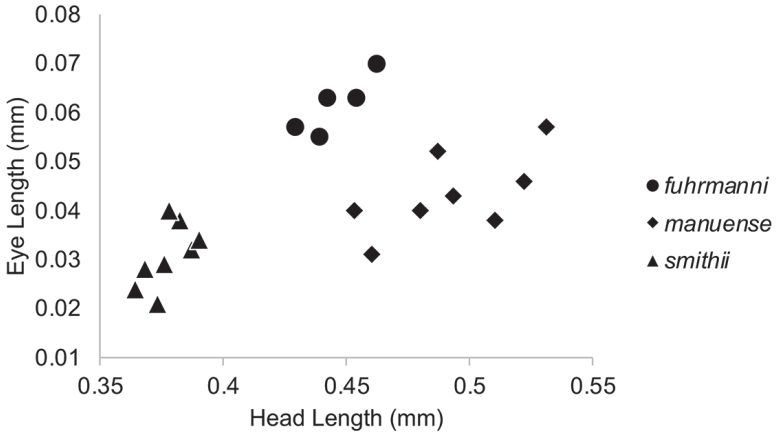


Figure 13. Bivariate plot of eye length vs. head length among measured *A. fuhrmanni*, *A. manuense* and *A. smithii* workers.

In the key to New World workers provided by LaPolla (2004), specimens of *A. manuense* will key to the lug for *A. fuhrmanni*. That lug would become a new couplet as follows:

1 Lateral portions of pronotum and mesopleuron with spare to no pubescence; ocular index between 12–15; cephalic index above 100.....***Acropyga fuhrmanni*** **(Forel)**

– Lateral portions of pronotum and mesopleuron with thick layer of pubescence; ocular index between 6–11; cephalic index less than 100 ....***Acropyga manuense*** **LaPolla & Schneider, sp. nov.**

Hemiptera Linnaeus, 1758
Xenococcidae Tang, 1992

Neochavesia podexuta **Schneider & LaPolla, sp. nov.**
https://zoobank.org/EA866C98-2812-44DC-8B50-0A59D80755B5
Fig. 14

Description. ***Adult female*** **(*N* = *7*).** In life, body bright white to cream colored and free of wax. Mounted on microscope slide, body elongate-pyriform, 1.35–1.58 mm long, 0.55–0.73 mm wide at widest point; head and thorax dilated with widest point at metathorax and abdominal segment I. Abdomen constricted after segment III; segments IV–VII gently tapering in width posteriorly with another constriction between segments VII and VIII. Dorsal posterior half of abdominal segment VIII sclerotized; anterior half membranous and free of setae, forming a distinctive bald patch; width of segment 145 µm wide. Anal lobes well developed and separated from abdominal segment VIII on venter and margins of dorsum by an intersegmental line. Anal lobes diverging with a roughly U-shaped notch between them, each rounded at posterior end. Dorsum of each anal lobe with numerous long flagellate setae, longest about 135 µm, situated at posterior end, with those at anterior end about 35 µm; ventral surface with similar setae 32–90 µm long. Anal ring roughly triangular, without cells or setae, 65 µm wide; anterior end lying along the intersegmental division that separates the anal lobes from abdominal segment VIII, posterior edge removed from the apical notch between lobes by about 1X length of anal ring. Long antennae widely spaced on dorsal head margin; basal segment set into a notch on the head and articulating; each with four segments, 652–663 µm in overall length; average lengths of segments (base to apex) 56 µm, 297 µm, 95 µm, 215 µm; the apical segment appearing partially divided, indicating an obsolete fifth segment; few flagellate setae on basal antennal segment, numerous such setae on all other segments, 30–55 µm long. Legs well developed; average length of metatrochanter + femur 212 µm long; metatibia + tarsus 150 µm long; tarsus swollen basally and abruptly tapering; with metaclaw 70–80 µm long, longer than tarsus. Ratio of length of metatibia to tarsus, 1.60; leg segments with multiple stout flagellate setae. Labium 3-segmented, 147 µm long, longer than clypeolabral shield, 70 µm wide; basal segment with three pairs of setae; eight pairs of setae on terminal seg-

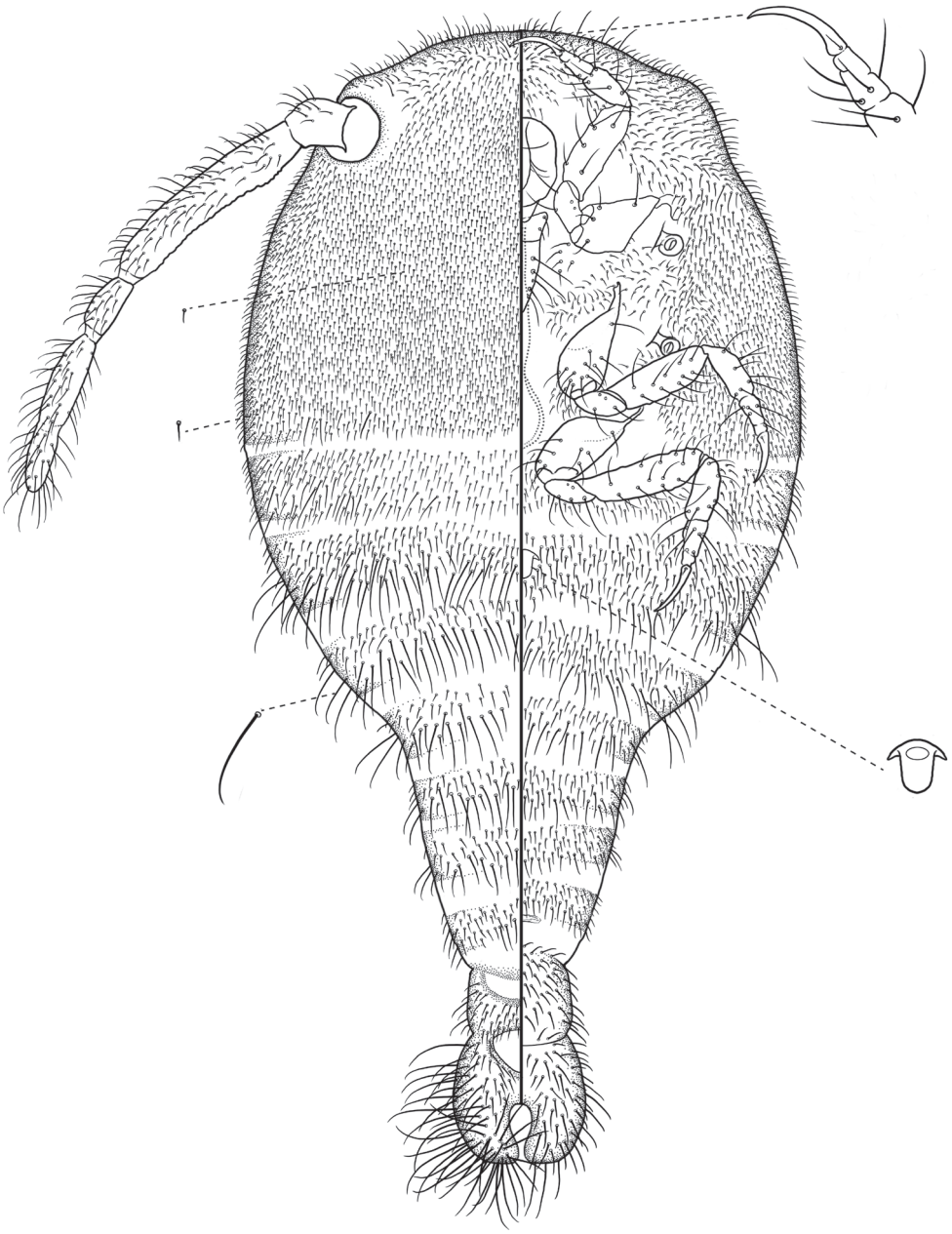


Figure 14. *Neochavesia podexuta* sp. nov. Adult female, full body view, illustrated from the holotype and paratypes. Illustration by Taina Litwak (USDA, ARS, Systematic Entomology Laboratory) with edits by SAS.

ment. One round circulus present, situated towards center of abdominal segment II, 16 μm in diameter, conical and projecting from derm, cup-shaped internally. Spiracles normal, 35 μm in diameter at widest point.

Dorsal surface of head and thorax crowded with slender flagellate setae, about 17 μm long, few approaching 45 μm at posterior end of metathorax, most with small setal collars, longer setae with slightly wider collars; abdominal segments with similar setae but less densely crowded after segment I; on each segment, setae at anterior end shorter and finer than posterior setae, ranging from 19–75 μm on segment I, upwards of 95 μm on segments II–VI, shorter setae 25–40 μm on VII–VIII, longest setae on anal lobes, from 32–135 μm. Venter with similar setation; less densely crowded on head and with greater variation in setal lengths, 15–40 μm; thoracic margin to submargin similar to dorsum; thoracic submedian similar to ventral head; abdominal segments I–IV similar to dorsum, segments V–VIII with shorter setae, anal lobes with numerous long setae but generally shorter than those found on dorsum. Pores and ducts absent.

Material examined. ***Holotype*:** Peru • 1 adult female; Madre de Dios, Las Cruces, Manu Paradise Lodge, from *Acropyga manuense* nest behind lodge, in soil around small rotting branches; 13.055°S, 71.544°W; 31.v.2019; J.S. LaPolla and S.A. Schneider leg.; UNMSM (nest ID PER01-02; prep S0401E). ***Paratypes*:** Peru • 6 adult females; same data as holotype; USNM (nest ID PER01-01; preps S0400A,B,C,D,E,F) • 1 immature female; same data as holotype; USNM (nest ID PER01-02; prep S0401A).

Informal synonyms. This species was previously referred to as "*Neochavesia* undescribed" in Schneider et al. (2022).

Etymology. The epithet is a noun in apposition, referring to the distinctive bald patch located just anterior to the anal opening. The Latin *'podex'*, meaning fundament/anus, was combined with *'exutus'*, meaning bared or stripped.

Remarks. *Neochavesia podexuta* bears a distinctive bald patch on the dorsal anterior surface of abdominal segment VIII. On slide-mounted specimens, it often appears as though this segment, including the anal lobes, has become detached from the rest of the body although it is still intact. In life, species of *Neochavesia* hold their abdomen in a curled position over their dorsum, resembling the tail of a scorpion; this bald membranous patch is located where the cuticle would curve inward. Adult females of *Neochavesia podexuta* are similar to *N. cephalonodus*, *N. eversi*, *N. iwokramae*, and *N. lapollai* in possessing antennae that articulate at the basal segment with a sclerotized prominence (forming a socket) on the head. They also lack a pair of setae on the middle labial segment, a characteristic shared among these species as well. The new species is most akin to *N. eversi*; the former can be distinguished from the latter by the bald patch on VIII described above and by their longer antennae. In *N. podexuta*, the body is about 2.0–2.5 times longer than the antennae with the second segment almost 300 μm long; whereas in *N. eversi*, the body is roughly 3.5 times the length of the antennae with the second segment only about 150 μm long.

Direct association between *A. manuense* and *N. podexuta* was confirmed by collecting ants and root mealybugs into a nest-box and observing interactions (Schneider et al. 2022). Ants gathered root mealybugs into protective clusters within the nest-box and were observed actively tending them. These observations were made over a 48-hour period in field-based laboratory conditions.

Key to adult females of *Neochavesia* Williams & Granara de Willink, 1992

Adapted from Schneider and LaPolla (2011) and Williams (2004).

1 Anal lobes fused with abdominal segment VIII, without intersegmental line; antennae situated toward ventral head margin **2**

– Anal lobes separated from abdominal segment VIII by intersegmental line; antennae situated on lateral margin or dorsally on head **4**

2 Trilocular pores present on head and thorax ..... ***Neochavesia caldasiae*** **(Balachowsky)**

– Trilocular pores absent **3**

3 Claws over 1/2 length of tarsi; one circulus present on third abdominal segment; posterior abdominal segments with rows of rigid thorn-like setae ..... ***Neochavesia linealuma*** **Schneider & LaPolla**

– Claws between 1/4 and 1/3 length of tarsi; two circuli present on abdominal segments II and III; all setae on abdominal segments flagellate ..... ***Neochavesia weberi*** **(Beardsley)**

4 Antennae normally five segmented **5**

– Antennae normally four segmented **7**

5 Second antennal segment 203–293 μm long; anal ring transversely elliptical and situated between anal lobes and abdominal segment VIII; many long stout setae on head margin ..... ***Neochavesia lapollai*** **Williams**

– Second antennal segment 81–185 μm long; anal ring round to triangular and situated near proximal base or in middle of anal lobes between anterior edge and base of U-shaped notch between anal lobes; head without long stout setae **6**

6 Second antennal segment 81–95 μm long, antennae articulating with prominences on head; anal ring situated in middle of anal lobes between anterior edge and base of U-shaped notch between anal lobes ..... ***Neochavesia iwokramae*** **Williams**

– Second antennal segment 168–185 μm long, antennae not articulating with prominence on head; anal ring situated near proximal base of anal lobes ..... ***Neochavesia trinidadensis*** **(Beardsley)**

7 Claws shorter than tarsi; second antennal segment 365–415 μm long; prominences enlarged giving head a swollen appearance ..... ***Neochavesia cephalonodus*** **Schneider & LaPolla**

– Claws longer than tarsi; second antennal segment not exceeding 300 μm in length, prominences on head relatively small **8**

8 Body roughly 2.0–2.5 times longer than antennae, with second antennal segment almost 300 μm in length; dorsal anterior surface of abdominal segment VIII membranous and free of setae, appearing bald ..... ***Neochavesia podexuta*** **Schneider & LaPolla, sp. nov.**

– Body roughly 3.5 times longer than antennae, with second antennal segment about 150 μm in length; dorsal anterior surface of abdominal segment VIII sclerotized and bearing setae ..... ***Neochavesia eversi*** **(Beardsley)**

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RESEARCH ARTICLE

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Three new species of the primitively segmented spider genus *Songthela* (Mesothelae, Liphistiidae, Heptathelinae) from Hunan Province, China

Yan Zhang[1], Zhaoyang Chen[1], Daiqin Li[2], Xin Xu[1]

1 *College of Life Sciences, Hunan Normal University, Changsha 410081, Hunan Province, China* **2** *Department of Biological Sciences, National University of Singapore, 14 Science Drive 4, 117543, Singapore*

Corresponding author: Xin Xu (xuxin@hunnu.edu.cn)

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Abstract

Three new species of the primitively segmented spider genus *Songthela* Ono, 2000 are identified and described from Hunan Province, China, based on morphological characters of males and females: *S. anhua* Zhang & Xu, **sp. nov.** (♂♀), *S. longhui* Zhang & Xu, **sp. nov.** (♂♀), and *S. zhongpo* Zhang & Xu, **sp. nov.** (♂♀). All the new *Songthela* species belong to the *multidentata*-group according to male palp and female genital morphology.

Keywords

Araneae, morphology, taxonomy, trapdoor spiders

Introduction

The primitively segmented spider family Liphistiidae Thorell, 1869 is the basal lineage among spiders, which contains species with a limited dispersal ability and high endemicity (Bristowe 1976; Haupt 2003; Xu et al. 2015a, b). Members of liphistiids retain some plesiomorphic arachnid traits, such as abdominal tergites (Fig. 1) and spinnerets situated in the middle of abdominal venter (Bristowe 1975; Haupt 2003;

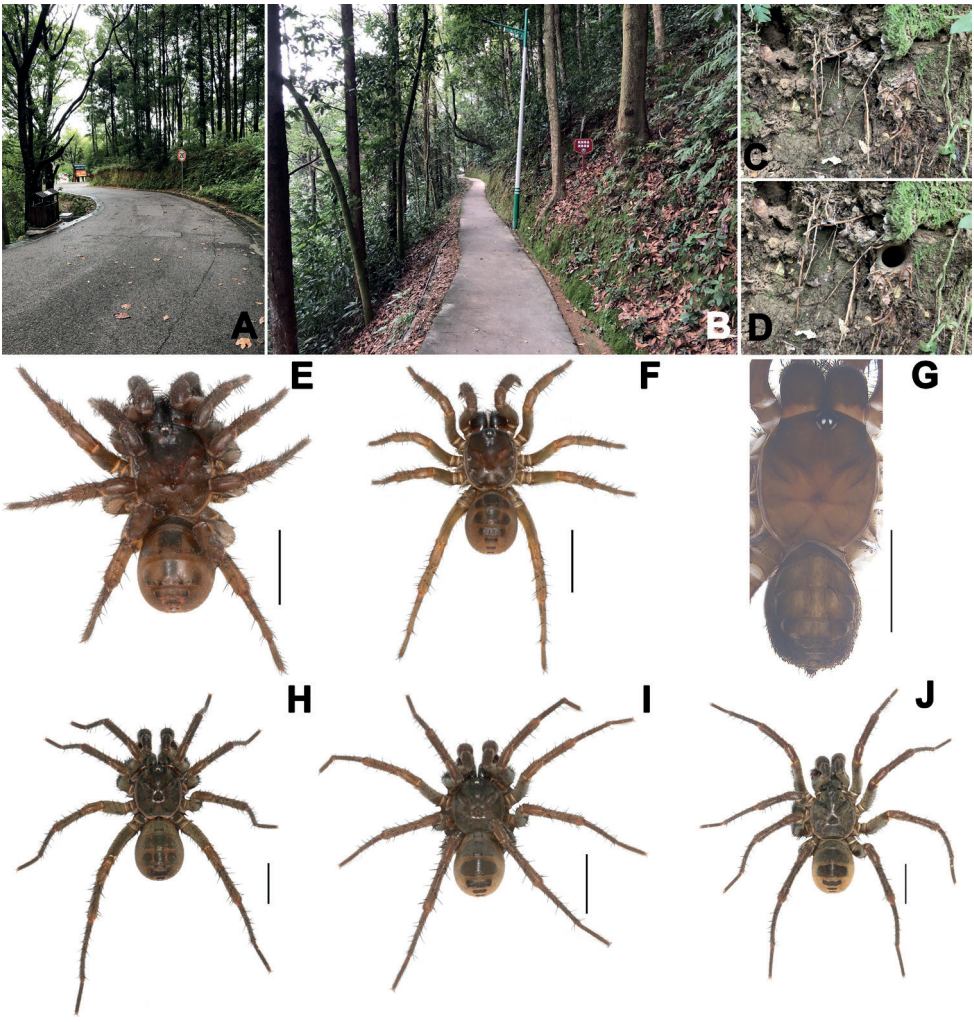

Figure 1. Microhabitat (**A–D**) and general somatic morphology (**E–J**) of three new *Songthela* species **E–G** female **H–J** male **E, H** *Songthela zhongpo* Zhang & Xu, sp. nov. **F, I** *Songthela longhui* Zhang & Xu, sp. nov. **G, J** *Songthela anhua* Zhang & Xu, sp. nov. Scale bar: 5 mm.

Schwendinger and Ono 2011; Xu et al. 2015a). Although a few alternative taxonomic classifications for this group did exist (Kishida 1923; Haupt 1983, 2003; Ono 2000; Schwendinger and Ono 2011), the classification system of a single family Liphistiidae consisting of eight genera in two subfamilies, Liphistiinae Thorell, 1869 and Heptathelinae Kishida, 1923, was established based on the evidence from morphology, monophyly, phylogeny, and fossils (Xu et al. 2015a, b), and has been widely accepted by most arachnologists since then (Schwendinger et al. 2019; Ono and Aung 2020; Yu et al. 2021). Recently, Li (2022) elevated the two subfamilies, Liphistiinae and Heptathelinae, to family ranks, Liphistiidae and Heptathelidae, but provided no additional justification for the taxonomic classification change. Breitling (2022) argued against

Li's two-family classification system based on nomenclature, morphology, molecular data and fossils, and recommended to maintain a single family Liphistiidae. We agree with Breitling's argumentation, and follow the classification that we have previously proposed (Xu et al. 2015a, b, 2021), which supports two subfamilies in the family Liphistiidae because all members of Liphistiidae share the same plesiomorphic traits mentioned above, although the members of Liphistiinae have signal lines around their burrow entrances, which are often used as one of the diagnostic characters to separate Liphistiinae from Heptathelinae.

Currently, the genus *Songthela* Ono, 2000, belonging to the subfamily Heptathelinae, contains 35 described species, of which, 34 are distributed in southern China (Chongqing, Guizhou, Hubei, Hunan, Sichuan, Yunnan, Zhejiang); one species, *S. sapana* (Ono, 2010) is found in northern Vietnam (World Spider Catalog 2023). Until now, 20 *Songthela* species are known from Hunan Province, and they are divided into three species groups based on morphology and molecular data: *bispina*-group, *multidentata*-group, and *unispina*-group (details see Li et al. 2022).

In this study, we diagnose and describe three new *Songthela* species collected from Hunan Province, China based on male palp and female genital morphology.

Materials and methods

We collected the specimens alive from Hunan Province, China (Fig. 2), brought subadults back to the laboratory, and reared them until they reached maturation. We removed the right four legs of adults, preserved them in 100% ethanol, and stored them at –80 °C for molecular work. We preserved the remaining body of each specimen in 80% ethanol as vouchers for morphological examination. All type and voucher specimens are deposited at the College of Life Sciences, Hunan Normal University, Changsha, Hunan Province, China.

We examined and dissected the specimens using an Olympus SZ61 stereomicroscope. The soft tissues of female genitalia were removed and degraded using 10 mg/ml pancreatin (Bomei Biotech Company, Hefei, Anhui, China) for at least 3 h at the room temperature. Male palp and female genitalia were observed and photographed using the digital camera CCD mounted on an Olympus BX53 compound microscope, and then generated compound focused images using Helicon Focus v.6.7.1. All measurements are given in millimeters. Leg and palp measurements are given in the following order: leg total length (femur + patella + tibia + metatarsus + tarsus), palp total length (femur + patella + tibia + tarsus).

Abbreviations used are: **ALE** = anterior lateral eyes; **AME** = anterior median eyes; **BC** = bursa copulatrix; **BL** = body length; **CL** = carapace length; **Co** = conductor; **CT** = contrategulum; **CW** = carapace width; **DT** = dorsal extension of terminal apophysis of tegulum; **E** = embolus; **GA** = genital area; **GS** = genital stalk; **MA** = marginal apophysis of tegulum; **OL** = opisthosoma length; **OW** = opisthosoma width; **PC** = paracymbium; **PLE** = posterior lateral eyes; **PME** = posterior median eyes; **RC** = receptacular cluster; **T** = tegulum; **TA** = terminal apophysis of tegulum.

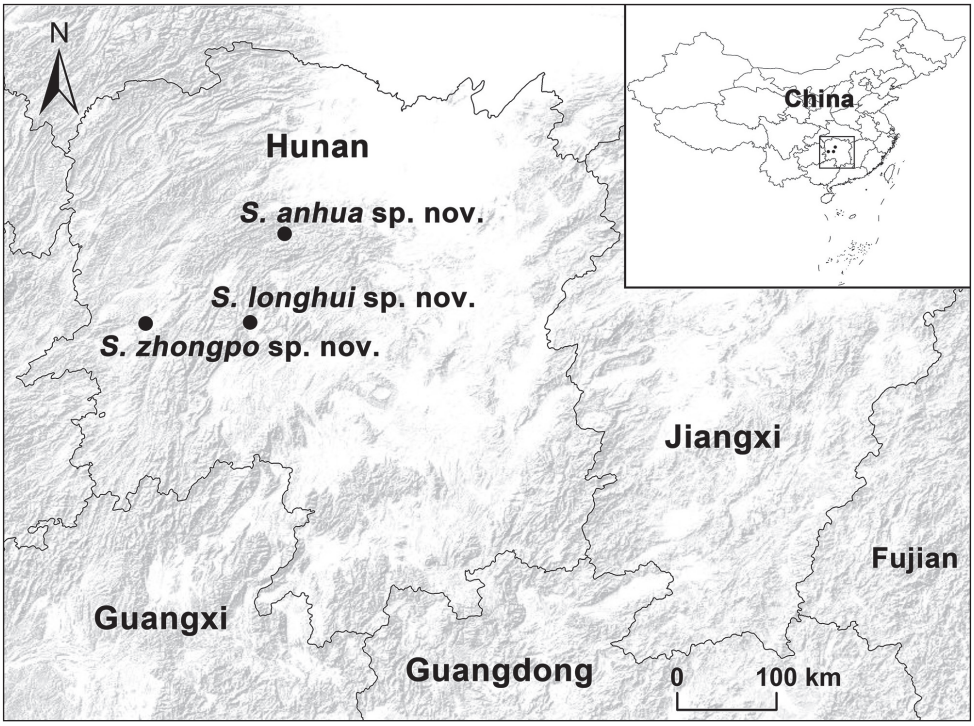

Figure 2. Map showing the type localities of the three new *Songthela* species in Hunan Province, China.

Taxonomy

Family Liphistiidae Thorell, 1869
Subfamily Heptathelinae Kishida, 1923

Genus *Songthela* Ono, 2000

Type species. *Heptathela hangzhouensis* Chen, Zhang & Zhu, 1981.

Diagnosis. Males of *Songthela* differ from those of all other Heptathelinae genera by smooth conductor with one or two apical spines and by conductor middle portion having several teeth (Figs 3B, E, 4A–C, 6A, B); by embolus having a wide and flat opening (Figs 3D, 4D, 6D); and by contrategulum having densely serrated margin (Figs 3D, 4D, 6D); females of *Songthela* can be distinguished from those of all other liphistiid genera by two pairs of receptacular clusters separated from each other, median ones with obviously tubular genital stalks, four receptacular clusters situated at the anterior margin of the bursa copulatrix, or middle ones situated at the anterior margin of the bursa copulatrix and lateral ones located relatively dorsolaterally, or all four located dorsally (Figs 3J–M, 5A–F, 7A–H).

Distribution. China (Chongqing, Guizhou, Hubei, Hunan, Sichuan, Yunnan, Zhejiang) and Vietnam (Lao Cai).

***Songthela anhua* Zhang & Xu, sp. nov.**
https://zoobank.org/508E6FAF-B31C-4680-AFEA-7935331007AC
Fig. 3

Type material. ***Holotype*:** China · 1 ♂; Hunan Province, Yiyang City, Anhua County, Moon Hill Park; 28.39°N; 111.22°E; alt. 125 m; 7 September 2021; Z.Y. Chen, X. Xu, Y. Zhan, Y. Zhang leg.; XUX-2021-007 (matured on 25 August 2022). ***Paratypes*:** China · 1 ♂ 3 ♀; same data as for the holotype, alt. 127–144 m; XUX-2021-008, 012, 018 (matured on 25 August 2022), 019.

Diagnosis. Male of *S. anhua* sp. nov. resembles those of *S. tianzhu* Chen, Li, Li & Xu, 2021, *S. yuping* Chen, Li, Li & Xu, 2021, and *S. xiangnan* Li, Liu, Li & Xu, 2020 by conductor with blade-shaped apical spine (Fig. 3C–E, H, I), but can be distinguished from *S. tianzhu* by tegulum with smaller terminal apophysis and distinctly helicoid marginal apophysis (Fig. 3F, G), by conductor with wider apical spine and several short teeth in prolateral view (Fig. 3B, C, E, H, I); from *S. xiangnan* by wider apical spine of conductor lacking of bifid apex distally (Fig. 3C, E, H, I), and by contregulum with irregular dense dentate margin (Fig. 3C, D); from *S. yuping* by tegulum with slightly narrower dorsal extension of terminal apophysis (Fig. 3F, G); from those of *S. longhui* sp. nov. and *S. zhongpo* sp. nov. by conductor with slightly shorter and blade-shaped apical spine (Fig. 3B–E, H, I), by tegulum with slightly narrower dorsal extension of terminal apophysis (Fig. 3F, G); from those of other species of *multidentata*-group by conductor with blade-shaped apical spine (Fig. 3C–E, H, I); from those of other *Songthela* species by middle part of conductor with several short teeth (Fig. 3B–E, H, I).

Females of *S. anhua* sp. nov. can be distinguished from those of *S. longhui* sp. nov. and *S. pluma* Yu, Li & Zhang, 2018 by median receptacular clusters slightly larger than lateral ones, and middle genital stalks separated from each other basally (Fig. 3J, K); from *S. zhongpo* sp. nov. by trapeziform anterior margin of bursa copulatrix, median receptacular clusters with slightly longer genital stalks (Fig. 3J–K); from those of other species of *multidentata*-group by median receptacular clusters separated from each other basally and posterior margin of genital area wider and flat (Fig. 3J–M); from those of other *Songthela* species by four receptacular clusters situated at the dorsal side of bursa copulatrix (Fig. 3J–M).

Description. Male (holotype; Fig. 1J). Carapace black brown; opisthosoma yellow brown, with 12 black brown tergites attached a pair of thick bristles, the second to fifth larger than others and the fourth largest; sternum narrow, much longer than wide; a few pointed hairs running over ocular area; chelicerae robust with promargin of cheliceral groove with 14 denticles of variable size; legs with sturdy hairs and spines; 8 spinnerets. Measurements: BL 13.28, CL 6.42, CW 5.70, OL 6.19, OW 4.85; ALE > PLE > PME > AME; leg I 20.58 (5.80 + 2.53 + 4.25 + 5.27 + 2.73), leg II 19.69 (5.54 + 2.52 + 4.18 + 4.88 + 2.57), leg III 22.95 (5.56 + 2.69 + 4.28 + 6.95 + 3.47), leg IV 28.29 (7.32 + 3.03 + 5.69 + 7.97 + 4.28).

***Palp*.** Prolateral portion of paracymbium unpigmented and unsclerotised, with several setae and spines on the tip (Fig. 3A–C). Contregulum with an obviously

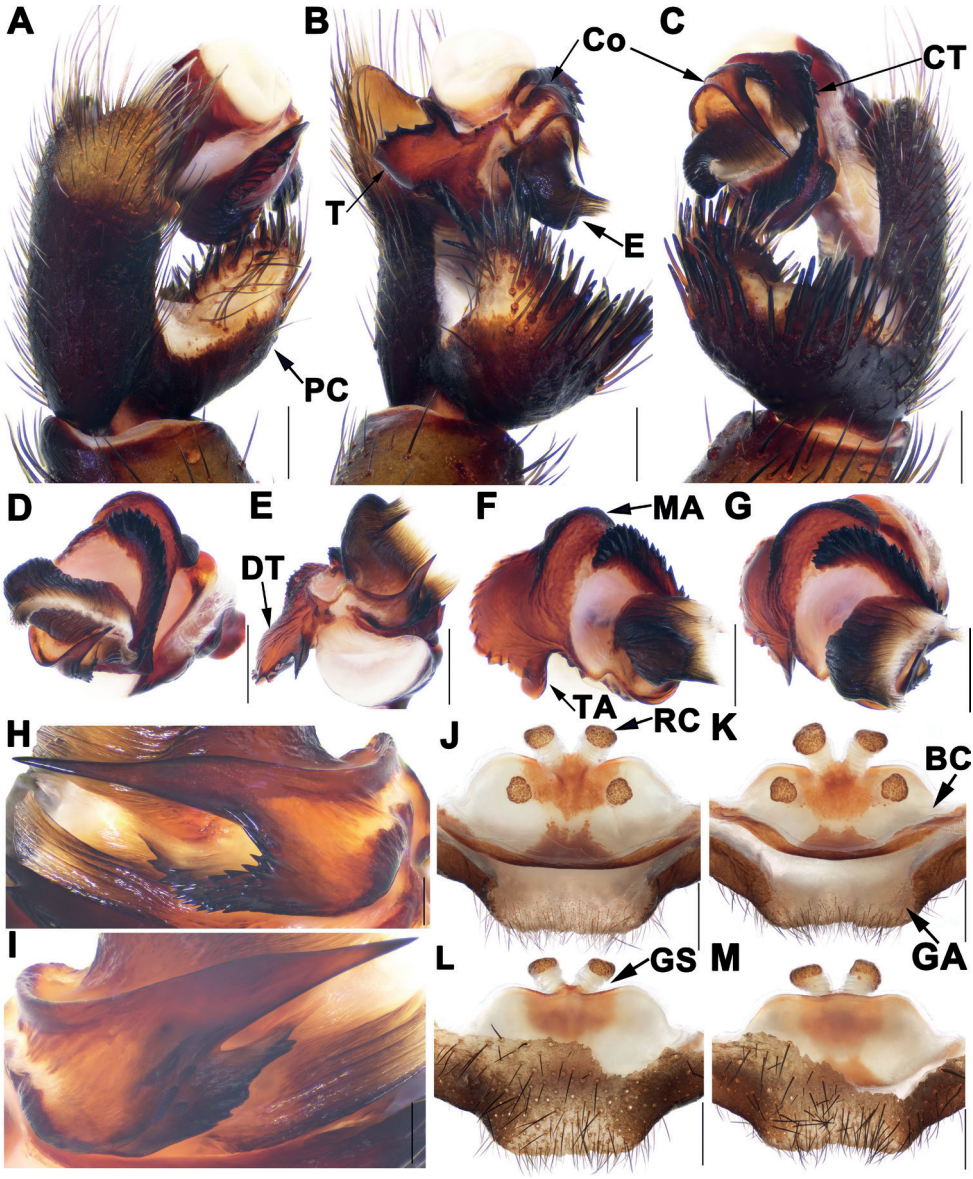

Figure 3. Male and female genital anatomy of *Songthela anhua* Zhang & Xu, sp. nov. **A–C** left palp **A** prolateral view **B** ventral view **C** retrolateral view **D–G** right palp **D** prolateral view **E** ventral view **F** retrolateral view **G** distal view **H** conductor of left palp **I** conductor of right palp **J, K** vulva dorsal view **L, M** vulva ventral view **A–C, H** XUX-2021-007 (holotype) **D–G, I** XUX-2021-018 **J, L** XUX-2021-008 **K, M** XUX-2021-012. Scale bars: 0.5 mm (**A–G, J–M**); 0.1 mm (**H, I**).

triangular apophysis proximally and two irregular dentate edges distally (Fig. 3C, D). Tegulum with a helicoid marginal apophysis, a dentate dorsal extension of the terminal apophysis, and a thumb-like terminal apophysis retrolaterally (Fig. 3F, G). Conductor

lamellar, fused with embolus ventroproximally, with a blade-shaped apical spine pointed to the one-third of opening of embolus proximally, and the middle portion inserted with several teeth (Fig. 3B–E, H, I). Embolus largely sclerotized with a wide opening, several ribbed ridges, and with a twisted top in ventral view (Fig. 3B–E, G).

Female (XUX-2021-008; Fig. 1G). Carapace yellow brown and opisthosoma dark brown in alcohol, with 12 dark brown tergites attached a pair of thick bristles, the second to fifth larger than others and the fourth largest; sternum narrow, much longer than wide; a few pointed hairs running over ocular area; chelicerae robust with promargin of cheliceral groove with 12 denticles of variable size; legs with sturdy hairs and spines; 7 spinnerets. Measurements: BL 10.18, CL 5.16, CW 4.52, OL 4.43, OW 3.57; ALE > PLE > PME > AME; palp 9.82 (3.37 + 1.81 + 2.41 + 2.23), leg I 10.97 (3.66 + 1.83 + 2.16 + 1.96 + 1.36), leg II 10.29 (3.21 + 1.79 + 1.86 + 2.06 + 1.37), leg III 9.71 (2.91 + 1.74 + 1.22 + 2.27 + 1.57), leg IV 14.37 (4.22 + 1.60 + 2.49 + 3.72 + 2.34).

***Female genitalia*.** Two pairs of receptacular clusters situated on the dorsal side of the bursa copulatrix; the middle pair of receptacular clusters with long genital stalks and larger than the lateral ones, the middle stalks separated from each other; the posterior margin of the bursa copulatrix sclerotized; the posterior margin of the genital area wide (Fig. 3J–M).

Variation. Males and females vary in body size, cheliceral teeth, and spinnerets. Range of measurements in males (N = 2): BL 11.94–13.28, CL 5.59–6.42, CW 5.07–5.70, OL 6.08–6.19, OW 4.80–4.85; the number of cheliceral teeth varies from 9–14 (N = 2); there are 7 or 8 spinnerets. Females (N = 3): BL 10.18–11.51, CL 5.16–5.57, CW 4.52–4.84, OL 4.43–5.66, OW 3.57–4.04; the number of cheliceral teeth varies from 12–13 (N = 3); there are 7 or 8 spinnerets. In addition, male palp and female genitalia also show intraspecific variations: in males, the left palp is slightly different from the right palp, e.g. the tegulum of left male palp with three teeth basally in ventral view (Fig. 3B), but they are missing in right male palp (Fig. 3E, F); the number of teeth located in middle portion of conductor also varies between left and right palp (Fig. 3C, E, H, I); in females, the relative position of the middle receptacular clusters situated on the dorsal side of the bursa copulatrix is slightly different (Fig. 3L, M).

Etymology. The species epithet, a noun in apposition, refers to the type locality.

Distribution. Hunan (Anhua), China

***Songthela longhui* Zhang & Xu, sp. nov.**

https://zoobank.org/EBBC224B-1404-41B6-B08B-EC8D3A5749AB

Figs 4, 5

Type material. ***Holotype*:** China · 1 ♂; Hunan Province, Shaoyang City, Longhui County, Jinshiqiao Town, Huangjinjing Village; 27.58°N; 110.90°E; alt. 550 m; 18 September 2021; Z.Y. Chen, X. Xu, Y. Zhan, Y. Zhang leg.; XUX-2021-275 (matured on 25 August 2022). ***Paratypes*:** China · 1 ♂, 5 ♀; same data as for the holotype, alt. 552 m; XUX-2021-278, 281, 282, 282A (matured on 25 August 2022), 283, 285A.

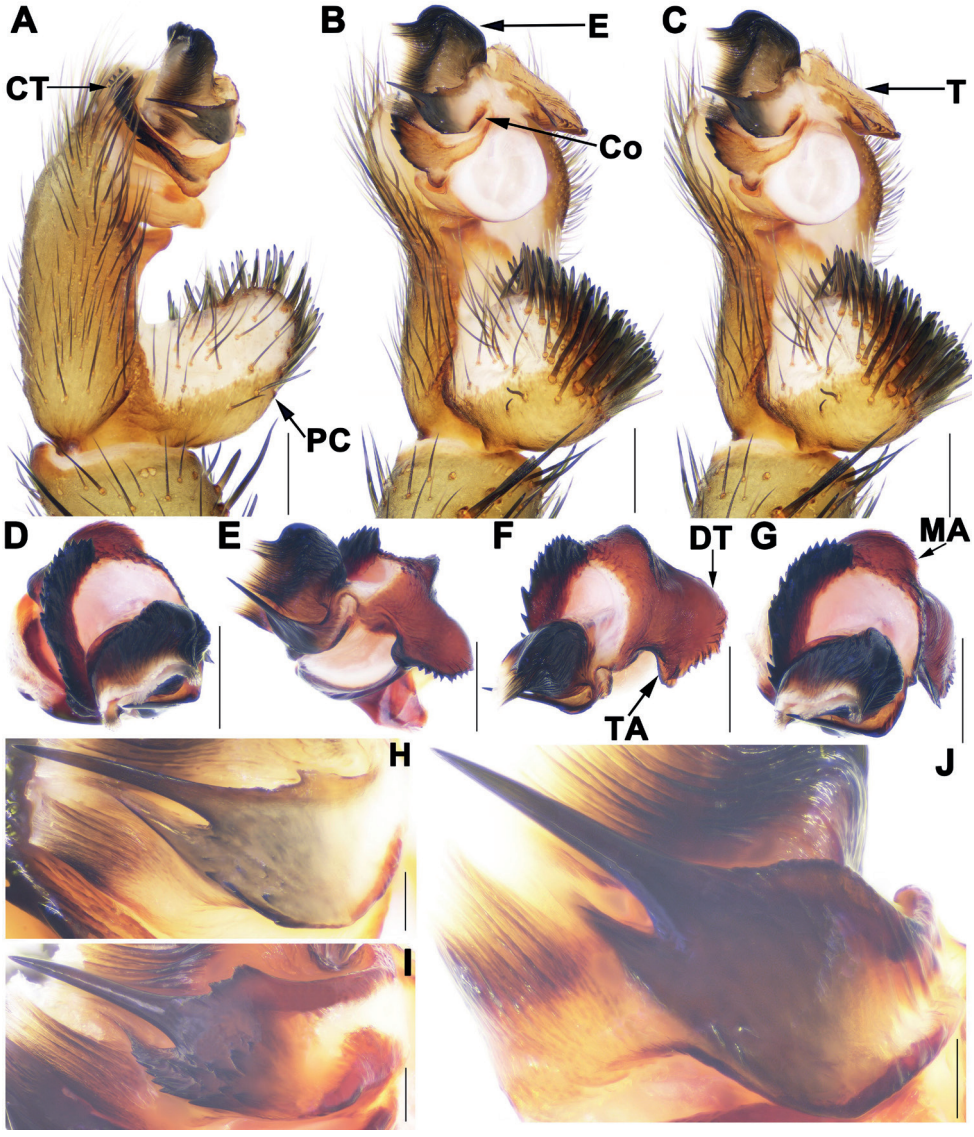

Figure 4. Male genital anatomy of *Songthela longhui* Zhang & Xu, sp. nov. **A, D** palp prolateral view **B, E** palp ventral view **C, F** palp retrolateral view **G** palp distal view **H–J** conductor ventral view **A–C, H** XUX-2021-275 (holotype) **D–G, J** XUX-2021-282A **I** XUX-2021-287. Scale bars: 0.5 mm (**A–G**); 0.1 mm (**H–J**).

Diagnosis. Male of *S. longhui* sp. nov. resembles those of *S. dapo* Li, Chen, Liu, Li & Xu, 2022, *S. lingshang* Li, Chen, Liu, Li & Xu, 2022, *S. multidentata* Li, Chen, Liu, Li & Xu, 2022, *S. pluma* and *S. xiujian* Li, Chen, Liu, Li & Xu, 2022 by conductor with needle-shaped apical spine (Fig. 4A, B, E, H–J), but can be distinguished from those of *S. dapo* and *S. lingshang* by tegulum with smaller dorsal extension of

terminal apophysis (Fig. 4C, F), and conductor with slightly narrower base of apical spine (Fig. 4A, H–J); from *S. multidentata* by conductor with longer apical spine (Fig. 4A, B, E, H–J), and contrategulum with larger apophysis proximally (Fig. 4A, B, D); from *S. pluma* by tegulum with smaller terminal apophysis (Fig. 4F), and contrategulum with one irregular dentate margin (Fig. 4A, D); from *S. xiujian* by contrategulum with larger apophysis proximally (Fig. 4A, B, D); from *S. anhua* sp. nov. by apical spine of conductor needle-shaped (Fig. 4A, B, H–J), by tegulum with slightly smaller terminal apophysis and wider dorsal extension of terminal apophysis (Fig. 4C, F); from *S. zhongpo* sp. nov. by apical spine of conductor with slightly narrower base (Fig. 4A, H–J); from those of other species of *multidentata*-group by needle-shaped apical spine of conductor (Fig. 4A, E, H–J); from those of other *Songthela* species by middle part of the conductor with several small spines (Fig. 4A, B, E, H–J).

Females of *S. longhui* sp. nov. can be distinguished from *S. anhua* sp. nov. by Y-shaped median genital stalks, lateral receptacular clusters with distinct short genital stalks, and deeper depressions in dorsal view (Fig. 5A–C); from *S. pluma* by lateral receptacular clusters with slightly longer genital stalks, and two larger and deeper depressions in dorsal view (Fig. 5A–C); from *S. zhongpo* sp. nov. by median receptacular clusters with longer genital stalks (Fig. 5A–C); from those of other species of *multidentata*-group by median receptacular clusters with longer genital stalks, and Y-shaped median genital stalks, lateral ones with distinct genital stalks (Fig. 5A–C); from those of other *Songthela* species by four receptacular clusters located at dorsal side of bursa copulatrix and median genital stalks fused together basally (Fig. 5A–C).

Description. Male (holotype). Carapace brown; opisthosoma yellow brown, with 12 brown tergites attached a pair of hard and thick bristles, the second to fifth larger than others and the fourth largest; sternum narrow, much longer than wide; a few pointed hairs running over ocular area; chelicerae robust with promargin of cheliceral groove with 11 denticles of variable size; legs with sturdy hairs and spines; 6 spinnerets. Measurements: BL 11.94, CL 5.36, CW 4.63, OL 5.91, OW 4.72; ALE > PLE > PME > AME; leg I 16.52 (4.72 + 2.10 + 3.32 + 4.05 + 2.33), leg II 16.34 (4.37+ 2.09 + 3.13 + 4.23 + 2.52), leg III 19.10 (5.17 + 2.07 + 3.37 + 5.47 + 3.02), leg IV 23.98 (5.80 + 2.44 + 4.65 + 7.31 + 3.78).

***Palp*.** Paracymbium unpigmented and unsclerotised prolaterally, numerous setae and spines on the tip (Fig. 4A–C). Contrategulum with an arched apophysis proximally and irregular dentate edge (Fig. 4A, B, D). Tegulum with a semi-circular marginal apophysis and dentate dorsal extension of the terminal apophysis, and with a small terminal apophysis retrolaterally (Fig. 4C, F, G). Conductor having a long apical spine pointed to the one-third of opening of embolus proximally, the middle part covered with several small teeth, and the smooth base fused with embolus (Fig. 4A, B, E, H–J). Embolus largely sclerotized, with a wide and flat opening, several longitudinal ribs in middle and distal portion (Fig. 4A, B, D, E, G).

Female (XUX-2021-281; Fig. 1F). Carapace dark reddish brown and opisthosoma light brown, with 12 dark brown tergites attached a pair of thick bristles, the second to fifth larger than others and the fourth largest; sternum narrow, much longer than wide; a few pointed hairs running over ocular area; chelicerae robust with promargin

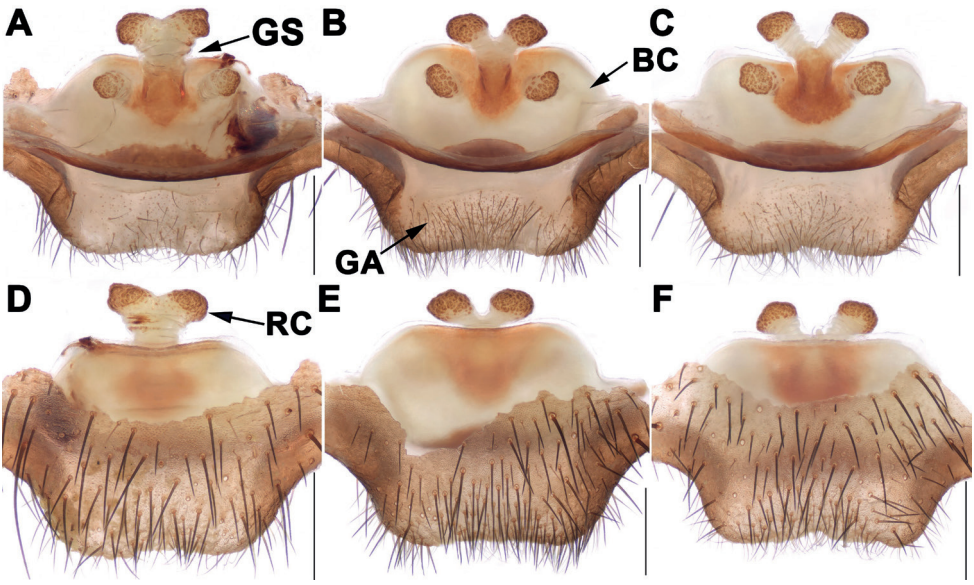

Figure 5. Female genital anatomy of *Songthela longhui* Zhang & Xu, sp. nov. **A–C** vulva dorsal view **D–F** vulva ventral view **A, D** XUX-2021-281 **B, E** XUX-2021-282 **C, F** XUX-2021-278. Scale bars: 0.5 mm.

of cheliceral groove with 12 denticles of variable size; legs with sturdy hairs and spines; 7 spinnerets. Measurements: BL 11.52, CL 5.20, CW 4.33, OL 5.73, OW 4.51; ALE > PLE > PME > AME; palp 9.41 (3.36 + 1.56 + 1.90 + 2.59), leg I 10.69 (3.41 + 1.72 + 2.12 + 2.03 + 1.41), leg II 10.56 (3.29 + 1.76 + 1.82 + 2.14 + 1.55), leg III 11.23 (3.22 + 1.80 + 1.97 + 2.58 + 1.66), leg IV 15.96 (4.56 + 2.07 + 2.82 + 4.22 + 2.29).

Female genitalia. Two pairs of receptacular clusters with distinctly genital stalks, situated on the dorsal wall of the bursa copulatrix; the median ones similar to or slightly larger than the lateral ones, the Y-shaped middle genital stalks; the posterior margin of the bursa copulatrix sclerotized, the posterior margin of the genital area wide, two deeper depressions in dorsal view (Fig. 5A–F).

Variation. Males and females vary in body size, cheliceral teeth and spinnerets. Range of measurements in males (N = 2): BL 10.98–11.94, CL 4.95–5.36, CW 4.52–4.63, OL 5.60–5.91, OW 4.22–4.72. There are 6 or 7 spinnerets (N = 2). Females (N = 5): BL 5.56–11.86, CL 4.27–5.48, CW 3.61–4.58, OL 4.29–5.79, OW 3.27–4.60. The number of cheliceral teeth varies from 12 to 13 (N = 5). In addition, male palp and female genitalia also show intraspecific variations: in males, the middle part of conductor with more teeth (Fig. 4H, I) or less teeth (Fig. 4J); tegulum with a relatively larger terminal apophysis (Fig. 4C) or slightly smaller (Fig. 4E). In females, the middle Y-shaped genital stalk fused totally with only two receptacular clusters separated from each other (Fig. 5A, D) or fused basally and separated in the middle (Fig. 5B, C, E, F).

Etymology. The species epithet, a noun in apposition, refers to the type locality.

Distribution. Hunan (Longhui), China

***Songthela zhongpo* Zhang & Xu, sp. nov.**
https://zoobank.org/A5692990-DD85-4BDA-BE44-953DED723609
Figs 6, 7

Type material. ***Holotype*:** China · 1 ♂; Hunan Province, Huaihua City, Hecheng District, Zhongpo Forest Park; 27.57°N; 110.96°E; alt. 330 m; 17 September 2021; Z.Y. Chen, X. Xu, Y. Zhan, Y. Zhang leg.; XUX-2021-264 (matured on 3 August 2022). ***Paratypes*:** China · 3 ♂ 9 ♀; same data as for the holotype, alt. 300–345 m; XUX-2021-258, 259, 260, 261, 262 (matured on 18 September 2022), 263 (matured on 20 July 2022), 265, 266, 267 (matured on 26 July 2022), 267A, 267B, 267C.

Diagnosis. Male of *S. zhongpo* sp. nov. resembles those of *S. dapo*, *S. lingshang*, and *S. xiujian*, by apical spine of conductor with slightly wider base (Fig. 6A, D, E, H–K), but can be distinguished from *S. dapo* by tegulum with smaller terminal apophysis (Fig. 6C, F, G); from *S. lingshang* by contrategulum with slightly larger teeth (Fig. 6D, F, G, L), conductor with fewer teeth in middle part (Fig. 6A, D, E, H–K), and tegulum with a small terminal apophysis (Fig. 6C, F, G); from *S. xiujian* by tegulum with arched marginal apophysis (Fig. 6G), and contrategulum with slightly smaller apophysis proximally (Fig. 6A, L); from *S. anhua* sp. nov. by apical spine of conductor narrower and longer (Fig. 6A, B, D, H–K); from *S. longhui* sp. nov. by apical spine of conductor with slightly narrower base (Fig. 6A, H–K), and surface of dorsal extension of the tegular terminal apophysis with several ridges (Fig. 6G); from those of other species of *multidentata*-group by contrategulum with two dentate margins in middle part (Fig. 6D, L), by apical spine of conductor with slightly wider base and gradually becomes elongated distally (Fig. 6A, D, E, H–K); from those of other *Songthela* species by middle part of the conductor with several teeth (Fig. 6A, B, D, E, H–K).

Female of *S. zhongpo* sp. nov. can be distinguished from *S. anhua* sp. nov. by the lateral receptacular clusters with slightly longer genital stalks, and arched anterior margin of bursa copulatrix (Fig. 7A–D); from *S. longhui* sp. nov. by median receptacular clusters with shorter genital stalks (Fig. 7A–D); from *S. multidentata* by median receptacular clusters with thicker genital stalks (Fig. 7A–D), from *S. tianzhu* by lateral genital stalks slightly longer (Fig. 7A, D); from those of other species of *multidentata*-group by median receptacular clusters with slightly thicker genital stalks, and lateral ones with distinct genital stalks (Fig. 7A–H); from those of other *Songthela* species by two pairs of receptacular clusters situated on dorsal wall of bursa copulatrix (Fig. 7A–H).

Description. Male (holotype). Carapace black brown; opisthosoma dark brown, with 12 brown tergites attached a pair of thick bristles, the second to fifth larger than others and the fourth largest; sternum narrow, much longer than wide; a few pointed hairs running over ocular area; chelicerae robust with promargin of cheliceral groove with 11 denticles of variable size; legs with sturdy hairs and spines; 7 spinnerets. Measurements: BL 13.53, CL 5.96, CW 5.44, OL 7.19, OW 5.94; ALE > PLE > PME > AME; leg I 18.97 (5.30 + 2.29 + 3.95 + 4.93 + 2.50), leg II 19.13 (4.99 + 2.33 + 3.93 + 5.24 + 2.64), leg III 21.49 (5.25 + 2.46 + 3.91 + 6.52 + 3.35), leg IV 27.19 (6.62 + 2.84 + 5.17 + 8.59 + 3.97).

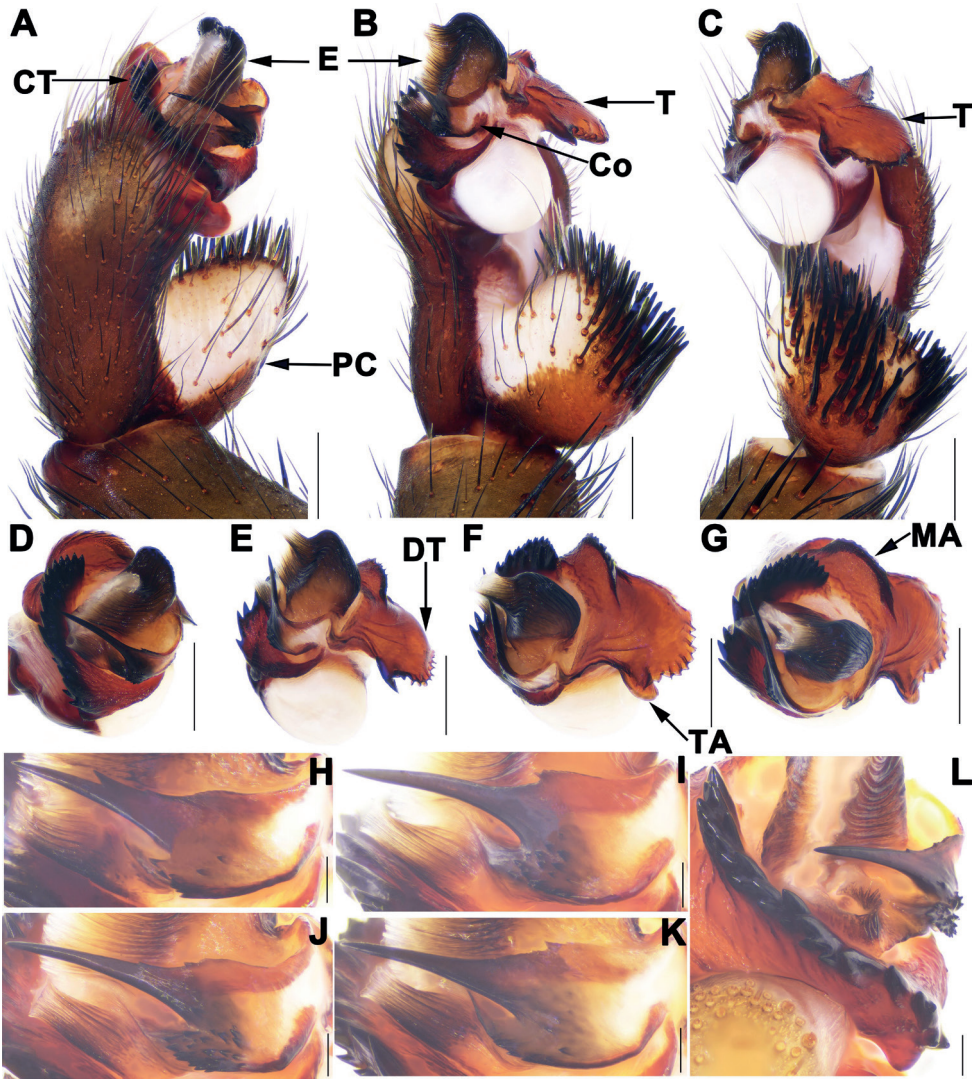

Figure 6. Male genital anatomy of *Songthela zhongpo* Zhang & Xu, sp. nov. **A, D** palp prolateral view **B, E** palp ventral view **C, F** palp retrolateral view **G** palp distal view **H–K** conductor ventral view **L** contrategulum prolateral view **A–C, J, L** XUX-2021-264 (holotype) **D–G, I** XUX-2021-263 **H** XUX-2021-262 **K** XUX-2021-267. Scale bars: 0.5 mm (**A–G**); 0.1 mm (**H–L**).

Palp. Paracymbium unpigmented and unsclerotised prolaterally, with several setae and spines on the tip (Fig. 6A–C). Contrategulum with a triangular apophysis proximally and with a dentate edge in distal and proximal portions, while with two dentate margins in the middle part (Fig. 6A, D, F, G, H–K). Tegulum with an arched helicoid marginal apophysis, a helicoid dorsal extension of the terminal apophysis, and a thumb-shaped terminal apophysis retrolaterally (Fig. 6C, E–G). Conductor fused

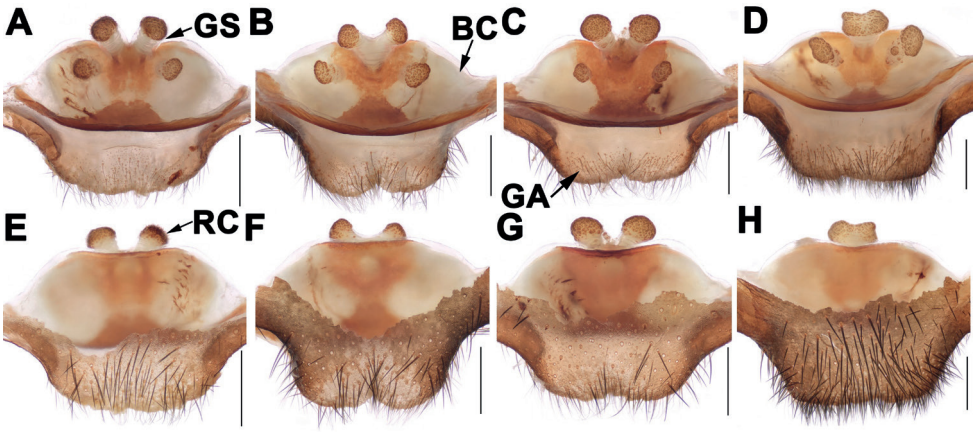

Figure 7. Female genital anatomy of *Songthela zhongpo* Zhang & Xu, sp. nov. **A–D** vulva dorsal view **E–H** vulva ventral view **A, E** XUX-2021-258 **B, F** XUX-2021-259 **C, G** XUX-2021-261 **D, H** XUX-2021-265. Scale bars: 0.5 mm.

with embolus basally and having several teeth in the middle part, the long apical spine with a spinule basally and pointed to the one-fourth of opening of embolus proximally (Fig. 6A, B, D–K). Embolus largely sclerotized, with a wide and flat opening, numerous longitudinal ribs in middle and distal portion (Fig. 6B, D–F).

Female (XUX-2021-258). Carapace reddish brown and opisthosoma light brown, with 12 dark brown tergites attached a pair of thick bristles, the second to fifth larger than remaining ones and the fourth largest; sternum narrow, much longer than wide; a few pointed hairs running over ocular area; chelicerae robust with promargin of cheliceral groove with 11 denticles of variable size; legs with sturdy hairs and spines; 7 spinnerets. Measurements: BL 9.32, CL 4.62, CW 3.95, OL 3.93, OW 3.31; ALE > PLE > PME > AME; palp 8.57 (3.05 + 1.56 + 1.84 + 2.12), leg I 9.17 (2.57 + 1.79 + 1.82 + 1.76 + 1.23), leg II 8.57 (1.96 + 1.65 + 1.77+ 1.84 + 1.35), leg III 9.72 (2.62 + 1.58 + 1.74 + 2.27 + 1.51), leg IV 14.28 (4.07 + 1.90 + 2.67 + 3.61 + 2.03).

Female genitalia. Four receptacular clusters situated on the dorsal side of the bursa copulatrix; the middle ones with thick genital stalks close to each other, fused together basally and separated from each other distally (Fig. 7A–C), or the middle genital stalks fused as one (Fig. 7D); the lateral receptacular clusters similar to or smaller than the middle ones; the posterior margin of the bursa copulatrix sclerotized, the posterior margin of the genital area wide and straight (Fig. 7A, D), or incurved in the middle (Fig. 7B, C).

Variation. Males and females vary in body size, cheliceral teeth and spinnerets. Range of measurements in males (N = 4): BL 12.54–13.80, CL 4.96–6.09, CW 5.29–5.89, OL 6.02–7.19, OW 4.23–5.94. The number of cheliceral teeth varies from 11 to 13. There are 6 or 8 spinnerets (N = 4). Females (N = 9): BL 9.32–13.77, CL 4.62–6.40, CW 3.95–5.49, OL 3.93–6.32, OW 3.31–5.14. The number of cheliceral teeth varies from 10 to 12. There are 7 or 8 spinnerets (N = 9). In addition, male palp and female genitalia also show intraspecific variations: in males, the apical spine of

conductor with a spinule in the middle part (Fig. 6H) or basally (Fig. 6A, D, I–K); the middle of conductor with more teeth (Fig. 6I, L) or relatively few teeth (Fig. 6H, K). In females, the middle pair of receptacular clusters similar (Fig. 7B) to or slightly larger than the lateral ones (Fig. 7A, C), the middle genital stalks fused together basally and separated from each other distally (Fig. 7A, C), or the middle genital stalks Y-shaped (Fig. 7B), or fused together totally (Fig. 7D).

Etymology. The species epithet, a noun in apposition, refers to the type locality.

Distribution. Hunan (Huaihua), China

Remarks. The three new species from Hunan Province, China can be assigned into the *multidentata*-group based on the following characters of both male palp and female genital morphology: 1) conductor of male palp with one apical spine and the middle part covered several teeth; 2) female genitalia with two pairs of receptacular clusters situated on the dorsal side of the bursa copulatrix; and 3) the posterior margin of the bursa copulatrix of female genitalia pigmented and sclerotised.

Acknowledgements

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RESEARCH ARTICLE

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Review of the Palaearctic species of *Miscogasteriella* Girault, 1915 (Chalcidoidea, Pteromalidae)

Ekaterina V. Tselikh[1], Jaehyeon Lee[2], Deok-Seo Ku[2]

1 *Zoological Institute, Russian Academy of Sciences, St Petersburg 199034, Russia* **2** *The Science Museum of Natural Enemies, Geochang 50147, Republic of Korea*

Corresponding author: Ekaterina V. Tselikh (tselikhk@gmail.com)

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Abstract

Palaearctic species of the genus *Miscogasteriella* Girault, 1915 are reviewed. *Miscogasteriella olgae* **sp. nov.** from South Korea and *M. vladimiri* **sp. nov.** from Japan are described. Type material of *M. nigricans* (Masi) and *M. sulcata* (Kamijo) is redescribed and illustrated. *Miscogasteriella nigricans* is recorded from the Palaearctic region for the first time. An identification key to females of all Palaearctic species of *Miscogasteriella* is given.

Keywords

Description, key, new record, new species, parasitoid, Trigonoderinae

Introduction

The pteromalid genus *Miscogasteriella* Girault, 1915 (type species *Miscogasteriella longiventris* Girault, 1915) belongs to the family Pteromalidae, subfamily Trigonoderinae (Burks et al. 2022), and is distributed in the Palaearctic, Oriental, and Australian regions. Until present, it comprised ten species, with only *Miscogasteriella sulcata* (Kamijo, 1962) being found in the Palaearctic region (Kamijo 1962; Tselikh et al. 2017; Noyes 2019).

Eight other species of *Miscogasteriella*, *M. bijoyi* Sureshan & Nihkil, 2013, *M. burmanica* (Hedqvist, 1968), *M. flavipes* (Masi, 1927), *M. jayasreeae* Sureshan, 1999, *M. keijli* Narendran, 2012, *M. nigricans* (Masi, 1927), *M. perakensis* (Hedqvist, 1968), *M. yemenica* Narendran & van Harten, 2007 are distributed in the Oriental region (Masi 1927; Hedqvist 1968; Sureshan 1999; Narendran and Harten 2007; Narendran 2012; Sureshan and Nikhil 2013; Noyes 2019).

Two species, *M. niger* (Bouček, 1988) and *M. longiventris* Girault, 1915, are distributed in the Australian region (Girault 1915; Bouček 1988; Noyes 2019).

Unfortunately, the biology is unknown for all species of *Miscogasteriella*, but mostly they were collected near dead trees in forests, suggesting similar hosts to other Trigonoderinae.

The aim of this work is to describe two new species of *Miscogasteriella* from South Korea and Japan, and to redescribe and illustrate the species *M. nigricans* and *M. sulcata*. An identification key to females of all Palaearctic species of *Miscogasteriella* is also provided.

Materials and methods

The specimens examined in this study are deposited in the collections of the Deutsches Entomologisches Institut (Eberswalde, Germany; **DEI**), the Department of Life Sciences of the Yeungnam University (Gyeongsan, Republic of Korea; **YNU**), the National Institute of Biological Resources (Incheon, Republic of Korea; **NIBR**), the Science Museum of Natural Enemies (Geochang, Republic of Korea; **SMNE**), the Korea National Arboretum (Pocheon, Republic of Korea; **KNA**), the Entomological Laboratory of the Hokkaido University (Sapporo, Japan; **EIHU**), the Ehime University Museum (Matsuyama, Japan; **EUM**), and the Zoological Institute of the Russian Academy of Sciences (St Petersburg, Russia; **ZISP**).

Morphological terminology, including sculpture and wing venation, follows Bouček and Rasplus (1991), Gibson (1997), and Burks et al. (2022). The flagellum consists of two anelli, six funicular segments, and the four-segmented clava. The following abbreviations are used: **POL** – posterior ocellar line, the minimum distance between the posterior ocelli; **OOL** – ocello–ocular line, the minimum distance between a posterior ocellus and compound eye; **C1–C4** – claval segments; **PST** – parastigma; **M** – marginal vein; **S** – stigmal vein; **PM** – postmarginal vein; **F1–F6** – funicular segments; **Mt2–Mt8** – metasomal tergites (Mt1 – petiole). The scape is measured without the radicle; the pedicel is measured in lateral view. The distance between the clypeal lower margin and the toruli is measured from the lower margins of the toruli. Eye height is measured as the maximum diameter, eye length as the minimum diameter. The mesosoma and metasoma are measured in lateral view, the latter including the ovipositor sheaths.

Specimens were examined using Olympus SZX12, Nikon SMZ745T and Zeiss SteREO Discovery V20 stereomicroscopes. Photographs were taken with a Canon EOS 70D digital camera mounted on an Olympus SZX10 microscope (ZISP specimens), and a Digital Sight PS-Fi2 camera mounted on a Nikon SMZ745T microscope (EIHU specimens). The acquired images were then processed with Helicon Focus.

Taxonomy

Class Hexapoda Blainville, 1816
Order Hymenoptera Linnaeus, 1758
Family Pteromalidae Dalman, 1820
Subfamily Trigonoderinae Bouček, 1964

Genus *Miscogasteriella* Girault, 1915

Miscogasteriella Girault, 1915: 196–197. Type species *Miscogasteriella longiventris* Girault, 1915, by original designation.

Glyptosticha Masi, 1927: 348–349. Type species *Glyptosticha flavipes* Masi, 1927, by original designation. Subjective synonym of *Miscogasteriella* Girault, 1915 in Bouček (1988: 402).

Trigonoderoides Kamijo, 1962: 121–122. Type species *Glyptosticha nigricans* Masi, 1927, by original designation and monotypy. Subjective synonym of *Miscogasteriella* Girault, 1915 in Heydon (1997: 5, 13, 73).

Diagnosis. Vertex of head smooth (Figs 4, 13, 20, 28). Clypeal margin with angular median tooth (Fig. 3) or weakly emarginate (Figs 12, 19, 27); tentorial pits distinct, but shallow (Figs 3, 12, 19, 27); antennal formula 11264 female (Figs 2, 11, 22, 30) and 11210 male (Figs 17, 25, 33); scutellum with distinct frenal area (Figs 5, 14, 24, 31); propodeum with medial longitudinal depression (Figs 14, 24, 31) or median pit (Fig. 5); fore wing without speculum (Fig. 29) or in form of a narrow line near basal vein (Figs 7, 15, 21).

Distribution. Palaearctic, Oriental and Australian regions.

Key to Palaearctic species of *Miscogasteriella* based on females

1 Lower margin of clypeus with angular median tooth (Fig. 3). Antennal scape extending to middle ocellus, 1.31–1.35 times as long as eye length. Propodeum with costula (Fig. 5). Fore wing with PST 1.15–1.17 times as long as M (Fig. 7) ..... ***M. nigricans* (Masi, 1927)**

– Lower margin of clypeus weakly emarginate (Figs 12, 19, 27). Antennal scape not extending to middle ocellus, 0.89–1.05 times as long as eye length. Propodeum without costula (Figs 14, 24, 31). Fore wing with PST 0.55–0.83 times as long as M (Figs 15, 21, 29) **2**

2 F1 with 5–6 rows of sensilla (Fig. 22). Fore wing with PST 0.76–0.83 times as long as M (Fig. 21). Frenum with finely reticulate sculpture (Fig. 24). Propodeal lateral depressions 0.55–0.60 times as long as propodeum (Fig. 24) ..... ***M. sulcata* (Kamijo, 1963)**

– F1 with 3–4 rows of sensilla (Figs 11, 30). Fore wing with PST 0.55–0.67 times as long as M (Figs 15, 29). Frenum with alutaceous sculpture (Figs 14, 31). Propodeal lateral depressions 0.30–0.44 times as long as propodeum (Figs 14, 31) **3**

3 Combined length of pedicel and flagellum 1.75 times breadth of head. Dorsellum with distinct upper crenulate cross-line (Fig. 14). Scape (Figs 11, 12) and femora brown (Fig. 10). Metasoma with Mt2-Mt4 metallic blue-green with diffuse coppery lustre, Mt5–Mt8 brown with diffuse violet-coppery lustre (Fig. 16) ..... ***M. olgae* sp. nov.**

– Combined length of pedicel and flagellum 1.56–1.57 times breadth of head. Dorsellum without distinct upper crenulate cross-line (Fig. 31). Scape (Figs 27, 30) and femora yellowish-brown (Fig. 26); metasoma cupreous (Fig. 32)..... ***M. vladimiri* sp. nov.**

***Miscogasteriella nigricans* (Masi, 1927)**
Figs 1–8

Glyptosticha nigricans Masi, 1927: 353. Syntype female (DEI, examined) recognised by Masi, 1927: 353.

Type material. ***Syntype*:** female, "Taiwan, Hoozan Formosa H. Sauter, 1910", "TYPUS", "Dtsch. Entomol. Institut Berlin", "*Glyptosticha nigricans* ♀ Masi", "Coll. DEI Eberswalde", "*Trigonoderoides nigricans* (Masi) Det. K. Kamijo", "GBIF-ChalciSD ID: ChalD0419" (DEI).

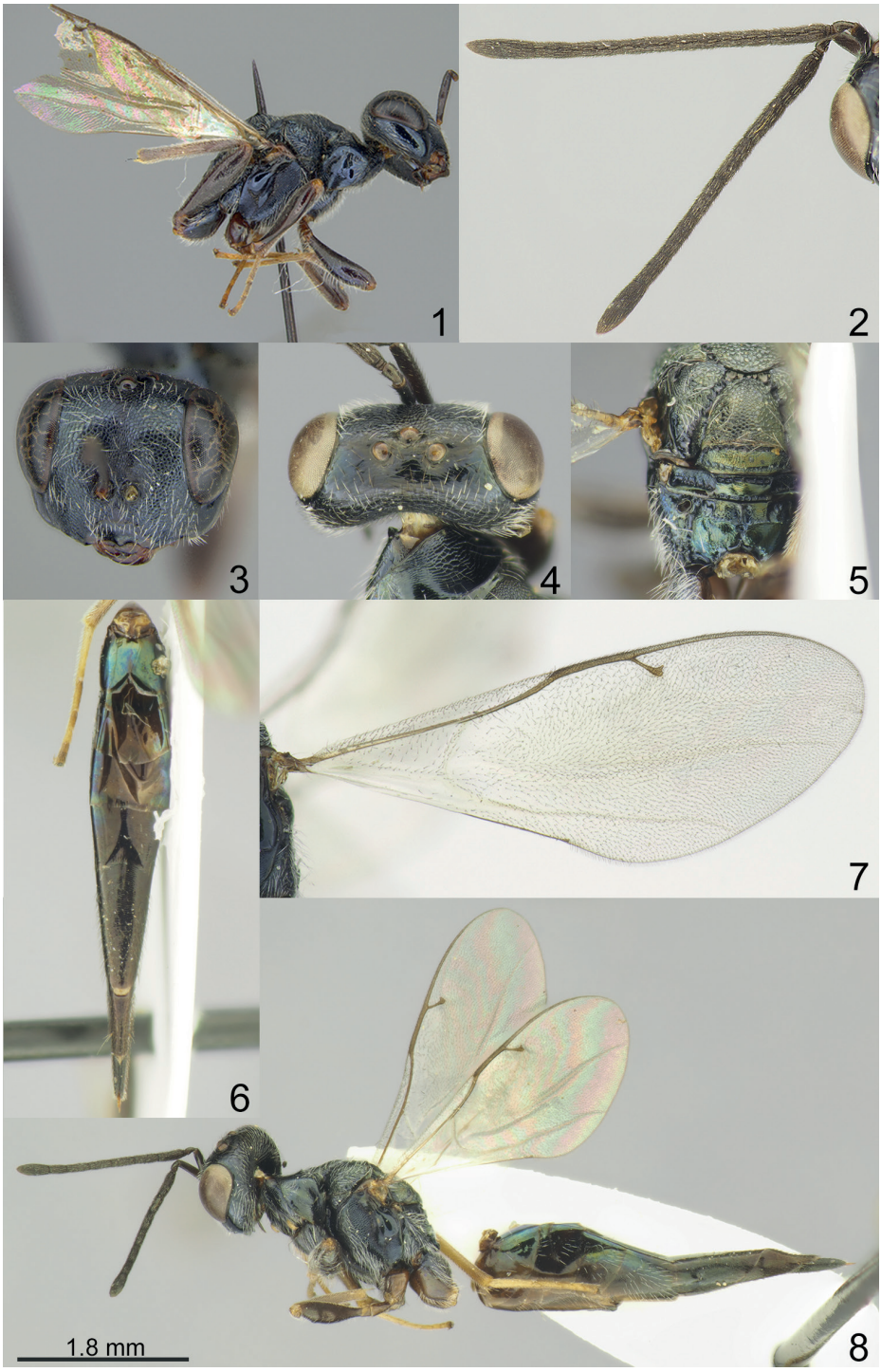
Additional material examined. Russia: 1 female, "Primorskii Reg., 40 km NE Spassk-Dalny Town, Dukhovskoe Vill, 1.VIII.1996, S. Belokobylskij" (ZISP).

Description. Female. Body length 7.70–9.60 mm; fore wing length 4.40 mm (wings of syntype are broken).

***Coloration*.** Head black. Antenna with scape, pedicel, and flagellum dark brown. Mesosoma black, pronotum and mesoscutum dorsally with metallic diffuse green-coppery lustre, propodeum dorsally with metallic diffuse blue-coppery lustre. All coxae and all femora brown; tibiae and tarsi yellowish-brown. Fore wing slightly infuscate, venation yellowish-brown. Metasoma dark brown, in dorsal view Mt2-Mt4 metallic blue-green with diffuse coppery lustre.

***Sculpture*.** Head in frontal view reticulate, head in dorsal view and clypeus smooth and shiny; mesosoma reticulate, but frenum finely reticulate; dorsellum alutaceous, with distinct upper and lower crenulate cross-line; propodeum weakly reticulate; metasoma weakly alutaceous and shiny.

***Head*.** Head in dorsal view 2.23–2.25 times as broad as long and 1.20–1.21 times as broad as mesoscutum; in frontal view 1.26–1.29 times as broad as high. POL 0.90–0.91 times as long as OOL. Eye height 1.40–1.50 times eye length and 2.80–3.00 times as long as malar space. Distance between antennal toruli and lower margin of clypeus 0.55–0.60 times distance between antennal toruli and median ocellus. Lower margin of clypeus with angular median tooth. Antenna with scape 0.87–0.90 times as long as eye height and 1.31–1.35 times as long as eye length; pedicel 1.80–2.00 times as long as broad and 0.25–0.37 times as long as F1; combined length of pedicel and flagellum 1.67–1.70 times breadth of head; F1 3.80–4.00 times as long as broad and



Figures 1–8. 1, 3 *Miscogasteriella nigricans* (Masi, 1927), female, syntype **2, 4–8** female, non-type **1** head and mesosoma, lateral view **2** antenna **3** head, frontal view **4** head, dorsal view **5** scutellum and propodeum, dorsal view **6** metasoma, dorsal view **7** fore wing **8** habitus, lateral view.

with 4–5 rows of sensilla, F3–F6 longer than broad; clava 3.07–3.40 times as long as broad, with micropilosity area on C3, and part of C2.

***Mesosoma*.** Mesosoma 1.80–1.95 times as long as broad. Scutellum 1.06–1.10 times as long as broad. Propodeum without nucha, with costula, 0.59–0.60 times as long as scutellum. Fore wing 2.65 times as long as maximum width; basal cell, cubital vein, basal vein pilose; speculum as narrow line near basal vein; PST 1.15–1.17 times as long as M, M 0.52–0.53 times as long as P and 2.67–2.80 times as long as S.

***Metasoma*.** Metasoma 5.20–5.55 times as long as broad, 1.96–2.05 times as long as mesosoma and 1.42–1.43 times as long as mesosoma and head; Mt8 2.25–2.40 times as long as broad.

Male. Unknown.

Distribution. Russian Far East, Taiwan.

***Miscogasteriella olgae* sp. nov.**

https://zoobank.org/ECA92916-6803-436B-984B-96DFA7DE2985

Figs 9–17

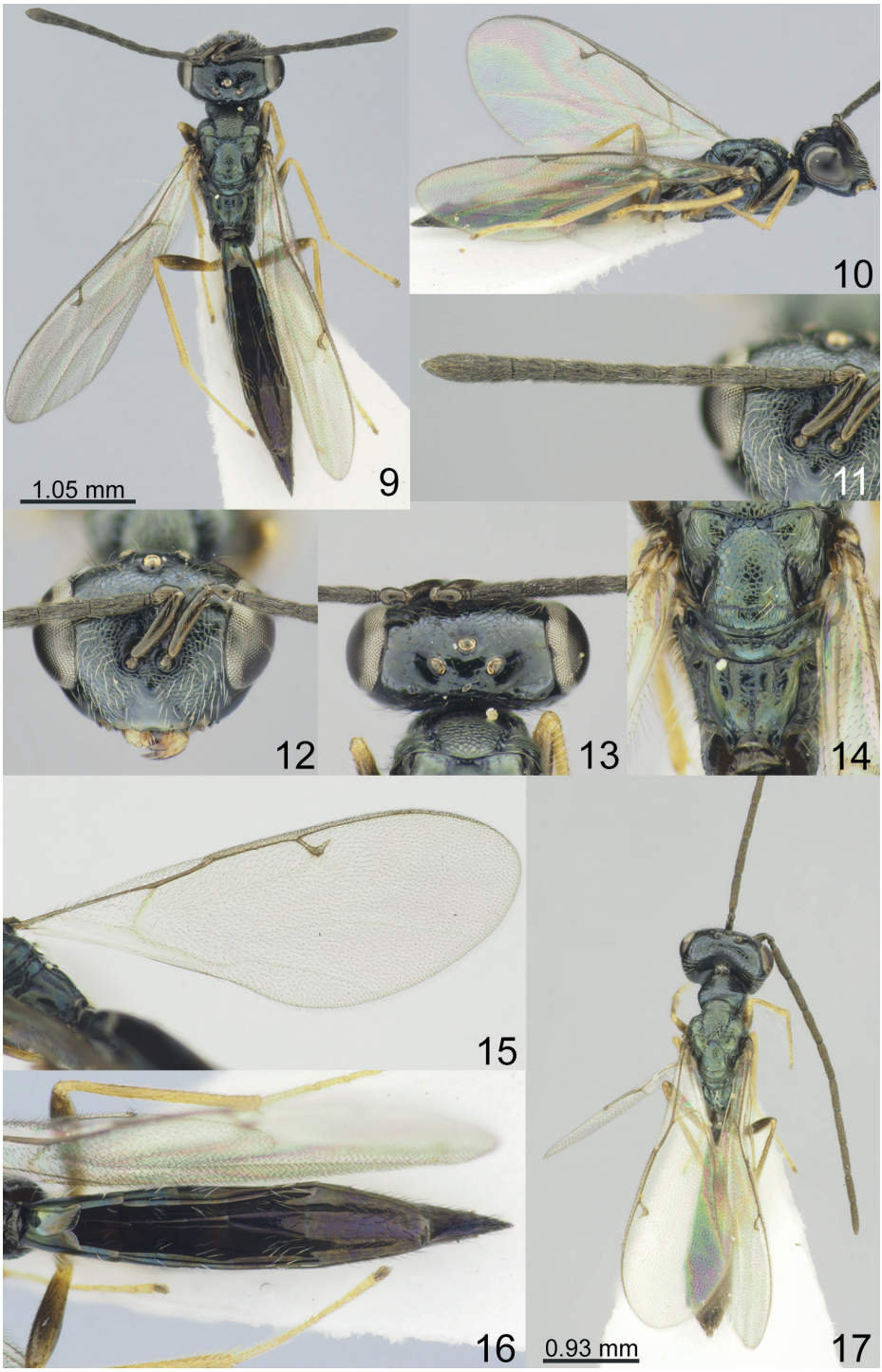
Type material. *Holotype*: female, South Korea: "Korea, Gyeongsangnam-do, Goseong-gun, Hail-myeon, Suyang-ri, 34°58'35"N, 128°12'08"E, 18.VI.2022, E. Tselikh" (NIBR). ***Paratypes*:** 3 males, same data as holotype (1 specimen in NIBR, 2 specimens in SMNE); 1 male, "Korea, Gyeongsangnam-do, Namhae-gun, Gohyeonmyeon, Daegok-ri, Hwabangsa temple, 34°51'07"N, 127°51'31"E, 19.VI.2022, E. Tselikh" (ZISP).

Description. Female. Body length 4.20 mm; fore wing length 3.20 mm.

***Coloration*.** Head black, dorsally with metallic blue lustre. Antenna with scape, pedicel, and flagellum brown. Mesosoma metallic blue-green with diffuse coppery lustre. All coxae brown with metallic blue lustre; all femora brown; tibiae, and tarsi yellow. Fore wing hyaline, venation yellowish-brown. Metasoma with Mt2-Mt4 metallic blue-green with diffuse coppery lustre, Mt5–Mt8 brown with diffuse violet-coppery lustre.

***Sculpture*.** Head in frontal view reticulate, head in dorsal view and clypeus smooth and shiny; mesosoma reticulate, but axilla and frenum alutaceous; dorsellum weakly alutaceous, with distinct upper crenulate cross-line, and without lower crenulate cross-line; propodeum weakly alutaceous; metasoma weakly alutaceous and shiny.

***Head*.** Head in dorsal view 2.30 times as broad as long and 1.65 times as broad as mesoscutum; in frontal view 1.30 times as broad as high. POL 0.80 times as long as OOL. Eye height 1.33 times eye length and 3.10 times as long as malar space. Distance between antennal toruli and lower margin of clypeus 0.78 times distance between antennal toruli and median ocellus. Lower margin of clypeus weakly emarginate. Antenna with scape 0.68 times as long as eye height and 0.90 times as long as eye length; pedicel 1.28 times as long as broad and 0.42 times as long as F1; combined length of pedicel and flagellum 1.75 times breadth of head; F1 3.00 times as long as broad and with 3–4 rows of sensilla, F3–F6 longer than broad; clava 3.05 times as long as broad, with micropilosity area on C3 and C2.



Figures 9–17. 1–16 *Miscogasteriella olgae* sp. nov., female, holotype **17** male, paratype **9** habitus, dorsal view **10** habitus, lateral view **11** antenna **12** head, frontal view **13** head, dorsal view **14** scutellum and propodeum, dorsal view **15** fore wing **16** metasoma, dorsal view **17** habitus, dorsal view.

***Mesosoma*.** Mesosoma 2.00 times as long as broad. Scutellum 1.05 times as long as broad. Propodeum without nucha and costula, 0.78 times as long as scutellum; medial longitudinal depression shallow, lateral depressions 0.44 times as long as propodeum. Fore wing 2.80 times as long as maximum width; basal cell, cubital vein, basal vein pilose; speculum absent; PST 0.55 times as long as M, M 0.53 times as long as P and 3.60 times as long as S.

***Metasoma*.** Metasoma 6.20 times as long as broad, 2.03 times as long as mesosoma and 1.37 times as long as mesosoma and head; Mt8 1.67 times as long as broad.

Male. Body length 3.50–3.70 mm; fore wing length 2.80–3.00 mm. Head in frontal view 1.24–1.25 times as broad as high. Distance between antennal toruli and lower margin of clypeus 0.90–0.93 times distance between antennal toruli and median ocellus. Antenna with scape 0.48–0.52 times as long as eye height and 0.68–0.70 times as long as eye length. Combined length of pedicel and flagellum 1.70–1.73 times breadth of head. Antennal formula 11210. Fore wing with M 3.78–3.80 times as long as S. Metasoma 5.00–5.15 times as long as broad, 1.68–1.70 times as long as mesosoma and 1.25–1.27 times as long as mesosoma and head. Otherwise, similar to female.

Etymology. The species is named in honour of the senior author's mother, Olga Tselikh.

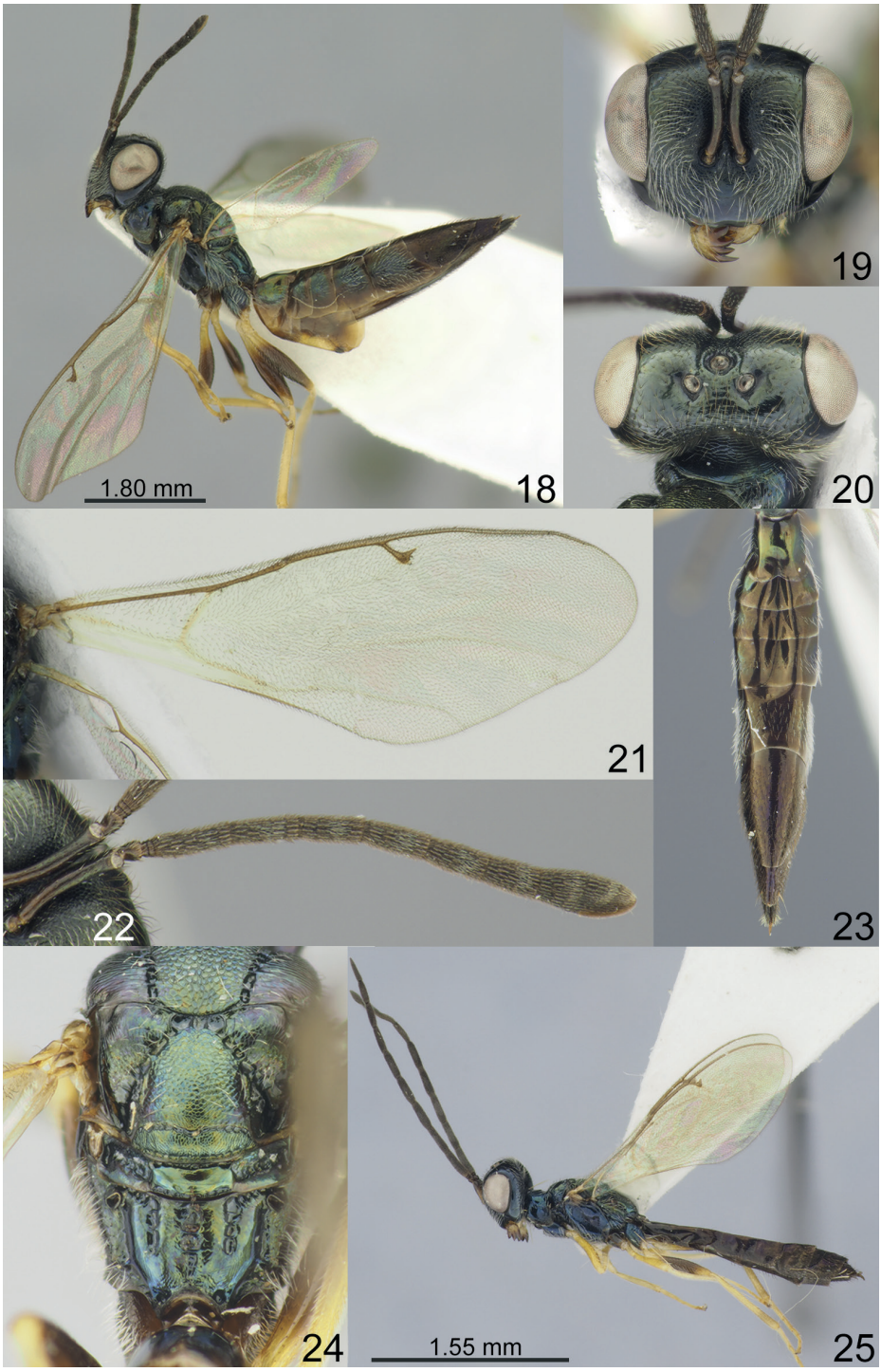
Distribution. Korean Peninsula.

***Miscogasteriella sulcata* (Kamijo, 1962)**
Figs 18–25

Glyptosticha sulcata Kamijo, 1962: 118. Holotype female (EIHU, examined) designated by Kamijo, 1962: 118.

Type material. *Holotype*: female, Japan: "Japan, Kyushu, 11.VIII.1955, K. Nohara", "Holotype *Glyptosticha sulcata* Kamijo ♀" (EIHU).

Additional material examined. South Korea: 2 females, "Busan, Gijang-gun, Jeonggwanmyeon, Gijang-cheongsonyeon-suryeonwon, 35°18'52"N, 129°09'57"E, 22.V–29.VI.2008, J.W. Lee"; 1 female, "Chungcheongbuk-do, Yeongdong-gun, Sangchon-myeon, Mulhan Valley, 35°49'53"N, 128°32'28"E, 23.V.2002, J.W. Lee"; 1 female "Miwon-ri, Miwon-myeon, Cheongwon-gun, 15–22.VII.05, J.H. Han"; 1 female, "Danyang-gun, Cheondong-ri, Mt. Sobaek, Temp. Bukbusa, 7.VII–2.VIII.2005, J.W. Lee"; 3 males, "Cheongwon-gun, Miwonmyeon, Miwon-ri, 9–16.IX.2005, J.H. Han" (all in YNU); 1 male, "Gyeongsangbuk-do, Kyeongju-si, Hyeongok-myeon, Namsa-ri, 2–09.IX.2015, J.T. Mun"; 1 female, "Cheongdo-gun, Unmunmyeon, Mt. Unmun, 35°38'09"N, 128°59'18"E, 23.V.2008, J.W. Lee"; 2 females, same locality, 15–29.IX.2005, J.O. Lim; 1 female, same locality, 23.V.2008, J.W. Lee; 2 females, same locality, 5–15.V.2009, J.W. Lee; 2 females, same locality, 30.V–16.VI.2009, C.J. Kim; 2 females, "Yeongju-si, Punggieup, Jungnyeong, 35°53'43"N, 128°26'22"E, 20.VIII–5.IX.2009, J.W. Lee"; 1 female, "Cheongdo-gun, Unmunmyeon, Haksodaepakpo, 35°38'15"N, 128°59'51"E, 2.VII–16.VIII.2013, J.W. Lee";



Figures 18–25. 18–24 *Miscogasteriella sulcata* (Kamijo, 1963), female, non-type **25** male, non-type **18** habitus, lateral view **19** head, frontal view **20** head, dorsal view **21** fore wing **22** antenna **23** metasoma, dorsal view **24** scutellum and propodeum, dorsal view **25** habitus, lateral view.

2 females, “Cheongdo-gun, Unmun-myeon, Ssalbawi, Mt. Unmun, 35°38'08"N, 129°01'27"E, 13.VII–16.VIII.2013, J.W. Lee”; 6 males, “Chilgok-gun, Dongmyeongmyeon, Hakmyeong-ri, San, 36°01'53"N, 128°33'47"E, 15.VII–29.VIII.2014, J.W. Lee”; 1 female, “Yeongcheon-si, Sinnyeong-myeon, Chisan-ri, San 141-4, 36°01'13"N, 128°42'26"E, 15.VII–29.VIII.2014, J.W. Lee”; 1 female, “Yeongcheon-si, Sinnyeong-myeon, Chisan-ri, San141-4, 36°01'13"N, 128°42'26"E, 30.VIII–25.IX.2014, J.W. Lee”; 1 female, “Bonghwa-gun, Myeongho-myeon, Gwanchang-ri, Mt. Cheongryang, 22.V.2015, J.W. Lee”; 1 female, “Bonghwa-gun, Jaesan-myeon, Galsan-ri, Irwolsan-gil, 36°49'22"N, 129°05'05"E, 7.VIII.2015, E.V. Tselikh, K.H. Ko” (all in YNU); 2 females, “Daehyeon-ri, Bukhu-myeon, Andong-si, 31.V–16.VI. 2021, 15.X–5. XI. 2021, Malaise Trap, K. Gimyeon”; 3 males, “Daedong-ri, Mari-myeon, Geochang-gun, 15.VIII–25.VIII.2021, 8.IX–23.IX.2021, Malaise Trap, L. Jaehyeon, J. Hyojin” (all in SMNE); 2 males, “Gyeonggi-do, Anyang-si, Manan-gu, Gwanak Arboretum, 37°18'05"N, 127°19'02"E, 5–19.VII.2007, J.O. Lim”; 3 females, 1 male, “Gapyeong-gun, Cheongpyeong-myeon, Mt. Homyeong, 1–26.V.2009, J.W. Lee”; 3 females, 2 males, same locality, 37°43'16"N, 127°19'23"E, 31.VII–17.VIII.2009, 27.V–10.VI.2009, J.O. Lim; 1 male, “Namyangju-si, Choan-myeon, Songchon-ri, Mt. Ungil, 37°34'43"N, 127°18'38"E, 26.VI–16.VII.2009, J.O. Lim”; 1 female, 22 males, same locality, 37°34'43"N, 127°18'40"E, 18.VIII–4.IX.2009, J.O. Lim; 2 females, 1 male, “Pocheon-si, Soheur-eup, Jikdong-ri, 51-7, Korea National Arboretum, 37°45'02"N,127°08'34"E, 29.VIII–14.X.2013, I.G. Kim” (all in YNU); 3 females, 5 males, “Soheul-eup, Pocheon-si, 24.V–12.VI.2017, 30.VI–17.VII.2017, 31.VI–16.VIII.2017, 37°45'02"N, 127°08'35"E, Kim, Kim, Nam” (all in KNA); 5 males, “Gyeongsangnam-do, Namhae-gun, Namhae-eup, Asan-ri, 34°51'07"N, 127°51'31"E, 19.VI.2022, S. Belokobylskij, E. Tselikh” (all in ZISP); 1 male, “Gangwon-do, Donghae-si, Samhwa-dong, Mureunggyegok, 2–10.X.2006, J.W. Lee”; 1 female, 1 male, “Wonju-si, Heungeop-myeon, Maeji-ri, 234,Yonsei University, 21.V–27.VI.2014, H.Y. Han” (all in YNU); 1 male, “Mandae-ri, Haean-myeon, Yuggu-gun, 30.VI.2014, H.T. Shin” (in KNA). Japan: 1 female, “Shikoku, Kochi Pref., Ashizurimisaki, 23.V.1983, M. Miyatake”; 1 female “Nagano Pref., Ueda City, Sugadairakougen, Tsukuba Univ., 36-31N/138-20E (about 1300 m), 9.IX.2013, S. Shimizu”; 1 male, “Niigata Pref., Nagaoka City, Suyoshi Town, Mt. Nokogiri-yama, (about 690 m), 21.VII.2014, S. Shimizu, R. Shimizu” (all in EUM).

Description. Female. Body length 6.90–8.00 mm; fore wing length 4.90–5.60 mm.

***Coloration*.** Head dark blue, in frontal view metallic diffuse coppery green lustre. Antenna with scape, pedicel, and flagellum dark brown. Mesosoma dark blue-green, in dorsal view with a diffuse coppery lustre, propodeum dorsally metallic blue and partly with coppery lustre. Fore and hind coxae dark blue, middle coxae dark brown; all femora apically yellow, basally brown; tibiae, and tarsi yellow. Fore wing slightly infuscate, venation yellowish-brown. Metasoma dark brown, in dorsal view Mt2 and Mt3-Mt4 laterally metallic blue-green with diffuse coppery lustre.

***Sculpture*.** Head in frontal view weakly reticulate, in dorsal view and clypeus smooth and shiny; mesosoma reticulate, but frenum finely reticulate; dorsellum shiny,

with distinct upper and lower crenulate cross-line; propodeum weakly reticulate; propodeum smooth and weakly reticulate only near medial longitudinal depression; metasoma weakly alutaceous and shiny.

Head. Head in dorsal view 2.20–2.27 times as broad as long and 1.44–1.46 times as broad as mesoscutum; in frontal view 1.29–1.40 times as broad as high. POL 0.70–0.72 times as long as OOL. Eye height 1.39–1.42 times eye length and 3.40–3.60 times as long as malar space. Distance between antennal toruli and lower margin of clypeus 0.79–0.82 times distance between antennal toruli and median ocellus. Lower margin of clypeus weakly emarginate. Antenna with scape 0.69–0.74 times as long as eye height and 0.94–1.05 times as long as eye length; pedicel 1.55–1.62 times as long as broad and 0.20–0.38 times as long as F1; combined length of pedicel and flagellum 1.53–1.78 times breadth of head; F1 3.30–4.00 times as long as broad and with 5–6 rows of sensilla, F3–F6 longer than broad; clava 2.67–2.87 times as long as broad, with micropilosity area on C3 and C2.

Mesosoma. Mesosoma 1.78–2.00 times as long as broad. Scutellum 1.07–1.10 times as long as broad. Propodeum without nucha and costula; 0.83–0.85 times as long as scutellum; medial longitudinal depression strong, lateral depressions 0.55–0.60 times as long as propodeum. Fore wing 2.80–2.89 times as long as maximum width; basal cell, cubital vein, basal vein pilose; speculum absent; PST 0.76–0.83 times as long as M, M 0.50–0.56 times as long as P and 3.00–3.35 times as long as S.

Metasoma. Metasoma 3.97–4.48 times as long as broad, 1.81–1.88 times as long as mesosoma and 1.36–1.38 times as long as mesosoma and head; Mt8 1.09–1.25 times as long as broad.

Male. Body length 3.40–6.20 mm; fore wing length 3.10–4.20 mm. All coxae dark blue; fore and middle femora yellow, hind femora brown. Eye height 1.25–1.30 times eye length and 2.70–3.00 times as long as malar space. Antennal formula 11210; scape 0.52–0.60 times as long as eye height and 0.69–0.75 times as long as eye length; pedicel as long as broad; combined length of pedicel and flagellum 2.80–3.15 times breadth of head; F1 4.80–5.00 times as long as broad. Fore wing with PST 0.61–0.69 times as long as M. Metasoma 1.00–1.28 times as long as mesosoma and head. Otherwise, similar to female.

Distribution. Korean Peninsula, Japan.

Miscogasteriella vladimiri sp. nov.

https://zoobank.org/FFB5BCA3-EE5E-45A8-A5AC-C3A3B4CD7441
Figs 26–33

Type material. ***Holotype*****:** female, "Japan, Shikoku Isl., Muroto, Tosa, 8.VI.1959, M. Miyatake" (ZISP). ***Paratype*****:** 1 female, "Japan, Shikoku Isl., Kuroson, Tosa, 30.IV.1956, M. Miyatake" (EUM).

Description. Female. Body length 5.00–5.20 mm; fore wing length 3.90–4.10 mm.

Coloration. Head dark brown. Antenna with scape yellowish-brown; pedicel, and flagellum brown. Mesosoma cupreous in lateral view with diffuse violet lustre. All

coxae brown with diffuse violet lustre; all femora, tibiae, and tarsi yellowish-brown. Fore wing slightly infuscate; venation yellowish-brown. Metasoma cupreous.

Sculpture. Head in frontal view weakly reticulate, in dorsal view and clypeus smooth and shiny; mesosoma reticulate, but axilla and frenum alutaceous; dorsellum shiny, without upper crenulate cross-line, and with lower crenulate cross-line; propodeum weakly reticulate; propodeum weakly reticulate propodeum weakly alutaceous; metasoma weakly alutaceous and shiny.

Head. Head in dorsal view 2.10–2.17 times as broad as long and 1.66–1.69 times as broad as mesoscutum; in frontal view 1.30–1.34 times as broad as high. POL 0.77–0.80 times as long as OOL. Eye height 1.27–1.33 times eye length and 2.90–3.20 times as long as malar space. Distance between antennal toruli and lower margin of clypeus 0.85–0.97 times distance between antennal toruli and median ocellus. Lower margin of clypeus weakly emarginate. Antenna with scape 0.67–0.73 times as long as eye height and 0.89–0.90 times as long as eye length; pedicel 1.40–1.53 times as long as broad and 0.40–0.45 times as long as F1; combined length of pedicel and flagellum 1.56–1.57 times breadth of head; F1 2.95–3.00 times as long as broad and with 3 rows of sensilla, F3–F6 longer than broad; clava 2.30–2.50 times as long as broad, with micropilosity area on C3 and C2.

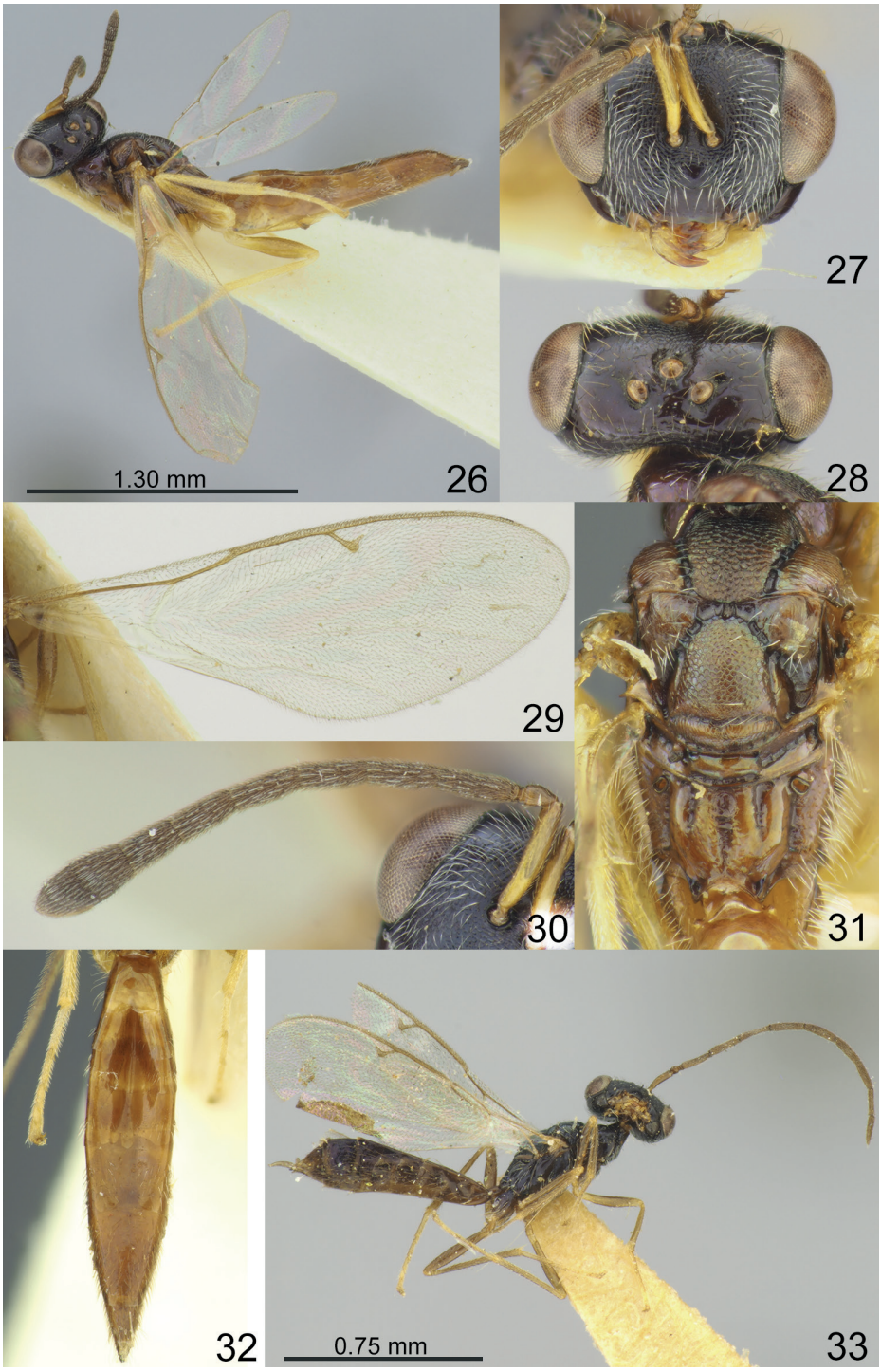
Mesosoma. Mesosoma 2.00–2.10 times as long as broad. Scutellum 1.09–1.10 times as long as broad. Propodeum without nucha and costula, 0.85–1.00 times as long as scutellum; medial longitudinal depression shallow, lateral depressions 0.30–0.35 times as long as propodeum. Fore wing 2.79–2.82 times as long as maximum width; basal cell, cubital vein, basal vein pilose; speculum absent; PST 0.62–0.67 times as long as M, M 0.55–0.60 times as long as P and 3.40–3.44 times as long as S.

Metasoma. Metasoma 4.00–4.65 times as long as broad, 1.77–1.95 times as long as mesosoma and 1.32–1.37 times as long as mesosoma and head; Mt8 1.00–1.10 times as long as broad.

Male. Body length 3.00 mm; fore wing length 2.60 mm. Eye height 1.13 times eye length and 3.40 times as long as malar space. Antennal formula 11210; scape 0.62 times as long as eye height and 0.70 times as long as eye length; pedicel 1.10 times as long as broad and 0.26 times as long as F1; combined length of pedicel and flagellum 1.78 times breadth of head; F1 4.67 times as long as broad and with 5 rows of sensilla. Mesosoma 2.00–2.10 times as long as broad. Scutellum 1.09–1.10 times as long as broad. Propodeum without nucha and transversal carina, 0.85–1.00 times as long as scutellum; medial longitudinal depression shallow, lateral depressions 0.30–035 times as long as propodeum. Fore wing 2.79–2.82 times as long as maximum width; basal cell, cubital vein, basal vein pilose; speculum absent; PST 0.62–0.67 times as long as M, M 0.55–0.60 times as long as P and 3.40–3.44 times as long as S. Metasoma 1.33 times as long as mesosoma and as long as mesosoma and head. Otherwise, similar to female.

Etymology. The species is named in honour of the senior author's father, Vladimir Tselikh.

Distribution. Japan.



Figures 26–33. 26–32 *Miscogasteriella vladimiri* sp. nov., female, holotype **33** male, paratype **26** habitus, lateral view **27** head, frontal view **28** head, dorsal view **29** fore wing **30** antenna **31** scutellum and propodeum, dorsal view **32** metasoma, dorsal view **33** habitus, lateral view.

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Land snail diversity in central China: revision of *Laeocathaica* Möllendorff, 1899 (Gastropoda, Camaenidae), with descriptions of seven new species

Min Wu[1], Wang Shen[1], Zhong-Guang Chen[2]

1 *School of Life Sciences, Nanjing University, Nanjing 210023, China* **2** *Jiangxi Province Key Laboratory of Watershed Ecosystem Change and Biodiversity, Center for Watershed Ecology, Institute of Life Science and School of Life Sciences, Nanchang University, Nanchang 330031, China*

Corresponding author: Min Wu (minwu1969@aliyun.com)

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Abstract

Central China harbors the native dart-sac-bearing camaenids *Laeocathaica*. The genus is revised and seven new species are proposed based on museum material and newly collected specimens. This work confirmed that most *Laeocathaica* species have restricted habitats. The comparison of the dart sac apparatus among the dart-sac-bearing camaenid genera indicated the importance of the presence of the proximal accessory sac that might be analogous to the membranous/muscular sac surrounding the proximal dart sac and/or the distal region of the vagina near the atrium, which also plays a significant role in the diagnosis of *Laeocathaica* species based on its number, symmetry and position on the dart sac. Species with similar shell morphology were studied using geometric morphometric methods to detect variations in shell shape. A molecular phylogenetic analysis based on 16S and ITS2 sequence data of partial *Laeocathaica* species and many other dart-sac-bearing taxa suggested that *Laeocathaica* might be monophyletic. Furthermore, the present phylogeny indicated that *Stilpnodiscus*, *Cathaica*, *Bradybaena*, and *Pseudobuliminus* might be polyphyletic and therefore the taxonomy of dart-sac-bearing camaenids in this region requires a thorough revision. This work reconfirms that the Southern Gansu Plateau is important as a hotspot for malacodiversity conservation on the Chinese mainland.

Keywords

Anatomy, Central China, Helicoidea, molecular phylogeny, morphology, taxonomy

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Introduction

Laeocathaica Möllendorff, 1899 comprises more than twenty species, most of which were described by O. von Möllendorff. It is a group of sinistrally-shelled camaenids indigenous to Central China, an area that includes western Hubei, Chongqing (administratively part of Sichuan before 1997), Sichuan, southern Gansu, and western Shaanxi (works before 1934 listed in References; Wu and Chen 1998; Chen and Zhang 2004; Páll-Gergely et al. 2022). This genus is characterized by a sinistral shell with a conic to strongly depressed spire, usually with a sharp carina, more or less reflexed aperture, broad umbilicus and weak or strong apertural barriers on the young shell. However, their shell morphological phenotypic variation is so wide that most shell characters can also be observed in other dart-sac-bearing camaenids of China, such as toothless and toothed aperture of juvenile/mature shell, rounded and carinate periphery, narrow and broad umbilicus, scaly and smooth periostracum, banded color pattern and so on, which makes us question, whether it is a monophyletic group (Páll-Gergely et al. 2022). It is noteworthy that in the original paper on the introduction of this genus Möllendorff (1899) noticed that this group might be distinguished from other related genera by "juniora labro interno munita", which means "during postembryogenesis several sets of teeth, different from those developed at adult stage in shape and/or number, present and remained to adult stage" (Schileyko 2004). In comparison to the shell characteristics, which are not always reliable taxonomic markers, the characteristics of genitalia are considered important to the systematics of dart-sac-bearing camaenids. Unfortunately, the genital anatomy of *Laeocathaica* species described so far has been insufficiently investigated, except for very few species (Wiegmann 1900; Schileyko 2004), whose absence makes the delimitation of the genus problematic.

This paper examines the shell morphology and genital anatomy of *Laeocathaica* using museum material and recent field collections and proposes seven new species. A molecular phylogeny based on 16S and ITS2 sequence data of a subset of *Laeocathaica* species and other dart-sac-bearing taxa is constructed to explore whether *Laeocathaica* is monophyletic.

Materials and methods

Specimen preparation and observation

Animals in most cases were relaxed by drowning in water before being transferred to 70% ethanol for fixation, which was replaced with ethanol of the same concentration

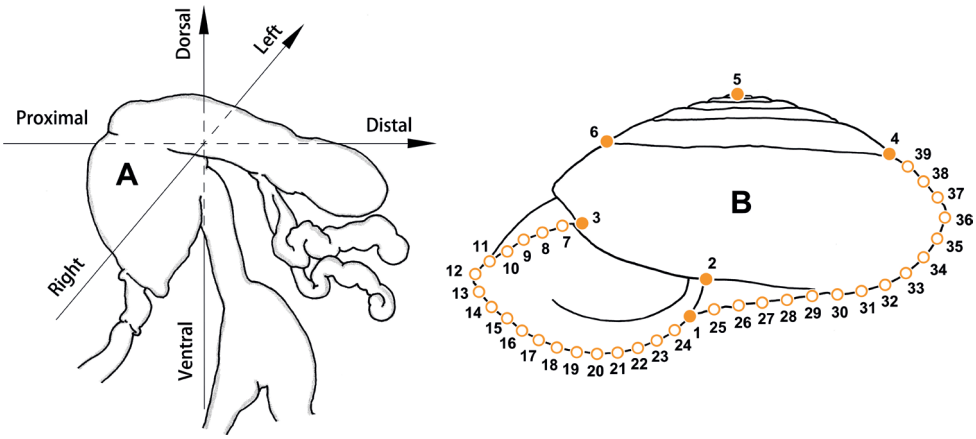

Figure 1. A directions used to describe dart sac apparatus **B** design of landmarks (solid dots) and semi-landmarks (empty dots).

after 3 days. To observe the animals with evaginated dart sac apparatus, before fixation the animal was drowned in water with 5% ethanol, 10% ethanol and 15% ethanol, in each solution for ~ 60 min. Photographs for illustrations (by MW) and geometric morphometric analyses (by WS) were taken using a Canon camera. The shells were measured with digital vernier calipers to the nearest 0.1 mm. Whorls were counted following Kerney and Cameron (1979) to the nearest 0.125 (= $^{1}/_{8}$) whorls. Shells were observed under a scanning electron microscope Sigma 500. The penis was dissected at the opposite side of penial retractor insertion. The dart sac was dissected by cutting the dorsal part of the dart sac (see Fig. 1A) along the line from the atrium to the dart sac chamber. Directions used in the general descriptions of genitalia: proximal = towards the genital atrium; distal = away from the genital atrium. For directions used in the description of dart sac apparatus, refer to Fig. 1. Illustrations of genitalia were drawn based on actual photos (by MW). The corresponding Chinese name for person, new species, or locality is present only once in square bracket when necessary.

Map preparation

Distribution maps were created using ArcGIS Desktop 10.8 under GCS_WGS_1984 coordinate system. In addition, mapping was carried out to map both the distribution limit and the distribution pattern of *Laeocathaica* species (Fig. 2A). The nearby places where *Laeocathaica* was not found, represented by the counties/cities where the field work was carried out at one or more sites, are as follows: **Gansu Province:** Lixian [礼县], Qingyang [庆阳], Huanxian [环县], Huining [会宁县], Lanzhou [兰州]; **Guizhou Province:** Libo [荔波县], Jiangkou [江口县], Shibing [施秉县], Guiyang [贵阳市], Zhenning [镇宁县], Xishui [习水县], Meitan [湄潭县], Majiang [麻江县], Xifeng [息烽], Tongzi [桐梓县], Sansui [三穗县]; **Hubei Province:** Xianning [咸丰县], Wufeng [五峰县], Shennongjia in Hubei [湖北神农架], Zigui [秭归县],

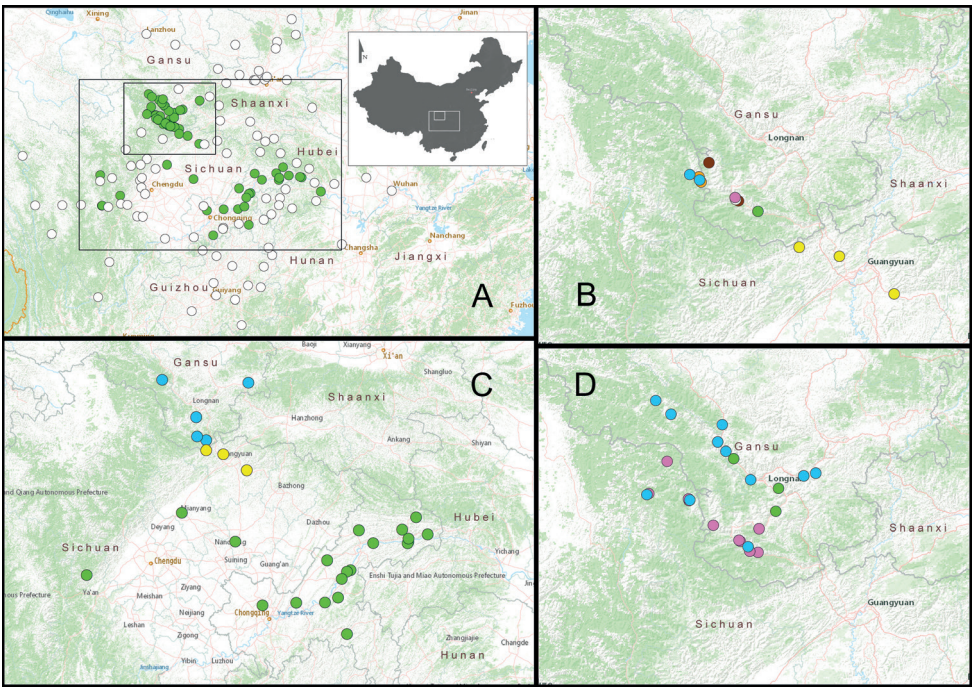

Figure 2. A distribution map of all known species of *Laeocathaica* Möllendorff, 1899 except *L. anceyi* (Möllendorff in Ancey, 1889), *L. hisanoi* Páll-Gergely, 2022, and *L. leucorhaphe* Möllendorff, 1899 whose precise localities are not known; white dots: the localities where no *Laeocathaica* species was ever found **B** distribution of the new species described in this paper, yellow dots: *L. qingchuanensis* Wu, sp. nov., green dot: *L. zhengpingliui* Wu, sp. nov., brown dots: *L. parapolytyla* Wu, sp. nov., white dot: *L. qiminglii* Wu, sp. nov., pink dot: *L. cheni* Wu, sp. nov., blue dots: *L. qishilii* Wu, sp. nov., orange dots: *L. nordsiecki* Wu, sp. nov. **C** distribution of *L. carinifera* (H. Adams, 1870) (green dots), *L. qingchuanensis* Wu, sp. nov. (yellow dots), and *L. stenochone* Möllendorff, 1899 (blue dots) **D** distribution of *L. amdoana* Möllendorff, 1899 (green dots), *L. distinguenda* Möllendorff, 1899 (pink dots), and *L. tropidorhaphe* Möllendorff, 1899 (blue dots) **C** equivalent to the larger box in (**A**), **B, D** equivalent to the smaller box in (**A**).

Xingshan [兴山县], Hefeng [鹤峰县], Enshi [恩施], Dangyang [当阳市], Jianshi [建始县], Wuchang [武昌], Jingshan [京山县], Lichuan [利川县], Xuanen [宣恩县]; **Hunan Province:** Taojiang [桃江县], Songtao [松桃苗族自治县], Xiushan [秀山县]; **Shaanxi Province:** Zhenping[镇坪县], Fengxian [凤县], Liquan [礼泉县], Luochuan [洛川县], Pingli [平利县], Yichuan [宜川县], Ziyang [紫阳县], Yanchang [延长县], Chunhua [淳化县], Huaxian [华县], Jingyang [泾阳县], Sanyuan [三原县], Linyou [麟游县], Shangnan [商南县], Baoji [宝鸡县], Liquan [礼泉县], Hanzhong [汉中市], Shiquan [石泉县], Huangling [黄陵县], Liuba [留坝县], Longxian [陇县], Xiba [西坝县], Langao [岚皋县]; **Sichuan Province:** Maoxian [茂县], Wenchuan [汶川县], Emei [峨眉], Luding [泸定县], Qingchengshan [青城山], Pingwu [平武县], Tianquan [天全县], Chongqing [崇庆县], Xicang [西昌], Mianzhu [绵竹县], Xinjin [新津], Yibin [宜宾], Leshan [乐山], Danba [丹巴县], Yaan [雅安市],

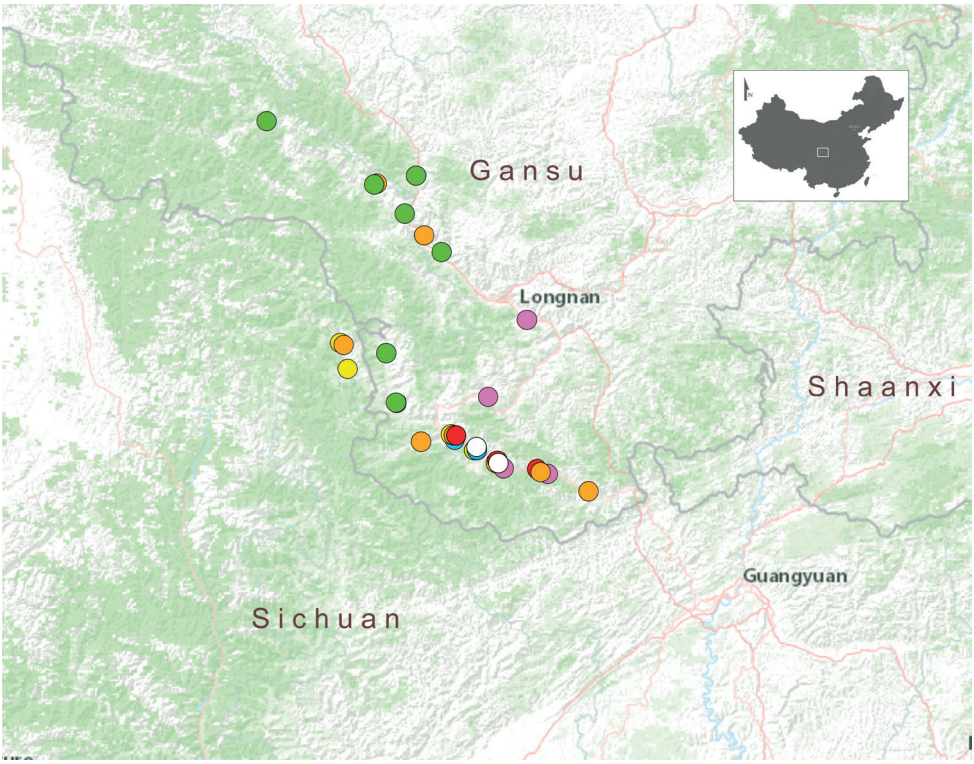

Figure 3. Distribution map of *Laeocathaica dityla* Möllendorff, 1899 (green dots), *L. odophora* Möllendorff, 1899 (pink dots), *L. pewzowi* Möllendorff, 1899 (white dots), *L. phaeomphala* Möllendorff, 1899 (blue dots), *L. polytyla* Möllendorff, 1899 (yellow dots), *L. potanini* Möllendorff, 1899 (red dots), and *L. prionotropis* Möllendorff, 1899 (orange dots). Range of the map is defined by the rectangle in the thumbnail.

Xiangcheng [乡城], Yajiang [雅江市], Batang [巴塘], Litang [理塘县], Dege [德格县], Dujiangyan [都江堰市], Panzhihua [攀枝花市], Songpan [松潘县], Heishui [黑水县], Hejiang [合江县], Lixian [理县], Wangcang [旺苍县], Nanjiang [南江县], Tongjiang [通江县], Xiaojin [小金县]; **Chongqing:** Wulong [武隆县], Chengkou [城口县], Hechuan [合川], Qianjiang [黔江县], Nanchuan [南川县]. It should be noted that the map (Fig. 2A) is far from complete, as any survey carried out in such a vast area could normally have provided very limited information about its malacofauna, not to mention that these places comprise 91 counties/cities of seven provinces, covering an area of ~ 1,080,000 km^2 (calculated from Fig. 2A).

Geometric morphometric analyses

Geometric morphometric methods (GMM) were used to investigate the relationship between some species that exhibits conchological similarities. The morphological variation analyses of the shells were performed in the tps series software including tpsUtil32

(Rohlf 2004), tpsDig32 (Rohlf 2005), and MorphoJ (Klingenberg 2011) using geometric morphometric methods based on the landmarks and semi-landmarks on the profile of the aperture-viewed shell (Schilthuizen et al. 2012; Wu et al. 2019a). The landmarks and semi-landmarks treated equally in the analyses were designed as follows: LM_1, the crossing of peristome and right profile of body whorl; LM_2, the columella insertion; LM_3, the left insertion of peristome onto body whorl; LM_4 and LM_6, the right and left terminal points on last suture, respectively; LM_5, apex of shell; $LM_{7–24}$, eighteen semi-landmarks on the peristome between LM_3 and LM_1 by length; $LM_{25–39}$, fifteen semi-landmarks on the right profile between LM_1 and LM_4 by length (Fig. 1B).

The material used in the GMM analyses were intact mature shells and the high-quality published photos, including *Laeocathaica amdoana* Möllendorff, 1899: HBUMM05639 (2 specimens; the information of each collection lot is showed under each species in the section Systematics), -05640 (3), -05646 (5), -08147 (6), -08432 (3) and SMF 8952 (1); *Laeocathaica distinguenda* Möllendorff, 1899: HBUMM05417 (5), -05434 (1), -05436 (1), -05473 (10), -05554 (4), -05565a (3), -05571 (3), -05576b (1), -06536 (3), -06556 (3), -06579 (2), -00674 (8), -08429 (2), CZG202008-w10 (4), CZG202008-w5 (5), SMF 8959 (1) and SMF 95024 (1); *L. tropidorhaphe* Möllendorff, 1899: HBUMM00450 (3), -00486 (2), -00508 (5), -00526 (1), -00527 (2), -05600 (8), -05621 (4), -05664 (6), -05692 (7), -05719 (4), -06621 (3), -08425 (7), CZG202008-w1 (2), SMF 9074 (1), SMF 9075 (1), SMF 9077 (1) and fig. 7D in Páll-Gergely et al. (2022) (paratype of *Laeocathaica dangchangensis* Chen & Zhang, 2004; 1); *L. carinifera* (H. Adams, 1870): HBUMM00006 (1), -01573 (5), -00228 (2), -04064 (5), -04162 (7), -04217 (8), -04219 (5), -04235 (5), -08443 (4), NHMUK V. W. McAndrew coll. Acc. No. 1563 (1), SMF 24265 (1), SMF 95116 (1) and fig. 12A in Páll-Gergely et al. 2022 (syntype; 1); *L. qingchuanensis* Wu, sp. nov.: HBUMM01179a (5), -04264 (2), -08195 (5), -08196 (4) and -08200 (9); and *L. stenochone* Möllendorff, 1899: HBUMM05495 (5), -05764a (1), -05767 (2), -05772 (4), -08431 (3), -08433 (1), SMF 8951 (1), SMF 9071 (1) and fig. 12D in Páll-Gergely et al. 2022 (lectotype; 1).

Molecular studies and phylogenetic analyses

Whole genomic DNA was extracted from a piece of the foot muscle using the Animal Genome Quick Extraction Kit (B518221, Sangon Biotech). All PCR reactions were performed in 50 μL volumes containing 5 μL 10× reaction buffer containing 25 mm $MgCl_2$, 10 mm of each dNTP, 1 μL of Taq polymerase (5 U/μL), 1 μL of 10–100 ng template DNA and ddH_2O. Thermal cycling was performed on an Eastwin ETC811. PCR amplicons were inspected on a 1% agarose gel for quality and fragment size, then were sequenced on an automated sequencer. Primers used for partial fragment of 16S were 16Sar-L (5'-CGCCTGTTTATCAAAAACAT-3') /16Sbr-H (5'-CCGGTCTGAACTCAGATCACGT-3') (Palumbi et al. 2002). The conditions for thermal cycling: an initial denaturing step at 94 °C for 2 min, 35 cycles of denaturing at 94 °C for 30 s, annealing at 58 °C for 30 s and extending at 72 °C for 30 s, and final

extending step of 72 °C for 10 min. A partial fragment of the ITS2 gene was amplified using the primer pair LSU-1 (5'-CTAGCTGCGAGAATTAATGTGA-3')/ LSU-3 (5'-ACTTTCCCTCACGGTACTTG-3') (Wade and Mordan 2000). The conditions for thermal cycling: 2 min at 94 °C for pre-denaturing, 35 circles of 30 sec at 94 °C, 30 sec at 58 °C and 60 sec at 72 °C.

Chromatographs and sequences were first studied and compiled in sequencer 4.5. DNA sequences of both genes were aligned by T-Coffee with standard parameters (Di Tommaso et al. 2011). Then the badly aligned parts (marked green and purple in T-Coffee, indicating inferior alignment) were deleted. For the subsequent analyses a concatenated matrix of 91 (incl. outgroup, table 1) × 1068 bp (incl. gaps) was used. The model selection was made using "Models" in MEGA 7.0.26 (Kumar et al. 2015). The dataset was analyzed by Bayesian Inference (BI) in MrBayes 3.2.4 (Ronquist et al. 2012). While the dataset was analyzed using the Maximum Likelihood Analysis in raxmlGUI 2.0 beta (Edler et al. 2019), applying the GTRGAMMA+I model and reps 1,000. Three independent runs were performed in Bayesian Inference Analysis, each of which was performed for 1,000,000 generations and sampled every 1,000 generations, where the first 25% samples were discarded as burn-in. The convergence of the Markov Chain Monte Carlo simulations was investigated with tracer v. 1.7 (Rambaut et al. 2018) to confirm that all ESS values exceeded 200. *Helix pomatia* Linnaeus, 1758 (Table 3) was used as an outgroup for rooting phylogenetic trees. New DNA sequences were deposited in the NCBI GenBank under the accession numbers ON261686–ON261865 (Table 3).

Supraspecific classification

The generic classification of species adopted in this study mainly follows MolluscaBase (2021a–p; 2022a–c) (Table 3).

Abbreviations

AS accessory sac;
AO opening of accessory sac leading to dart chamber;
a.s.l. above sea level;
At atrium;
BC bursa copulatrix;
BCD bursa copulatrix duct;
DS dart sac;
Dt love dart;
DtC a chamber containing love dart;
DVM a membranous (or muscular) sac surrounding proximal dart sac and/or distal region of vagina near atrium;
Ep epiphallus;
fma fully mature animal(s) (i.e., shell(s) and soft parts);
fms fully mature empty shell(s);
FO free oviduct;
MG mucous glands;
juv juvenile;
P penis;
PAS proximal accessory sac, a blind sac on proximal dart sac (= DVM);

PO	opening of proximal accessory sac leading to dart sac chamber or dart chamber. In illustrations an PO is indicated by an asterisk or a red dot;	**PR**	penial retractor muscle;
		PS	penial sheath;
		Va	vagina;
		VD	vas deferens.

Depositories

CZG	Personal collection of Chen, Zhong-Guang [陈重光], China;
HBUMM	Mollusk collection of Museum of Hebei University (Baoding, China);
NHMUK	the Natural History Museum (London, UK);
SMF	Senckenberg Forschungsinstitut und Naturmuseum (Frankfurt am Main, Germany);
ZIN RAS	The Zoological Institute, Russian Academy of Sciences (St. Petersburg, Russia).

Results

Comparative examination of the terminal genital organs in *Laeocathaica*

The most complicated structure in the genital system of dart-sac-bearing camaenid species (here, we use "dart-sac-bearing camaenids" to replace the former subfamily Bradybaeninae), if present, is the dart sac apparatus, a sack-like structure on the vagina. The basic structure of a dart sac apparatus consists of a dart sac, the muscular blind tube that contains and can secrete the love dart, the penis insertion/opening and the vagina insertion/opening. The ventral side of the dart sac usually has an accessory sac that is distally connected by mucous glands and opens into the chamber containing the love dart or opening into the dart sac chamber. The mucous glands consist of several mucous gland tubes that are simply branched (i.e., only one tube or bifurcate tube) or complicatedly branched and covered, packaged and connected by a sheet of loose connective tissue that binds the mucous glands more or less tightly to the vagina (Fig. 4B). The nerve fibers that connect the mucous gland tubes (e.g., Wu 2019: fig. 5C), together with the proximal nerve fibers that connect the dart sac (incl. accessory sac), fuse into a main nerve fiber that is attached to the surface of the proximal oviduct before it enters the body wall of the animal. Bilateral symmetry (for directions see Fig. 1A) of a dart sac apparatus consisting of the above components has been observed in many genera of Bradybaeninae (Wu 2004). However, the position of the membranous sac surrounding the partial dart sac and/or distal region of the vagina proximal to the atrium (DVM) makes the dart sac asymmetric in some genera, e.g., in *Laeocathaica*. The DVM in dart-sac-bearing camaenid snails, has been ignored in many studies (e.g., those works before Wu and Guo 2003), or not particularly emphasized (e.g., in *Stilpnodiscus entochilus* Möllendorff, 1899, Wu (2004: fig. 16E): the sac around the space

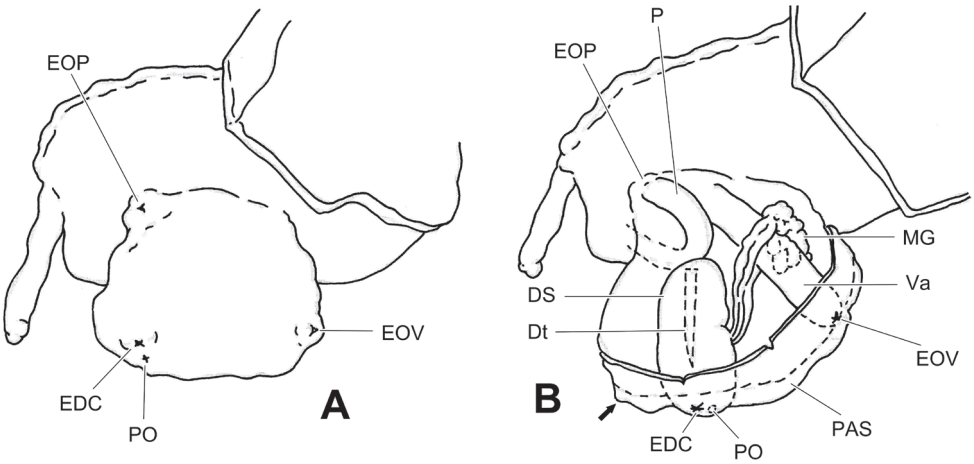

Figure 4. Terminal genitalia in the evaginated pouch in *Laeocathaica qishilii* Wu, sp. nov. (HBUMM08298-spec.8, paratype), showing relative position of dart sac apparatus, vagina, and penis **A** evaginated pouch of terminal genitalia **B** the exposed pouch. Arrow indicates the position of the proximal accessory sac. Abbreviations: DS – dart sac; Dt – love dart; EDC – entrance of dart chamber; EOV – external opening of vagina; EOP – external opening of penis; MG – mucous glands; P – penis; PAS – proximal accessory sac; PO – opening of proximal accessory sac leading to dart sac chamber or dart chamber; Va – vagina.

between V2 and V3), or treated by some authors as DVM (in *Trichobradybaena* Wu & Guo, 2003; in many species in Wu 2004; Wu 2019: table 1 for incomplete taxa, see below), or with alternative nomenclature referring to structures which are close in position and/or shape and blind or open into the dart sac chamber (i.e., "finger-shaped structure" in *Stilpnodiscus moellendorffi* Wu, 2001; "bladder" in *Laeocathaica polytyla* in Schileyko (2004); "bridge-like structure" in *Ponsadenia* spp. in Wu and Guo (2006); "proximal accessory sac", in *Traumatophora triscalpta* (Martens, 1875) in Wu (2019) and in *Pseudiberus* spp. where both blind ones or those open into the dart sac chamber were observed in Zhang et al. (2021)). The opening of the DVM was not recorded prior to observation in *T. triscalpta* (Wu 2019).

The so-called DVM structure cannot be distinguished from the proximal accessory sac in position, external morphology or internal structure. The fact that the conjunction of DVM structure and the proximal accessory sac was not observed in any Chinese bradybaenine genus (Wu 2019: table 1) suggests that they are originally the same organ. Consequently, in this work, the proximal accessory sac refers to "a membranous (or muscular) sac that partially surrounds the dart sac and/or distal region of the vagina proximal to the atrium" that does not differ from the DVM.

The proximal accessory sac, whose opening leads to the outside of the body (if is not blind) (Fig. 4), has been speculated to be the place where the fluid secreted by the mucous glands is stored (Zhang et al. 2021). Connecting with the chambers inside the dart sac apparatus, the PLS structure (e.g., in *Aegista* (*Aegista*) *accrescens* (Heude, 1882), Wu (2004: fig. 13C); *Aegista* (*Plectotropis*) *gerlachi* (E. Martens, 1881), Wu (2004: fig. 14B–D); in *Metodontia houaiensis houaiensis* (Crosse, 1882), Wu and Pro-

zorova (2006: fig. 3C), has yet to be proven that it is a modified PAS. When the dart sac apparatus in *Laeocathaica* is evaginated outwards to the body wall prior to dart shooting and epiphallus protrusion, an external sac is formed exposing the penial, vaginal and dart sac orifices and the proximal accessory sac (Fig. 4). Functionally, the proximal accessory sac forms a "cushion" (Fig. 4, arrowed) filled with the fluid secreted by the mucous glands during the pre-copulatory behavior. The shape, size, and number of openings of the proximal accessory sac are believed to be related to the compatibility of courtship behavior, which affects the efficiency of copulation.

In *Laeocathaica* it is most commonly observed that two proximal accessory sacs, the left and the right, each with a pore leading to the dart chamber or dart sac chamber, are dorsally separated and ventrally fused. For *Laeocathaica phaeomphala* Möllendorff, 1899, *L. polytyla* Möllendorff, 1899, and *L. tropidorhaphe*, the dart sac has no proximal accessory sac (Figs 23, 26, 34). The only species that has one proximal accessory sac is *Laeocathaica dolani* (Pilsbry, 1934) (Fig. 7). Two of the three species without proximal accessory sac have the elongated vagina part between atrium and dart sac (Figs 23A, 34A; Table 1). However, the third species *Laeocathaica polytyla* has neither a proximal accessory sac nor the elongated vagina part (Fig. 26). We can hardly guess how the love dart is to be exposed outside body through the long distance of the elongated vagina part, based on our knowledge of the normal situation of dart shooting in the genus, as showed in Fig. 4. The presence of two proximal accessory sacs in *Laeocathaica amdoana*, which has the relatively smallest proximal accessory sac in the genus (Fig. 6B, C), makes *L. amdoana* a species that may has a transitional state among the species that have large and ventrally fused proximal accessory sacs (e.g., in *L. carinalis* Chen & Zhang, 2004, Fig. 8), have large but ventrally separated proximal accessory sacs (e.g., in *L. zhengpingliui* Wu, sp. nov., Fig. 38) and have no proximal accessory sac (e.g., in *L. phaeomphala*, Fig. 23).

Unlike the structurally closed proximal accessory sac observed only in *Pseudiberus tectumsinense pingi* Zhang & Wu, 2021, the proximal accessory sac observed in all *Laeocathaica* species has an opening/pore leading to the dart chamber (for most species) or dart sac chamber (for *L. amdoana* only) instead of the proximal accessory sac opening leading only to dart sac chamber as observed in *Traumatophora* Ancey, 1887 (Wu 2019) and in *Pseudiberus* Ancey, 1887 (Zhang et al. 2021). In *Laeocathaica*, the proximal accessory sac pore is located at the distal end of the proximal accessory sac, opening into the proximal dart chamber, or at the central part of the proximal accessory sac, opening into the dart sac chamber. Accordingly, if the dart sac is evaginated during the mating of the snail, the pore is exposed to the outer environment or not deep in the dart chamber (Fig. 4).

The accessory sac in some *Laeocathaica* species is tiny in appearance and internally solid, with the mucous glands entering papilla (e.g., arrowed in Wu 2004: fig. 19B) missing (in *Laeocathaica amdoana*, *L. dityla* Möllendorff, 1899, *L. distinguenda*, *L. polytyla*, *L. potanini* Möllendorff, 1899, *L. stenochone*, *L. qishilii* Wu, sp. nov., *L. cheni* Wu, sp. nov.; Figs 6B, 14D, 16C, 26C, 28B, 32B, 36C, 39C). Even in species with an internally empty accessory sac, the mucous glands entering papilla is absent (in *Laeocathaica dolani*, *L. filippina* (Heude, 1882), *L. odophora* Möllendorff, 1899, *L. phaeomphala*,

Table 1. Some character states of the terminal genitalia in *Laeocathaica* Möllendorff, 1899.

Characters\Species	Vagina elongated above dart sac (+) or not (–)	Number of mucous glands	Branching of mucous gland duct complicated (+) or simple (–)	Blades of apical dart	Number of PAS	PAS: Symmetrical (+) or asymmetrical (–)	Number of PAS opening(s)	PAS: ventrally touching (+) or not (–)
L. amdoana Möllendorff, 1899	+	8	+	2	2 (tiny)	+	2	–
L. carinalis Chen & Zhang, 2004	–	4	–	/	2	+	2	+
L. carinifera (H. Adams, 1870)	–	6–7	+/–	/	2	–	2	+
L. christinae (H. Adams, 1870)	–	4–5	+	2	2	+	2	–
L. distinguenda Möllendorff, 1899	–	4–12	+/–	2	2	+	2	–
L. dityla Möllendorff, 1899	–	2–3	–	?	2	+	2	+
L. dolani (Pilsbry, 1934)	–	2–3	+	4	1	–	1	/
L. filippina (Heude, 1882)	–	5–7	+	?	2	+	2	+
L. odophora Möllendorff, 1899	–	5	–	2	2	–	2	+
L. powzowi Möllendorff, 1899	–	4	–	/	2	+	2	+
L. phaeomphala Möllendorff, 1899	+	8	–	/	0	/	/	/
L. polytyla Möllendorff, 1899	–	5	–	2	0	/	/	/
L. potanini Möllendorff, 1899	–	2–3	+	4	2	+	2	+
L. prionotropis Möllendorff, 1899	–	4–8	–	4	2	+	2	+
L. stenochone Möllendorff, 1899	–	5	+	2	2	+	2	+
L. tropidorhaphe Möllendorff, 1899	+	7–10	+	4	0	/	/	/
L. parapolytyla Wu, sp. nov.	–	4–5	–	/	0	/	/	/
L. *qishili* Wu, sp. nov.	–	2	+	2	2	+	2	+
L. qiminglii Wu, sp. nov.	/	/	/	/	/	/	/	/
L. zhengpingliui Wu, sp. nov.	+(somewhat)	6	–	0	2	+	2	–
L. cheni Wu, sp. nov.	–	4	–	2	2	+	2	+
L. qingchuanensis Wu, sp. nov.	+	6–8	–	/	2	+	2	+

L. prionotropis Möllendorff, 1899, *L. tropidorhaphe*; *L. zhengpingliui* Wu, sp. nov., and *L. qingchuanensis* Wu, sp. nov.; e.g., in Fig. 7B).

The penis of *Laeocathaica* is divided into three parts according to the structures that protrude on the inner wall. The proximal part consists of main/thicker pilasters. The central part is covered by cross-linked/network-like fine pilasters branched off from the main pilasters of the proximal part (e.g., in *Laeocathaica prionotropis*, Fig. 43D), or covered by isolated tongue-like/diamond-like granules that erect on the penis wall (in *L. cheni* Wu, sp. nov., Fig. 44F, H). The distal part is the distal end of the penis near the epiphallic opening, where the proximal mini-pilasters aggregate and form several short and more or less thick pilasters. All these three parts are intraspecifically stable, but more or less divergent among species. In the proximal part of the penis, it is characteristic that one (in most cases, i.e., in *Laeocathaica amdoana*, *L. carinalis*, *L. cheni* Wu, sp. nov., *L. distinguenda*, *L. dityla*, *L. dolani*, *L. odophora*, *L. polytyla*, *L. potanini* and *L. qishilii* Wu, sp. nov.) (Figs 41–44) or two (i.e., in *L. carinifera*, *L. prionotropis*, *L. tropidorhaphe*, *L. stenochone*, *L. parapolytyla* Wu, sp. nov., and *L. zhengpingliui* Wu, sp. nov.) (Figs 42–44) pairs of adjacent pilasters merge into one or two Y-shaped forks. In *Laeocathaica stenochone*, two pilasters form a Y-shaped fork (Fig. 43E, right arrow) and two other parallel pilasters merge into a rather thick pilaster (Fig. 43E, left arrow). Such a Y-shaped fork, formed by two adjacent pilasters, was not observed only in very few species (i.e., *Laeocathaica christinae* (H. Adams, 1870), *L. phaeomphala*, and *L. qingchuanensis* Wu, sp. nov.) (Figs 42C, D, 44E).

Systematics

Family Camaenidae Pilsbry, 1895

Genus *Laeocathaica* Möllendorff, 1899

Laeocathaica Möllendorff, 1899: 86; Richardson 1983: 77; Schileyko 2004: 1686.

Type species. *Helix* (*Plectotropis*) *christinae* H. Adams, 1870 (by original designation).

Description. Shell sinistral, strongly depressed to broadly conic, moderately solid, of 5–10.5 almost flat whorls. Last whorl abruptly descending in front, angulated to strongly keeled; rarely rounded. Coloration consists of whitish, corneous, or chestnut background and mostly with one or two dark sub-peripheral bands; besides, usually there are several fulvous, diffuse radial streaks. Protoconch usually with fine radial threads and/or fine granules that each is formed by a low hump deposited in a shallow socket. Sculpture of teleoconch whorls varying from fine, silky radial striation to rather strong ribbing; on basal surface below keel or angle this sculpture becomes much weaker. Aperture rounded to peach-shaped, oblique, margins usually more or less reflexed. Within aperture a ring-like thickening present. Apertural teeth absent or with one tuberculiform basal tooth and sometimes with another one on palatal wall. During postembryogenesis several sets of teeth, different from those developed at adult

stage in shape and/or number, present and remained to adult stage. Umbilicus moderate to very wide, ratio of umbilicus diameter to maximum diameter 0.21–0.50. Height 3.5–14 mm, maximum diameter 10.0–29.5 mm.

On left and right side of mantle edge, no leaf-shaped appendage present. Head wart between ommatophores present, weak, or developed. Jaw arcuate, with 3–8 more or less projecting ribs.

Slender vas deferens entering epiphallus at penial retractor muscle insertion. Penis generally clavate, rarely subcylindrical. Penis internally divided into three regions: the proximal part with narrow or thick longitudinal pilasters, among which one pair or two pairs of adjacent pilasters fuse into one Y-shaped fork or two Y-shaped forks (not in *Laeocathaica christinae*, *L. phaeomphala*, and *L. qingchuanensis* Wu, sp. nov.). The median part, composed of fine pilasters that weave into network or covered by isolated tongue-like/diamond-like granules erecting on penial wall. The distal part, near epiphallic opening, with mini-pilasters crowded and forming several short and thick pilasters. Epiphallic papilla absent. Penial sheath always present, surrounding proximal penis. Dart sac always present. Accessory sac presents at ventral dart sac, internally solid or narrowly empty. Mucous glands 2–12, each simply or complicatedly branched, entering accessory sac separately before being united into a common duct inside wall of accessory sac. Proximal section of dart sac with 0–2 PAS that if present, each has a tiny opening leading to dart chamber. Vagina between atrium and dart sac elongated only in a few species. Bursa copulatrix duct subcylindrical throughout (modified from Schileyko 2004).

Distribution. China: S Gansu, W Hubei, W Shaanxi, Chongqing, Sichuan.

Remarks. *Laeocathaica* species are granulate on the protoconch, which is smooth in actual observation due to erosion or weathering. In the original description of *Laeocathaica filippina*, Heude (1882) first mentioned the irregular white radiate stripes (1882), which were particularly noted by Möllendorff (1899) as "die stets vorhandenen Jugendlippen (the ever-present juvenile lips)" that joined the definition of *Laeocathaica*. Möllendorff (1899) also noticed in *Euhadra haplozona* Möllendorff, 1899 and *Euhadra eris* Möllendorff, 1899 such "ever-present juvenile lips" exist. The juvenile lips, which have remained on the mature shell, may be frequent and weak such as those of *L. minwui* Páll-Gergely, 2022 (Fig. 11A) and many other species, or sparse and strong as those of *Laeocathaica dityla* (Fig. 13D) and *L. parapolytyla* Wu, sp. nov. (Fig. 25). Regarding the genital organs, the Y-shaped forks present on the proximal part of inner wall of the penis were observed exclusively in most anatomically studied *Laeocathaica* species among the Chinese dart-sac-bearing camaenids.

Laeocathaica amdoana Möllendorff, 1899

Figs 2A, D, 5A, B, 6, 41A, B, 46G, H, 50A, 51, 52E; Tables 1, 3

Laeocathaica amdoana Möllendorff, 1899: 92, pl. 5, fig. 5; – Gude 1902: 6; – Yen 1939: 148, pl. 15, fig. 31; – Páll-Gergely et al. 2022: 38, fig. 3A, B.
Laeocathaica stenochone amdoana – Wiegmann 1900: 104, pl. 3, figs 91–93.
Laeocathaica (*Laeocathaica*) *amdoana* –Zilch 1968: 173; – Richardson 1983: 77.

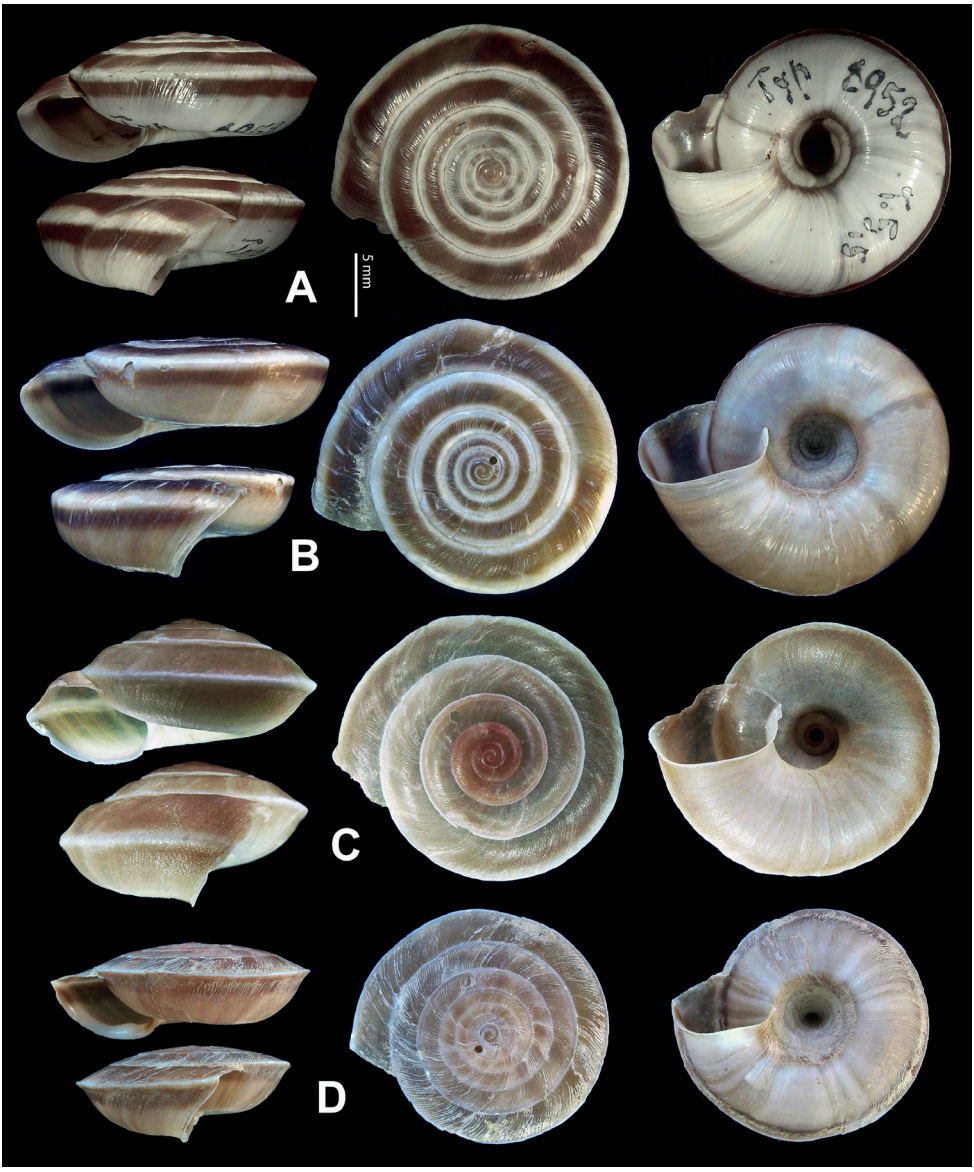

Figure 5. A, B *Laeocathaica amdoana* Möllendorff, 1899 **A** SMF 8952, lectotype **B** HBUMM05640-spec.1 **C** *L. dolani* (Pilsbry, 1934), HBUMM00069-spec.1 **D** *L. carinalis* Chen & Zhang, 2004, HBUMM08400-spec.1.

Museum material. ZIN RAS No. 2, 1 fma and 1 subadult, "*Aegista amdoana* Möllendorff.", Wen-Xian [文县], 1885-IX-8, coll. Potanin, det. Möllendorff. SMF 8952, lectotype, Ho-dshi-gou, Gansu, China. ex Potanin 853. Slg. O. v. Möllendorff. SMF 8953, paratype, Wen-hsien, SO-Gansu, China.

New material. HBUMM05600, numerous fma and juvs; southern slope of Beishan [北山], Wudu [武都], Longnan [陇南], Gansu Province, limestone hill

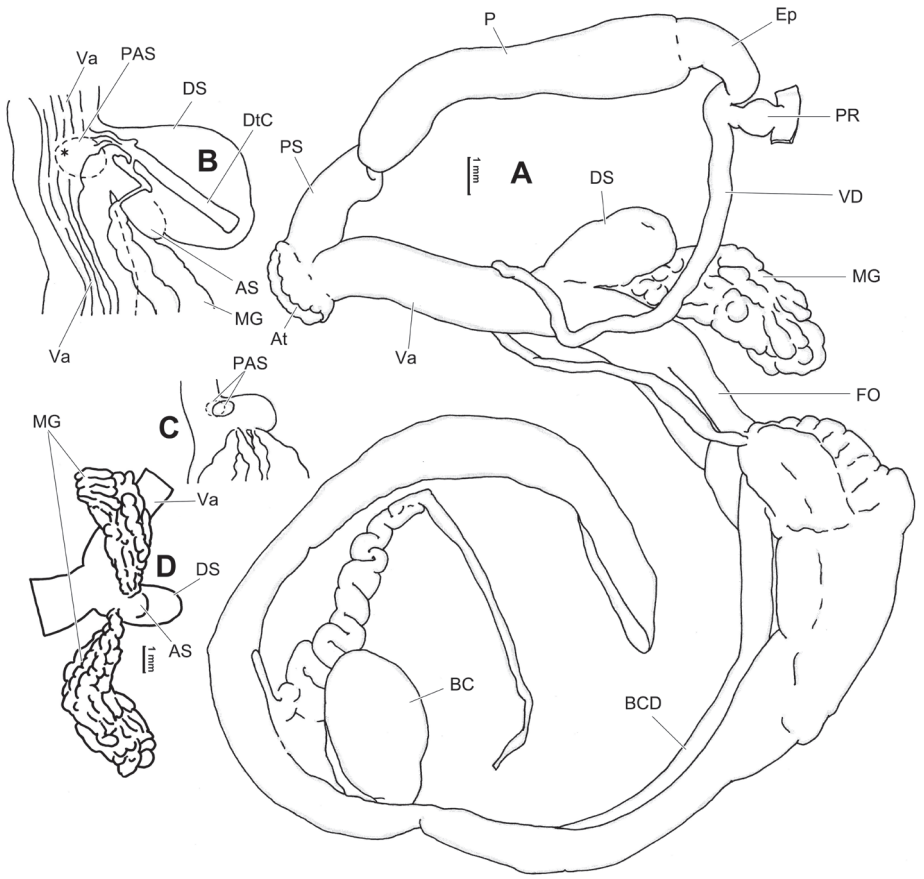

Figure 6. Genital anatomy of *Laeocathaica amdoana* Möllendorff, 1899, HBUMM05640-spec.1 **A** general view **B** left part of dart sac apparatus **C** right view of dart sac apparatus, showing position of proximal accessory sacs **D** ventral view of dart sac apparatus. Abbreviations: AS – accessory sac; At – atrium; BC – bursa copulatrix; BCD – bursa copulatrix duct; DS – dart sac; DtC – a chamber containing love dart; Ep – epiphallus; FO – free oviduct; MG – mucous glands; P – penis; PAS – proximal accessory sac; PR – penial retractor muscle; PS – penial sheath; Va – vagina; VD – vas deferens. Asterisk * indicates the opening of proximal accessory sac.

with sparse shrubs; 2006-X-02, coll. Liu, Jian-Min [刘建民], Zheng, Wei [郑伟]. HBUMM05640, numerous specimens, 2 fma dissected, Jiaogongzhen [角弓镇], Wudu, Gansu Province, (33.57°N, 104.64°E), broken limestone rocks, 2006-X-02, coll. Liu, J.-M. and Zheng, W. HBUMM05639, 4 fma and 1 juv, 1 fma dissected; Jiaogongzhen, Wudu, Gansu Province (33.57°N, 104.64°E), broken limestone rocks, 2006-X-02, coll. Liu, J.-M. and Zheng, W. HBUMM8147, 1 fma dissected: coll. data as HBUMM05640; DNA voucher HBUMM05626. HBUMM08147, 1 fma dissected, Wudu, Gansu Province, 927 m a.l.s., (33.346111°N, 105.044°E), adults on cliff and juvs on deadwood, 2017-VIII-05, coll. Shen, Xue-Fen [盛雪芬], etc.; DNA voucher HBUMM08147a. HBUMM08432, near Shichuanba [石川坝], Wenxian,

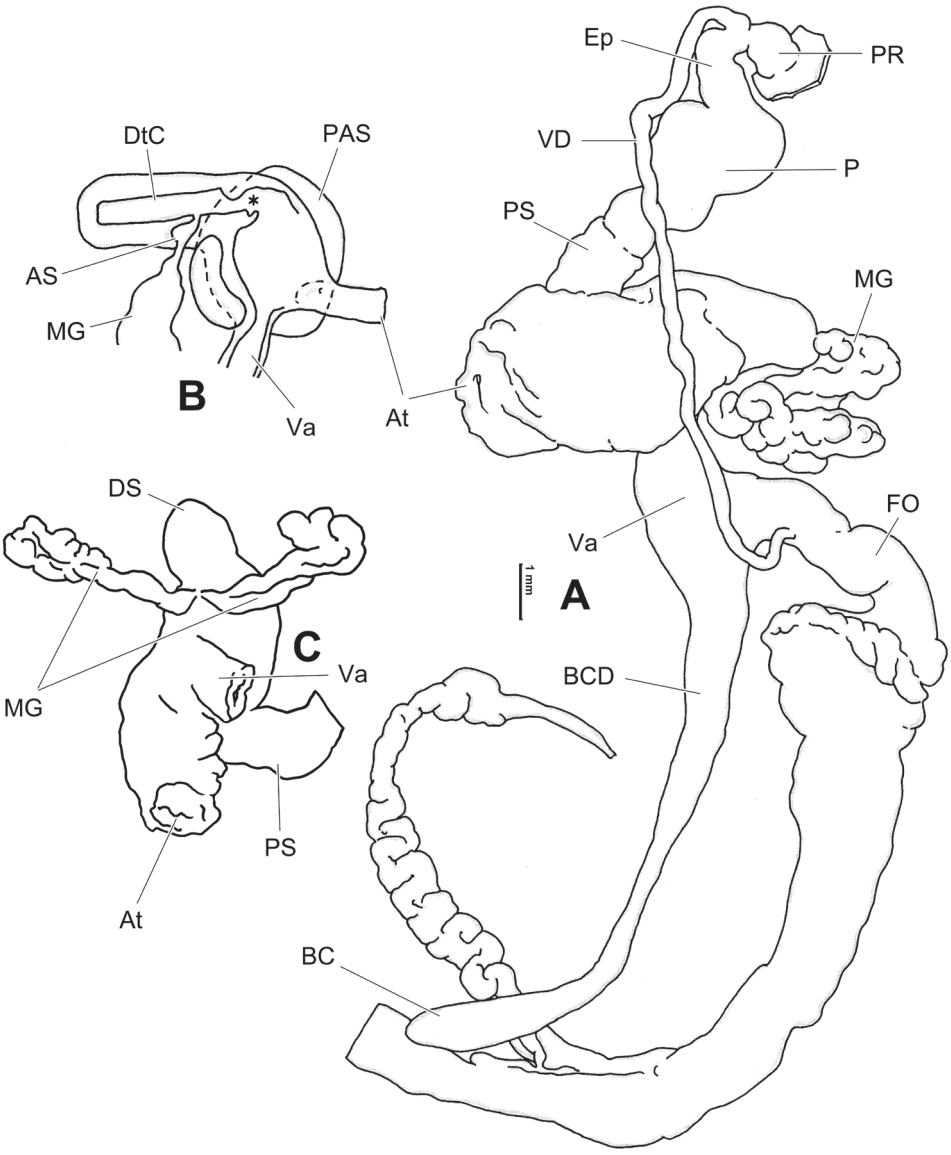

Figure 7. Genital anatomy of *Laeocathaica dolani* (Pilsbry, 1934) **A** general view, HBUMM08439-spec.1 **B** left view of dart sac apparatus, HBUMM08439-spec.1 **C** ventral view of dart sac apparatus, HBUMM00069-spec.1. Abbreviations: AS – accessory sac; At – atrium; BC – bursa copulatrix; BCD – bursa copulatrix duct; DS – dart sac; DtC – a chamber containing love dart; Ep – epiphallus; FO – free oviduct; MG – mucous glands; P – penis; PAS – proximal accessory sac; PR – penial retractor muscle; PS – penial sheath; Va – vagina; VD – vas deferens. Asterisk * indicates the opening of proximal accessory sac.

Gansu Province, near 33.17534°N, 105.019362°E; 2019-X-12, coll. Li, Qi-Ming [李启明]; DNA voucher HBUMM08432a.

Distribution. Gansu: Wudu, Wenxian (type locality).

Additional information of shell. Very fine and slim granules (~ 20 μm long) are present on the protoconch. After the fourth whorl, including the umbilical region, irregularly arranged spiral grooves are present. On teleoconch whorls, the growth lines are low and indistinct.

General anatomy. Eversible head wart lowly present. Jaw arcuate, with five projecting ribs.

Anatomy of genital organs. Penial sheath moderately long, covering ~ 1/3 of penis. Penis slightly expanded distally. Inside penis, two penial internal pilasters fusing into Y-shaped fork at proximal $^{1}/_{4}$, accompanied with 4–6 low pilasters. Distally inside penis, numerous fine pilasters merging into ~ 4 short but thick folds near opening of epiphallus. Vas deferens narrow throughout. Vagina between atrium and dart sac elongated, ~ 2 times longer than dart sac. Vagina between dart sac and insertion of bursa copulatrix duct short, ~ 3 mm in length. Dart sac ~ 1/3 length of penis. Love dart ~ 1.2 mm long, apically 2-bladed. Accessory sac small, internally solid, inserting into dart sac medially, opening to distal dart chamber. Mucous glands seven or eight, each complicatedly branched. Proximal accessory sacs two, not touching; each proximal accessory sac tiny, ~ 0.5 × 0.5 mm^2 (HBUMM05640-spec.1) or smaller (HBUMM05640-spec.2) in size; each with an opening leading to dart sac chamber. Bursa copulatrix duct of even diameter. Bursa copulatrix ovate.

Remarks. By shell sculpture, including that on the protoconch, this species (Fig. 46G, H) cannot be immediately distinguished from *Laeocathaica tropidorhaphe* (Fig. 46I, J) and *L. distinguenda* (Fig. 46A, B). It seems that *L. tropidorhaphe* forms a continuous variation of shell shape and the conchological delimitation among these three species that are geographically coexistent is not so distinct (Páll-Gergely et al. 2022). According to our observation, the key morphological features to practically distinguish the three species are:

(1) brownish/chestnut coloration. In *Laeocathaica amdoana* such coloration is usually (!) obviously darker and in *L. distinguenda* the coloration is usually very pale (in our Fig. 15C, it is a relatively darker shell). However, in HBUMM05479 (dissected, shell not pictured) the shell is in very pale dirty yellow except peripherally whitish.

(2) peripheral angulation. The level of angulation, in order is *Laeocathaica tropidorhaphe*> (>: stronger than; >>: much stronger than) *L. amdoana*>> *L. distinguenda*, which is also indicated by the geometric morphometric analyses: compared to *L. amdoana* (Fig. 5A, B; average shape 'b' in Fig. 50A) and *L. tropidorhaphe* (Fig. 33; average shape 'c' in Fig. 50A), the shell of *L. distinguenda* appears to be much broader in aperture and the periphery is very bluntly round (Möllendorff 1899).

(3) the structure of umbilicus. In both *Laeocathaica amdoana* and *L. tropidorhaphe*, the umbilicus is funnel-shaped and through which every whorl is visible. However, in *Laeocathaica distinguenda*, the penultimate whorl is much projecting and makes a suddenly enlarged umbilicus (Möllendorff 1899; our own observation, e.g., to compare Fig. 15 with Figs 5A, B, 33). *Laeocathaica amdoana*, *L. distinguenda*, and *L. tropidorhaphe* are clearly distinguishable based on genital features. *Laeocathaica amdoana*

and *L. tropidorhaphe*, both of which have a long vagina between dart sac apparatus and atrium that was not seen in *L. distinguenda*, can be distinguished by the presence of proximal accessory sac in the former species. *Laeocathaica tropidorhaphe* belongs to the three species in *Laeocathaica* that have no proximal accessory sac. In *Laeocathaica amdoana* there are two tiny proximal accessory sacs, and each has an opening leading to the dart sac chamber, which means the proximal accessory sacs could be functional compared to the blind one (i.e., without opening) observed in *Pseudiberus tectumsinense pingi* (Zhang et al. 2021). In addition, in *Laeocathaica amdoana* the dart is apically 2-bladed rather than 4-bladed in *L. tropidorhaphe*.

The phylogeny based on ITS2 and 16S suggests that *Laeocathaica amdoana* is sister to *L. distinguenda* and *L. tropidorhaphe* (Fig. 51). In Chen and Zhang (2004: 316, fig. 303), the species identified as *Laeocathaica amdoana* is dubious and looks like a *L. distinguenda*. For more comments, see *Laeocathaica tropidorhaphe*.

Laeocathaica anceyi (Möllendorff in Ancey, 1889)

Helix anceyi Möllendorff in Ancey, 1889: 205.
Laeocathaica anceyi – Pilsbry 1892: 215; – Gude 1902: 8.
Laeocathaica (*Laeocathaica*) *anceyi* – Richardson 1983: 77.

Examined specimens. None.

Distribution. Sichuan.

Laeocathaica carinalis Chen & Zhang, 2004

Figs 2A, 5D, 8, 41F, 47I, J; Table 1

Laeocathaica carinalis Chen & Zhang, 2004: 341, in Chinese, with erroneous text figure (fig. 334); – Páll-Gergely et al. 2022: 46, figs 9, 10.

New specimens. HBUMM08300, 3 fma, all dissected, ?Wenxian, Gansu Province, 2019-IV, coll. Li, Qi-Shi [李奇石]; DNA voucher HBUMM08300a. HBUMM8453, many fms, Shifangzhen [石坊镇], Wenxian, Gansu Province, near point (33.00509°N, 104.579061°E), 2021-IX-27, coll. Chen, Z.-G. HBUMM8455, Town of Wenxian, Gansu Province, near point (32.944361°N, 104.679819°E), 2020-VIII, coll. Chen, Z.-G.

Additional information of shell. In juveniles, regularly arranged fine threads and elongate granules are present on the protoconch, where in adults such sculpture is difficult to be observed because of erosion. Spiral grooves are present after the fourth whorl or only on apical body whorl, but are absent in umbilical side. The teleoconch has distinct and regularly arranged ribs, among which there is no fine threads.

Distribution. Gansu: Wenxian (type locality).

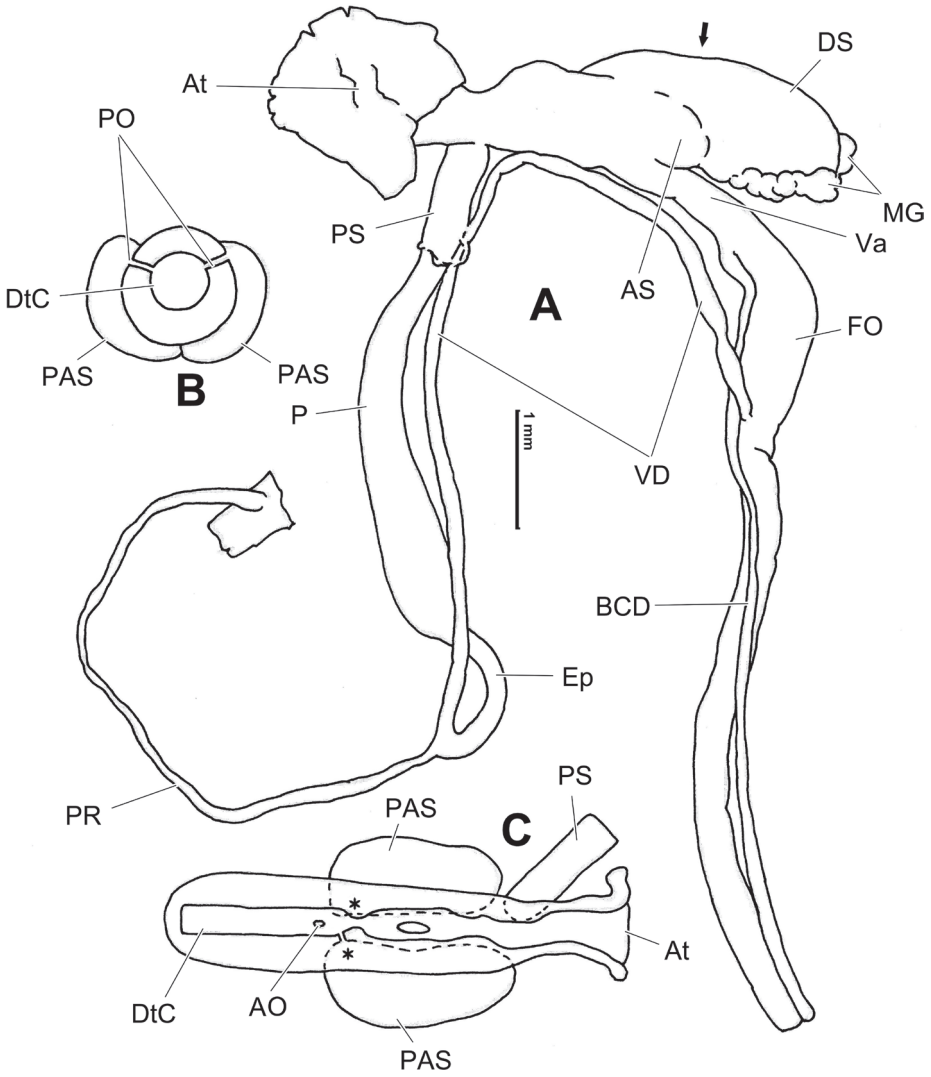

Figure 8. Genital anatomy of *Laeocathaica carinalis* Chen & Zhang, 2004, HBUMM08300-spec.1 **A** general view **B** cross-section of dart sac at the position arrowed in (**A**) **C** apical view of dart sac apparatus. Abbreviations: AS – accessory sac; At – atrium; BCD – bursa copulatrix duct; DS – dart sac; DtC – a chamber containing love dart; Ep – epiphallus; FO – free oviduct; MG – mucous glands; P – penis; PAS – proximal accessory sac; PO – opening of proximal accessory sac leading to dart chamber; PR – penial retractor muscle; PS – penial sheath; Va – vagina; VD – vas deferens. Asterisk * indicates the opening of proximal accessory sac.

General anatomy. Eversible head wart not prominent, perhaps due to specimen of not full maturity. Jaw arcuate, with five projecting ribs.

Anatomy of genital organs. Penial sheath moderately long, covering ~ 1/4 of penis. Penis slightly expanded distally. Accompanied with two or three lower pilasters, at proximal 1/2 of penis two thin penial pilasters fusing into one Y-shaped fork. Fine

pilasters of distal 1/2 penis weaving into delicate net. Near epiphallic opening numerous fine pilasters merging into ~ 4 short but thick folds. Vas deferens narrow throughout. Vagina between atrium and dart sac not elongated. Vagina between dart sac and insertion of bursa copulatrix duct ~ 1/2 length of dart sac. Dart sac ~ 2/3 length of penis. Information of love dart unknown. Accessory sac small. Mucous glands ~ 4, each complicatedly branched. Proximal accessory sacs two, symmetrical on dart sac, dorsally separated and ventrally touching, internally smooth (without pilasters), each with an opening leading to dart chamber near dart chamber opening. Bursa copulatrix duct of even diameter.

***Laeocathaica carinifera* (H. Adams, 1870)**
Figs 2A, C, 9, 10, 43G, 45I, J, 50B, 51, Tables 1, 3

Helix (*Plectotropis*) *christinae* var. *carinifera* H. Adams, 1870: 377.
Helix subsimilis Deshayes, 1874: 10, pl. 2, figs 28, 29; – Heude 1882: 22, pl. 20, fig. 18; – Standen 1905: 231.
Helix (*Plectotropis*) *subsimilis* – Ancey 1883: 7, pl. 2, figs 28, 29.
Helix christinae var. *carinifera* – Gredler 1884: 264 (= *Helix subsimilis* Deshayes, 1873); – Möllendorff 1884: 351.
Helix (*Cathaica*) *christinae* var. *subsimilis* – Pilsbry 1892: 214, pl. 49, figs 29–33.
Helix (*Cathaica*) *subsimilis* – Kobelt 1894: 713, pl. 203, figs 1–3.
Laeocathaica christinae carinifera – Richardson 1983: 78.
Laeocathaica (*Laeocathaica*) *subsimilis* – Zilch 1968: 175; – Richardson 1983: 79; Wu and Chen 1998: 107.
Cathaica subsimilis – Yen 1938: 456.
Laeocathaica subsimilis subsimilis – Yen 1939: 148, pl. 15, fig. 28.
Laeocathaica subsimilis – Möllendorff 1899: 44; – Wiegmann 1900: 96, pl. 3, figs 84–87; – Yen 1942: 283; – Gude 1902: 6; – Chen and Zhang 2004: 313, fig. 299.
Laeocathaica (*Laeocathaica*) *filippina* – Wu 2004: fig. 17.
Laeocathaica carinifera – Páll-Gergely et al. 2022: 50, fig. 12.

Museum material. *Laeocathaica subsimilis* (Deshayes, 1874): NHMUK V. W. McAndrew coll. Acc. no. 1563. SMF 95116, one fms; Szetschwan, Noerdl. der Stadt Juanjjuanj, China; ex Mus. Petersb. 1905 ex Potanin. Det. Möllendorff. SMF 24265, one fms and one near matured; Yang-dsy-gebiet; ex Heude. Slg. O. v. Möllendorff. SMF 294292, two juvs (the third one, a fms of *L. filippina*); Sytshuan, China; Slg. C. Bosch ex H. Rolle. SMF 24261, two fms; Liu-ba-ting, Shen-hsi, China; ex Potanin 451, Slg. O. v. Möllendorff. SMF 24258, three fms; O-Sytshuan; ex Möllendorff. Slg. W. Kobelt. SMF 24257, four fms; O-Sy-tshuan; ex. B. Schmacker, Slg. O. v. Möllendorff. SMF 24262, four fms; Sy-tshuan, Chung-king, W-M-China; ex Möllendorff, 1890, Slg. O. Böttger. SMF 24255, four fms; O-Sy-tshuan; ex L. Fuchs, Slg. O. v. Möllendorff. SMF 95712, one fms; Prov. Sze-chuen; Slg. C. R. Böttger, 1905. SMF 294294, one fms. China; Slg. C. Bosch ex Hermann Rolle. The species of following specimens

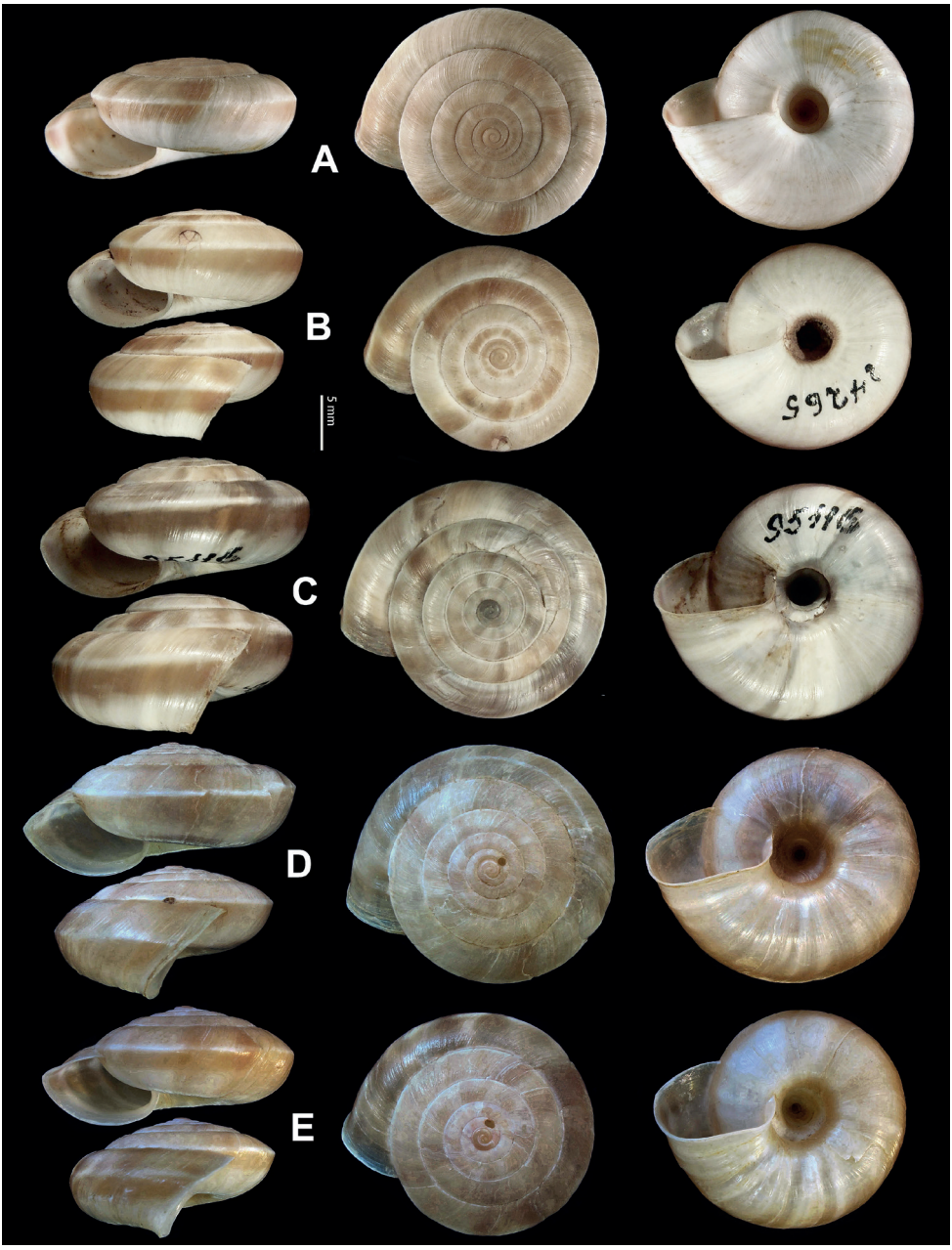

Figure 9. *Laeocathaica carinifera* (H. Adams, 1870) **A** NHMUK V. W. McAndrew coll. Acc. no. 1563 **B** SMF 24265 **C** SMF 95116 **D** HBUMM08443-spec.1 **E** HBUMM08443-spec.2.

are not decided: SMF 24260, one fms (with aperture not full matured), Kwan-juon-hszien (= Guangyuan) [广元县], Prov. Sze-Csuen, China, ex Kormos (Budapest). SMF 24256, three fms, Zw. Guan-yuan u. Dshau-hoa [昭化], Potanin 275, Slg. O.

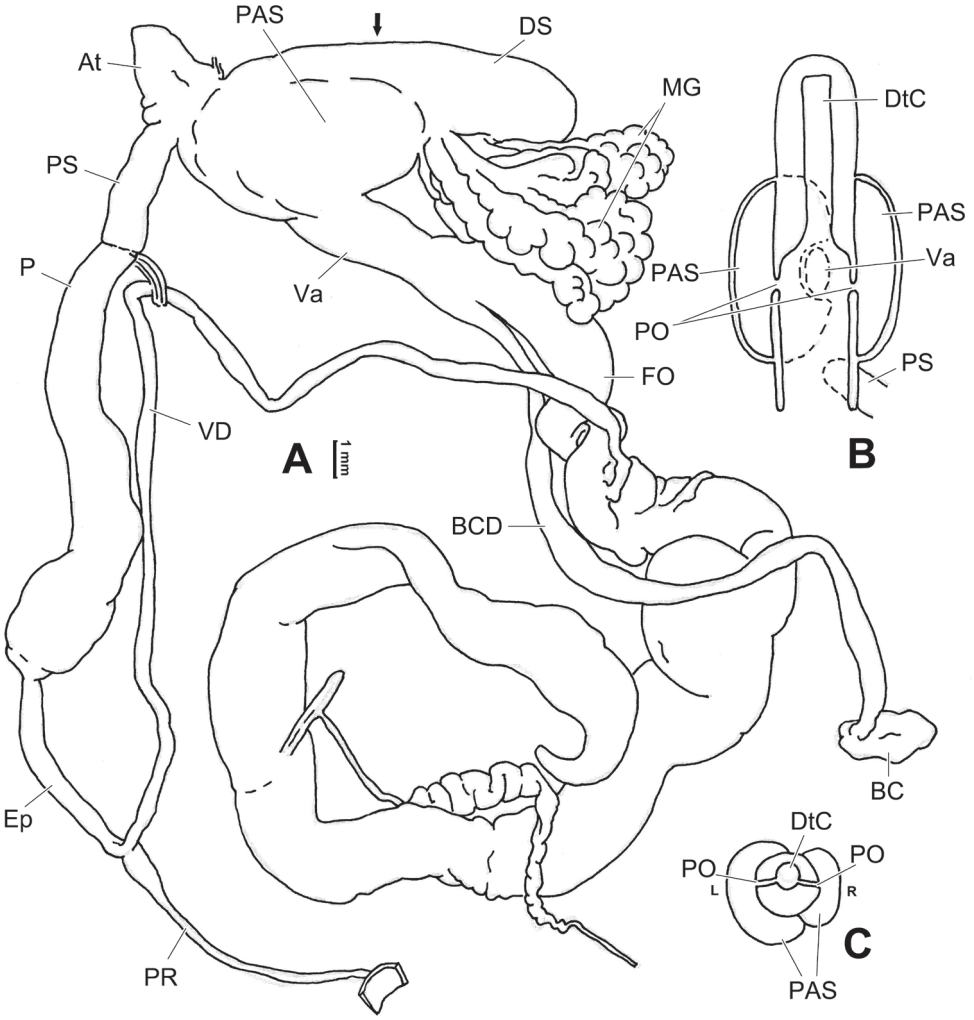

Figure 10. Genital anatomy of *Laeocathaica carinifera* (H. Adams, 1870), HBUMM08443-spec.1 **A** general view **B** apical view of dart sac apparatus **C** cross-section of dart sac at the position arrowed in (**A**). Abbreviations: AS – accessory sac; At – atrium; BC – bursa copulatrix; BCD – bursa copulatrix duct; DS – dart sac; DtC – a chamber containing love dart; Ep – epiphallus; FO – free oviduct; L – left; MG – mucous glands; P – penis; PAS – proximal accessory sac; PO – opening of proximal accessory sac leading to dart chamber; PR – penial retractor muscle; PS – penial sheath; R – right; Va – vagina; VD – vas deferens.

v. Möllendorff. SMF 24264, four fms, Lue-feng-kou bei Guan-yuan, ex Potanin 270, Slg. O. v. Möllendorff.

New material. HBUMM00006, 4 fma, 4 juvs; Xinjianxiang [新建乡], Nanchong [南充市], Sichuan Province, near point (30.963475°N, 105.842133°E); 1964-V-20, coll. Chen, De-Niu. [陈德牛]. HBUMM00228, 1 fma and 2 subadults; Beibei [北碚],

Chongqing [重庆], near point (29.809307°N, 106.411375°E); 1980, coll. Chen D.-N. HBUMM01573, 7 fma, 1 dissected; Muping [穆坪镇], Baoxingxian [宝兴县], Sichuan Province; the first hill to the south, between point A (1090 m a.s.l., 30.360333N 102.7255E) and point B (1021 m a.s.l., 30.341389N 102.783722E); limestone, 2 cm- thick litter layer, typical local vegetation type, seminatural, nearby cultivated with maize; 2003-VII-23, coll. Wu, Min [吴岷]. HBUMM03118, 4 juvs; Changping [长坪], Wanzhou [万州], Chongqing, near point (30.448543°N, 108.260695°E); 2003-VII-16, coll. Yuan, C. etc. HBUMM04064, many fma, 1 dissected; Meizixiang [梅子乡], Fengjiexian [奉节县], Chongqing, near point (430 m a.s.l., 31.178028°N, 109.341583°E); mixed rocks of slate and sandstone, semimature environment, very thin litter layer, nearby with eucalyptus trees; 2004-VII-18, coll. Wu, M. and Wu, Qin [吴琴]; DNA voucher HBUMM05121. HBUMM04162, numerous fma, 1 dissected, Shibaozhai [石宝寨], Zhongxian [忠县], Chongqing, 238 m a.s.l., 30.423083°N, 108.183972°E, shrubs and weed, purple sandy stone, humid, 2004-VII-16, coll. Wu, M., Wu, Q. and Qi, Gang [齐钢]; DNA voucher HBUMM05103. HBUMM04217, 10 fma; Tiejiacun [铁甲村], Jiangnanxiang [江南乡], Fengjiexian, Chongqing, 1005 m a.s.l., 30.956444°N, 109.468306°E; limestone, grass and shrubs, humid; 2004-VII-19, coll. Wu, M. and Wu, Q. HBUMM04219: many fma; same coll. data as HBUMM04064. HBUMM04232, several fma and juvs; near Xinmincun [新民村], Jiangnanxiang, Fengjiexian, Chongqing, 980 m a.s.l., 30.932583°N, 109.455639°E; mixed rocks of sandstone and limestone, grass and shrubs, humid, semi-farmland; 2004-VII-19, coll. Wu, M. and Wu, Q. HBUMM04235, 2 fma and 1 juv, 1 dissected, near town of Wuxixian [巫溪县], Chongqing, 339 m a.s.l., 31.402111°N, 109.634722°E; limestone, grass and shrubs, bare earth without litter layer; 2004-VII-22, coll. Wu, M.; DNA voucher HBUMM05131). HBUMM08443, 4 fma and 1 subadult, 4 dissected, Baidicheng [白帝城], Fengjie County, Chongqing, two kilometers away from the point (241 m a.s.l., 31.020194°N,, 109.472833°E), slate and sandy stones, woods with shrubs and trees, humid, 2004-VII-20, coll. Wu, M.

Distribution. Sichuan: Nanchong, Baoxing. Chongqing: Beibei, Changshouxian [长寿县], Fengduxian [丰都县] (type locality: Fungsiang gorge = Fengxiangxia [风箱峡]), Fengjiexian, Kaixian [开县], Liangpingxian [梁平县], Pengshuixian [彭水县], Shizhuxian [石柱县], Wanzhou, Wushanxian [巫山县], Wuxi, Yunyangxian [云阳县], Zhongxian. Shaanxi: Lueyang [略阳].

Additional information of shell. On adult shell the protoconch is granulate with thick granules of ~ 40 μm long, each of which looks like a hump in a pit. The obscurity of such granules is caused by erosion or weathering. Spiral grooves are absent throughout the shell. On teleoconch the growth lines are low but distinct.

General anatomy. Eversible head wart weak. Jaw arcuate, with four or five projecting ribs.

Anatomy of genital organs. Penial sheath moderately long, covering ~ 1/4–1/3 of penis. Penis somewhat expanded distally. A pair of penial internal pilasters fusing into one Y-shaped fork at proximal 1/3, and another pair fusing into one Y-shaped fork at proximal 1/2 of penis; some other low pilasters variably present. Distally inside penis, numerous fine pilasters merging into 6–8 short but thick folds near opening of

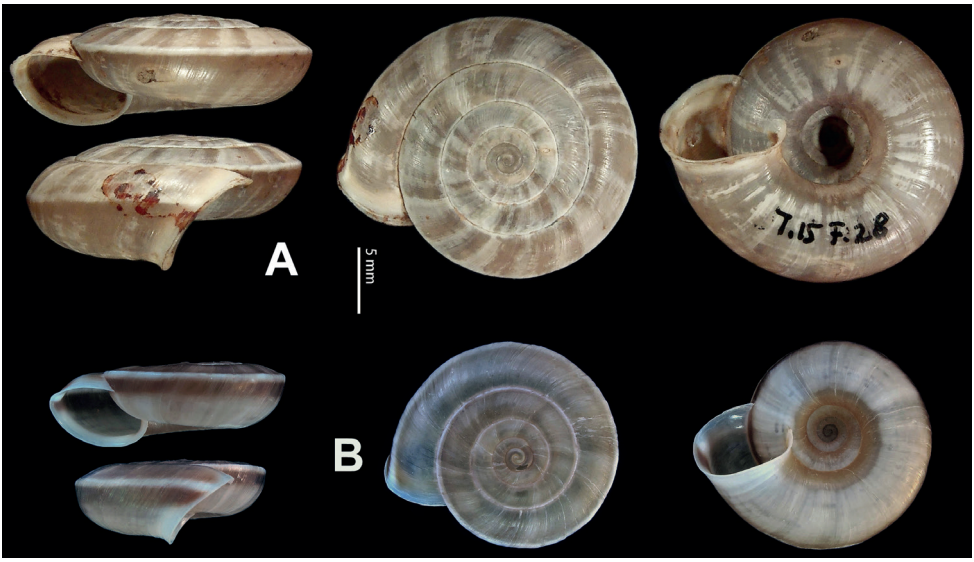

Figure 11. A *Laeocathaica minwui* Páll-Gergely, 2022, SMF 24255a **B** *L. christinae* (H. Adams, 1870), HBUMM01251-spec.1.

epiphallus. Vas deferens narrow throughout. Vagina between atrium and dart sac not elongated. Vagina between dart sac and insertion of bursa copulatrix duct approximately as long as or slightly shorter than 2/3 of dart sac. Dart sac ~ 1/2 of penis. Love dart ~ 2 mm long. Accessory sac spherical, internally almost solid, inserting into dart sac medially, opening to distal dart chamber. Mucous glands six or seven, each simply or complicatedly branched. Proximal accessory sacs two, asymmetrical, left one larger than right one, dorsally separated and ventrally touching, with internal pilasters, each with an opening leading to proximal dart chamber. Bursa copulatrix duct of even diameter. Bursa copulatrix ovate, small.

Remarks. See *Laeocathaica stenochone*.

***Laeocathaica christinae* (H. Adams, 1870)**

Figs 2A, 11B, 12, 42C, 45G, H; Table 1

Helix (*Plectotropis*) *christinae* H. Adams, 1870: 377, pl. 27, fig. 4, 4a.
Helix (*Plectopylis*) *christinae* – Ancey, 1882: 44.
Helix christinae – Dohrn, 1881: 596, pl. 174, figs 17–19; – Möllendorff 1884: 340, 351; – Gredler 1884: 264; – Heude 1885: 111, pl. 29, fig. 4; – Pilsbry 1892: 213, pl. 57, figs 15–17.
Laeocathaica christinae – Möllendorff 1899: 43; – Gude 1902: 6; – Yen 1942: 283, pl. 28, fig. 197; – Chen and Zhang 2004: 334, fig. 326; – Páll-Gergely et al. 2022: 54, fig. 13.
Laeocathaica (*Laeocathaica*) *christinae christinae* – Zilch 1968: 173.
Laeocathaica (*Laeocathaica*) *christinae* – Richardson 1983: 77.

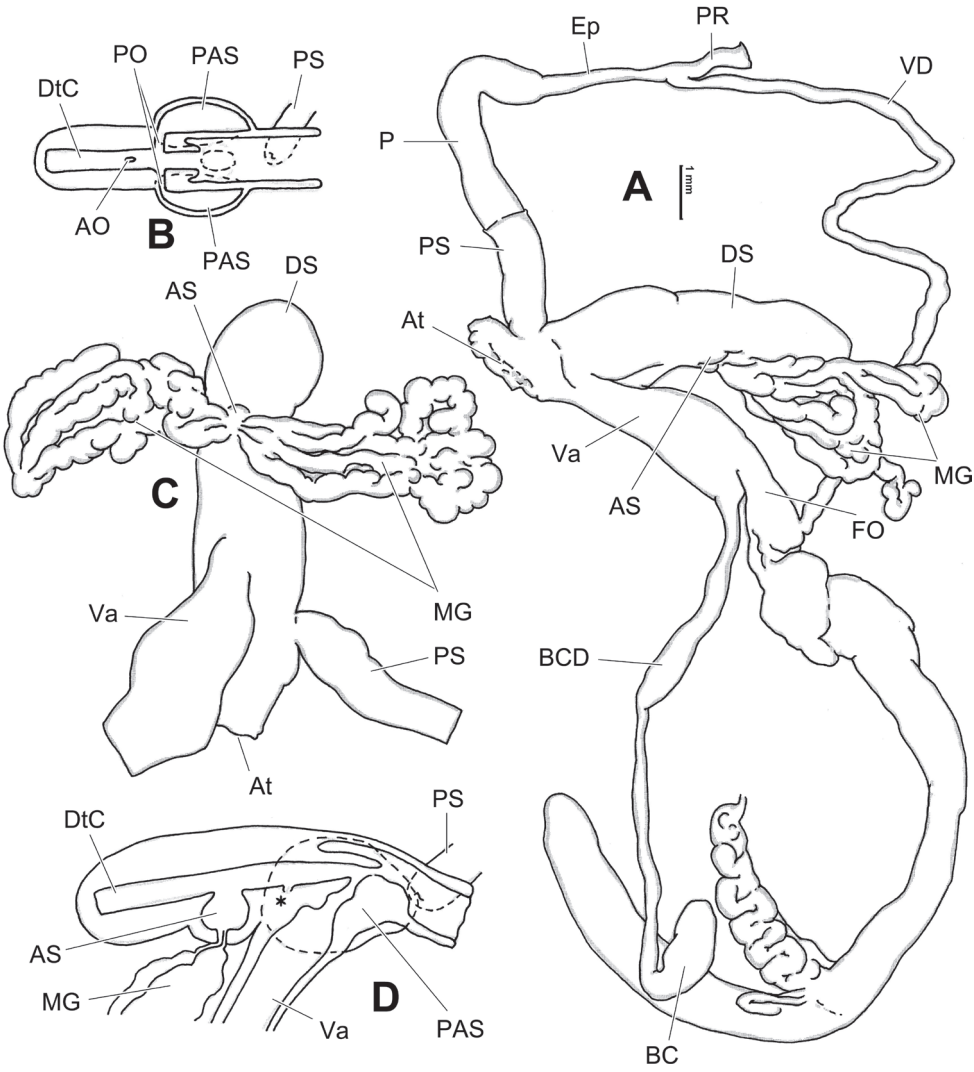

Figure 12. Genital anatomy of *Laeocathaica christinae* (H. Adams, 1870) **A, C** HBUMM01251-spec.1 **B, D** HBUMM04204-spec.1 **A** general view **B–D** apical, ventral, and left views of dart sac apparatus. Abbreviations: AO – opening of accessory sac leading to dart chamber; AS – accessory sac; At – atrium; BC – bursa copulatrix; BCD – bursa copulatrix duct; DS – dart sac; DtC – a chamber containing love dart; Ep – epiphallus; FO – free oviduct; MG – mucous glands; P – penis; PAS – proximal accessory sac; PO – opening of proximal accessory sac leading to dart chamber or dart sac chamber; PR – penial retractor muscle; PS – penial sheath; Va – vagina; VD – vas deferens. Asterisk * indicates the opening of proximal accessory sac.

Museum material. SMF 61056. Labeled with *L. subsimilis*: SMF 50089, two fms; W-Hupei, China; Slg. g. Maegele ex V. Gredler, 1906.

New material. HBUMM01251a, many fma, 1 fma dissected; Wuyuandong [无源洞] and nearby, Badong [巴东], Hubei Province, 254 m a.s.l., 31.027667°N,

110.420139°E, broad-leaved woods, limestone, humid, 2003-VIII-20, coll. Wu, M. HBUMM04204, Wuyuandong and nearby, Badong, Hubei Province, 255 m a.s.l., 31.026806°N, 110.422111°E, broad-leaved woods, limestone, humid, 2004-VII-31, coll. Wu, M., Wu, Q., Qi, G.

Distribution. Chongqing: Fengjie (type locality: Fungsiang gorge (= Fengxiangxia)); Hubei: Badong.

Additional information of shell. Tiny granules (~ 5 – ~ 50 μm) are densely and radially arranged throughout the protoconch. The erosion or weathering of sculpture on adult shell is not observed. Spiral grooves are absent throughout the shell. On teleoconch the growth lines are usually indistinct.

General anatomy. Eversible head wart weakly present. Jaw arcuate, with four projecting ribs.

Anatomy of genital organs. Penial sheath covering ~ 1/3 of penis. Penis tubular and equally thick. Inside penis, 5–6 narrow or thick pilasters present, Y-shaped fork formed by adjacent pilasters absent. Fine pilasters on distal end of penis merging into seven or eight thick folds. Vas deferens narrow throughout. Vagina between atrium and dart sac not elongated. Vagina between dart sac and insertion of bursa copulatrix duct ~ 1/2 length of dart sac. Dart sac slightly shorter than penis. Love dart ~ 5 mm long, apically 2-bladed. Accessory sac small but externally distinct, internally empty but spatially narrow, inserting into dart sac at middle part, opening to distal dart chamber. Mucous glands four (HBUMM04204-spec.14, spec.16) or five (HBUMM04204-spec.13, HBUMM01251a-spec.1), each complicatedly branched. Proximal accessory sacs two, symmetrical or the left one slightly larger (HBUMM04204-spec.14), dorsally and ventrally separated, each with a distal opening leading to dart chamber near its opening. Bursa copulatrix duct of even diameter. Bursa copulatrix ovate, small.

Remarks. This species is not known from NW Sichuan, so the specimens distributed in "Wentschun" [Wenchuan 汶川] identified as *Cathaica christinae* by Blume (1925; followed by Yen 1938), may indicate some other sinistral species. However, it could also be an erroneous site naming, as all field records except this indicate that no *Laeocathaica* species is distributed in Wenchuan.

Laeocathaica dejeana **(Heude, 1882)**

Figs 2A, 13A, B

Helix dejeana Heude, 1882: 21, pl. 20, fig. 17; – Möllendorff 1884: 340, 352.
Helix (*Cathaica*) *dejeana* – Pilsbry 1892: 215, pl. 49, figs 36–38.
Cathaica dejeana – Möllendorff, 1899: 73; – Yen 1938: 446; – Yen 1939: 141, pl. 14, fig. 46; – Yen 1942: 278.
Cathaica (*Pseudiberus*) *dejeana* – Gude 1902: 8.
Cathaica (*Campylocathaica*) *dejeana* – Richardson 1983: 51; – Chen and Zhang 2004: 270, fig. 255.
Laeocathaica dejeana – Wu 1999: 148, fig. 6.13-1; – Chen and Zhang 2004: 337, fig. 330; – Páll-Gergely et al. 2022: 56, fig. 15.

Figure 13. A, B *Laeocathaica dejeana* (Heude, 1882) **A** SMF 23919, lectotype **B** NHMUK1902.5.13.1-2 **C–E** *L. dityla* Möllendorff, 1899 **C** SMF 9086, lectotype **D** SMF 9087, paratype **E** HBUMM00698-spec.1.

Museum material. SMF 23919, lectotype. NHMUK 1902.5.13.1-2, 2 juv shells; W. Setchuan, W. China.

Distribution. Sichuan: western region (type locality) including Kangding [康定].

Additional information of shell. Protoconch has small granules. Spiral grooves are absent throughout the shell. Shell surface has tiny scales.

Anatomy of genital organs. Penis as long as dart sac, distally expanded. Vas deferens narrow throughout. Vagina between atrium and dart sac not elongated. Vagina between dart sac and insertion of bursa copulatrix duct ~ 1/2 length of dart sac. Love dart ~ 2 mm long, apically 2-bladed. Accessory sac small but distinguishable from outside, inserting into dart sac at middle part, opening to distal dart chamber. Mucous glands two, each complicatedly branched. Bursa copulatrix duct of equal thickness, as long as dart sac. Bursa copulatrix ovate (Wu 1999: 148, fig. 6.13-1).

Laeocathaica distinguenda Möllendorff, 1899

Figs 2A, D, 15, 16, 41D, E, 46A, B, 50A, 51; Tables 1, 3

Laeocathaica distinguenda Möllendorff, 1899: 93, pl. 5, fig. 6; – Gude 1902: 6; – Yen 1939: 149, pl. 15, fig. 32; – Yen 1942: 283; – Chen and Zhang 2004: 317, fig. 305.
Laeocathaica subsimilis distinguenda – Wiegmann 1900: 99, pl. 3, fig. 88.
Laeocathaica (*Laeocathaica*) *distinguenda* – Zilch 1968: 173; – Richardson 1983: 78.
Laeocathaica amdoana – Páll-Gergely et al. 2022: 38, fig. 5A.

Museum material. SMF 8959, lectotype; Thal des Pui-ho (= Baishuijiang) [白水江] b. Lum-du, Sy-tshuan, China; ex Potanin 906, Slg. O. v. Möllendorff. SMF 95024, paratype; SO-Gansu, NW-China; Slg. C. R. Böttger 1904 (ex Möllendorff!). "*Aegista distinguenda*", ZIN RAS No. 7, 3 fms. ZIN RAS No. 22, 1 fma and 1 subadult, between Nanping [南坪 = Jiuzhaigou 九寨沟县] and Sung-Pan (= Songpan), coll. Beresowskij, 1894, det. Möllendorff.

New material. HBUMM00674, numerous fma; Jianshanxiang [尖山乡], Wenxian, Gansu Province, 840 m a.s.l., 33.043291°N, 104.869226°E; 1998-IV-29, coll. Chen, D.-N. HBUMM05473, many fms, Jidushan [基督山] near Baishuijiang, Wenxian, Gansu Province, near point (32.94936°N, 104.699043°E); limestone and broad-leaved woods; 2006-IX-27; coll. Wu, M., Liu, J.-M., Zheng, W. and Gao, Lin-Hui [高林辉]. HBUMM05434, HBUMM05436, 2 fma dissected, Yuxushan [玉虚山], Wenxian, Gansu Province, 32.957259°N, 104.689152°E, shrubs and slate, 2006-IX-27, coll. Wu, M., Liu, J.-M., Zheng, W. and Gao, L.-H. HBUMM05415, 2 fma; hill foot of Yuxushan, Wenxian, Gansu Province; slate and shrubs, dry; 2006-IX-27, coll. Wu, M., Liu, J.-M., Zheng, W. and Gao, L.-H. HBUMM05417, numerous fma, 3 fma dissected, same data as HBUMM05436; DNA voucher HBUMM05407. HBUMM05434, 2 fma; same data as HBUMM05436. HBUMM05479, 2 fma; bank of Baishuijiang, Wenxian, Gansu Province, 32.946383°N, 104.685343°E, limestone and loess, broad-leaved woods, 2006-IX-27, coll. Wu, M., Liu, J.-M., Zheng, W. and Gao, L.-H.; DNA voucher HBUMM05442. HBUMM05554, 1 fma, 4 subadults. HBUMM05565a, many fma. HBUMM05571, many fma and subadults. HBUMM05576b, 1 fma: Hengdan [横丹], Wenxian, Gansu Province; north side of Baishuijiang River, along 212 Guodao, near point (32.864025°N, 104.859517°E); hillside, bushes; 2006-IX-29; coll. Wu, M., Liu, J.-M., Zheng, W. and Gao, L.-H. HBUMM06536, not dissected; town of Wenxian, Gansu Province, 1024 m a.s.l., 32.941111°N, 104.668889°E, 2011-VIII-08, coll. Wu,

M., Xu, Qin [徐沁], Budha, Prem; DNA voucher HBUMM06535. HBUMM06579, 2 fma, 4 fms and 1 juv (DNA voucher HBUMM06578). HBUMM06556, 2 fms: Fengchengsi [风成寺], Jiuzhaigouxian, Sichuan Province, 1515 m a.s.l., 33.256280°N, 104.238386°E; 2011-VIII-14, coll.Wu, M., Xu, Q. and Buhda, P.; DNA voucher HBUMM06555. HBUMM06646, 1 fma; Wenxian, Gansu Province, 1269 m a.s.l., 33.091944°N, 104.360833°E; 2011-VIII-9, coll. Wu, M., Xu, Q. and Buhda, P. HBUMM06736, 1 subadult; Eastern bank of Baishuijiang, Lihuacun [梨花村], Jiuzhaigouxian, Sichuan Province, 1425 m a.s.l., 33.267222°N, 104.234722°E; 2011-VI-14, coll.Wu, M., Xu, Q. and Buhda, P. HBUMM08148, 1 fma and several subadults; slope near river, Wenxian, Gansu Province, 807 m, 32.847111°N, 104.88775°E; grass and a few shrubs, on branches and rock cliff; 2017-VIII-6, coll. Sheng, X.-F. etc. HBUMM08429, 1 fma dissected; toward Danpuzhen [丹堡镇] on national road 212, Wenxian, Gansu Province, near 32.872636°N, 104.784372°E, on slope, 2019-X-13, coll. Li, Q.-M.; DNA voucher HBUMM08429a. CZG202008-w5, 8 fms, Zhangzhazhen [彰扎镇], Jiuzhaigouxian, Sichuan Province, near point (33.30674°N, 103.877345°E); 2020-VIII, coll. Chen, Z.-G. CZG202008-w9, Heihexiang [黑河乡], Jiuzhaigouxian, Sichuan Province, near (33.54941°N, 104.041691°E); 2020-VIII, coll. Chen, Z.-G. CZG202008-w10, 5 fms, whitish shells; Shijiba [石鸡坝], Wenxian, Gansu Province, near point (33.067936°N, 104.456784°E); 2020-VIII, coll. Chen, Z.-G.

Distribution. Gansu: Wenxian (type locality), Wudu (type locality), Zhouquxian (type locality); Sichuan: Jiuzhaigouxian (type locality).

Additional information of shell. The protoconch has the widespread granules each of which is ~ 20 – ~ 40 μm long and looks like a hump embedded in a shallow socket. All granules are present on densely arranged fine radial threads. Spiral grooves are shallowly present. The growth lines on teleoconch are more or less distinct but are irregularly arranged.

General anatomy. Eversible head wart present. Jaw arcuate, with 4–7 projecting ribs.

Anatomy of genital organs. Penial sheath moderately long, covering ~ 1/6–1/4 of penis. Penis slightly expanded distally. Inside penis, two penial pilasters forming one Y-shaped fork at proximal 1/3 penis (only indistinct in HBUMM05417); a rather thick pilaster that is made up of numerous thread-like longitudinal folds occupying proximal 1/3–2/3 of penis. Pilasters of median to distal penis weaving into a delicate net that bears regularly arranged diamond-shaped papillae, which are usually lost perhaps because of bad specimen condition. Distally inside penis, fine pilasters merging into 6–9 short and more or less thick folds near opening of epiphallus. Vas deferens narrow throughout. Vagina between atrium and dart sac not elongated. Vagina between dart sac and insertion of bursa copulatrix duct ~ 1/4 length of dart sac. Dart sac ~ 1/2 length of penis. Love dart ~ 9 mm long, apically 2-bladed. Accessory sac small but distinguishable from outside, internally solid, inserting into dart sac at middle part, opening to distal dart chamber. Mucous glands 4 (HBUMM08429, each complicatedly branched) – 12 (HBUMM05479, simply branched). Proximal accessory sacs two, symmetrical or the right one slightly larger, separated dorsally and ventrally, with a few internal pilasters, each with an opening leading to dart chamber near opening of dart chamber. Bursa copulatrix duct of even diameter. Bursa copulatrix ovate.

Remarks. The sculpture on protoconch and teleoconch of this species (Fig. 46A, B) resembles that of *Laeocathaica amdoana* (Fig. 46G, H). However, in *Laeocathaica distinguenda*, as in the most congeners of *Laeocathaica*, the part of the vagina between atrium and dart sac apparatus is not elongated.

For more comments, see *Laeocathaica tropidorhaphe*.

Laeocathaica dityla Möllendorff, 1899

Figs 2A, 3, 13C–E, 14, 41G, H, 45C, D; Table 1

Laeocathaica dityla Möllendorff, 1899: 99, pl. 6, fig. 8; – Sturany 1900: 22, pl. 1, figs 4–6; – Wiegmann 1900: 121, pl. 3, figs 108–111; – Gude 1902: 6; – Yen 1939: 150, pl. 15, fig. 42; – Chen and Zhang 2004: 332, fig. 324; – Páll-Gergely et. al.: 57, fig. 16.
Laeocathaica (*Laeocathaica*) *dityla* – Zilch 1968: 174; Richardson 1983: 78.

Museum material. SMF 9086, lectotype. SMF 9087, 1 paratype. SMF 9088, 1 paratype. ZIN RAS No.1, 1 fms.

New material. HBUMM00532, 2 juvs; Xinglongcun [兴隆村],Zhongzhaixiang [中寨乡], Wenxian, Gansu Province, near point (33.232415°N, 104.419075°E); 1998-V-19, coll. Chen, D.-N. and Zhang, Guo-Qing [张国庆] HBUMM00698, 1 fma and several juvs, 1 fma dissected; Daigusicun [代古寺村], Diebuxian [迭部县], Gansu Province, near point (34.004495°N, 103.940717°E), 1998-V-10, coll. Chen, D.-N. and Zhang, G.-Q. HBUMM05644, 4 fma and several fms; Jiaogongzhen, Wudu, Gansu Province (33.57°N, 104.64°E), broken limestone rocks, 2006-X-02, coll. Liu, J.-M. and Zheng, W. HBUMM05674, 1 fms; eastern bank of Bailongjiang [白龙江], Lianghekou [两河口], Dangchangxian [宕昌县], Gansu Province, near point (33.697332°N, 104.493015°E); limestone; 2006-X-02, coll. Zheng, W. and Gao, L.-H. HBUMM05685, 1 fma and 1 juv; western bank of Bailongjiang, Lianghekou, Dangchangxian, Gansu Province, near point (33.696791°N, 104.49129°E); limestone; 2006-X-02, coll. Zheng, W. and Gao, L.-H. HBUMM05710, 1 fms; Guantingzhen [官亭镇], Dangchangxian, Gansu Province, near point (33.82428°N, 104.538282°E); limestone hills, along 212 Guodao; 2006-X-3, coll. Zheng, W. and Liu, J.-M. HBUMM08449, 3 fms; Shijiba, Wenxian, Gansu Province, near point (33.067582°N, 104.457685°E); 2020-VIII, coll. Chen, Z.-G.

Distribution. Gansu: Wenxian, Diebuxian, Dangchangxian, Zhouquxian (type locality).

Additional information of shell. Tiny, low and sparsely arranged granules (~ 10 μm) on the smooth protoconch are present but difficult to be observed because of erosion or weathering. Spiral grooves are absent throughout the shell. On teleoconch the growth lines are not observed except on the part just following the protoconch.

General anatomy. Eversible head wart present but not prominent. Jaw arcuate, with four or five projecting ribs.

Anatomy of genital organs. Penial sheath rather short, covering ~ 1/8 of penis. Penis tubular and equally thick. Inside penis, two penial internal pilasters forming one

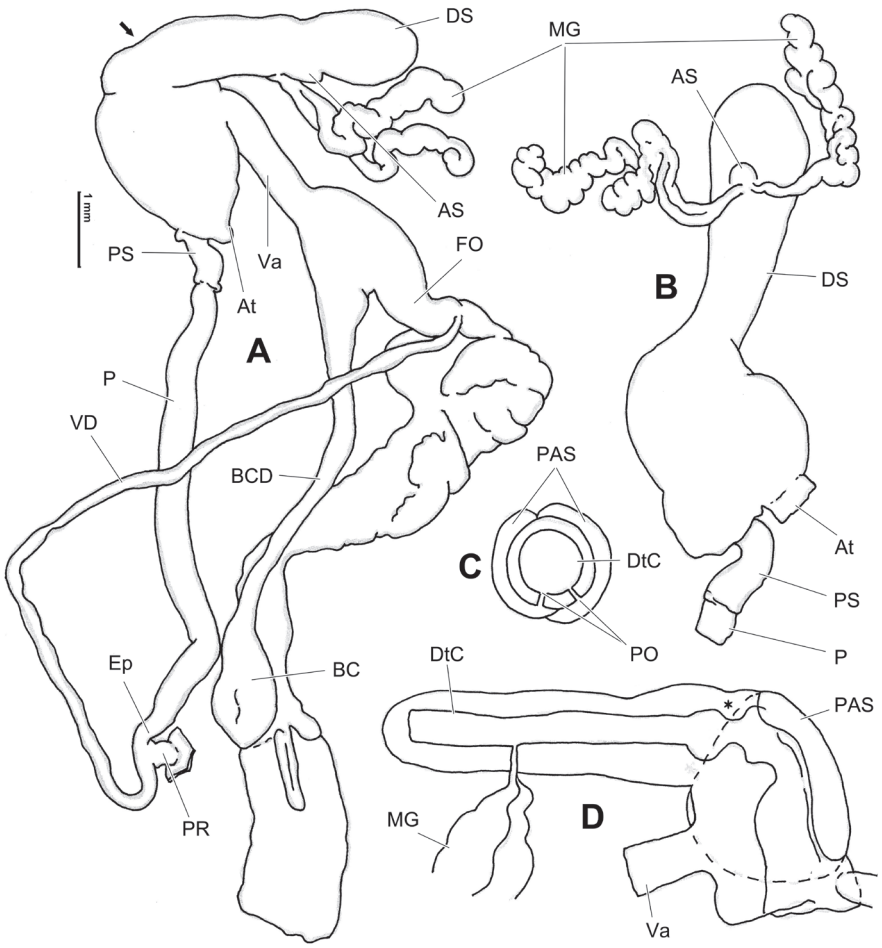

Figure 14. Genital anatomy of *Laeocathaica dityla* Möllendorff, 1899, HBUMM00698-spec.1 **A** general view **B** ventral view of dart sac apparatus **C** cross-section of dart sac at the position arrowed in (**A**) **D** left view of dart sac apparatus. Abbreviations: AS – accessory sac; At – atrium; BC – bursa copulatrix; BCD – bursa copulatrix duct; DS – dart sac; DtC – a chamber containing love dart; Ep – epiphallus; FO – free oviduct; MG – mucous glands; P – penis; PAS – proximal accessory sac; PO – opening of proximal accessory sac leading to dart chamber; PR – penial retractor muscle; PS – penial sheath; Va – vagina; VD – vas deferens. Asterisk * indicates the opening of proximal accessory sac.

Y-shaped fork at proximal 1/2 of penis, accompanied with another two thicker pilasters. Distal 1/2 of penis occupied by numerous isolated minute diamond-shaped papillae. Vas deferens narrow throughout. Vagina between atrium and dart sac not elongated. Vagina between dart sac and insertion of bursa copulatrix duct approximately as long as dart sac. Dart sac ~ 1/2 length of penis. Love dart ~ 4 mm long, apically 2-bladed and then rounded. Accessory sac small but distinguishable from outside, internally empty but spatially narrow, inserting into dart sac medially, opening to distal dart chamber. Mucous glands two (HBUMM00698-spec.2, spec.3) or three (HBUMM00698-

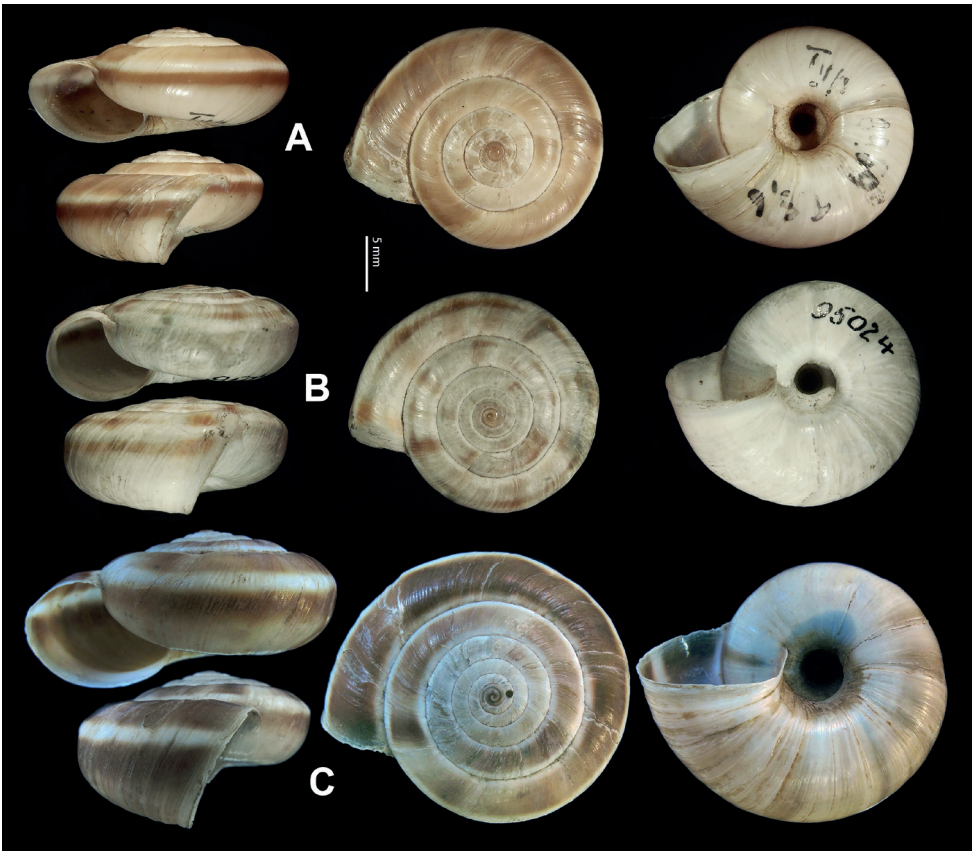

Figure 15. *Laeocathaica distinguenda* Möllendorff, 1899 **A** SMF 8959, lectotype **B** SMF 95024 **C** HBUMM054361.

spec.1), each a single tube. Proximal accessory sacs two, dorsally and ventrally touching, without internal pilasters, each with an opening leading to dart chamber near its opening. The right proximal accessory sac somewhat larger and with thicker wall than the left one. Bursa copulatrix duct basally slightly expanded. Bursa copulatrix ovate.

Remarks. This species has a very unique shell, but the anatomy of the terminal genitalia coincides with those of the congeners.

Laeocathaica dolani (Pilsbry, 1934)

Figs 2A, 5C, 7, 42A, B, 47C, D, 52F; Table 1

Cathaica (*Laeocathaica*) *dolani* Pilsbry, 1934: 16, pl. 3, fig. 4, 4a–c.
Cathaica dolani – Yen, 1938: 446.
Laeocathaica (*Laeocathaica*) *dolani* – Richardson 1983: 78.
Laeocathaica dolani – Chen and Zhang 2004: 335, fig. 328; – Páll-Gergely et al. 2022: 59, fig. 18A.

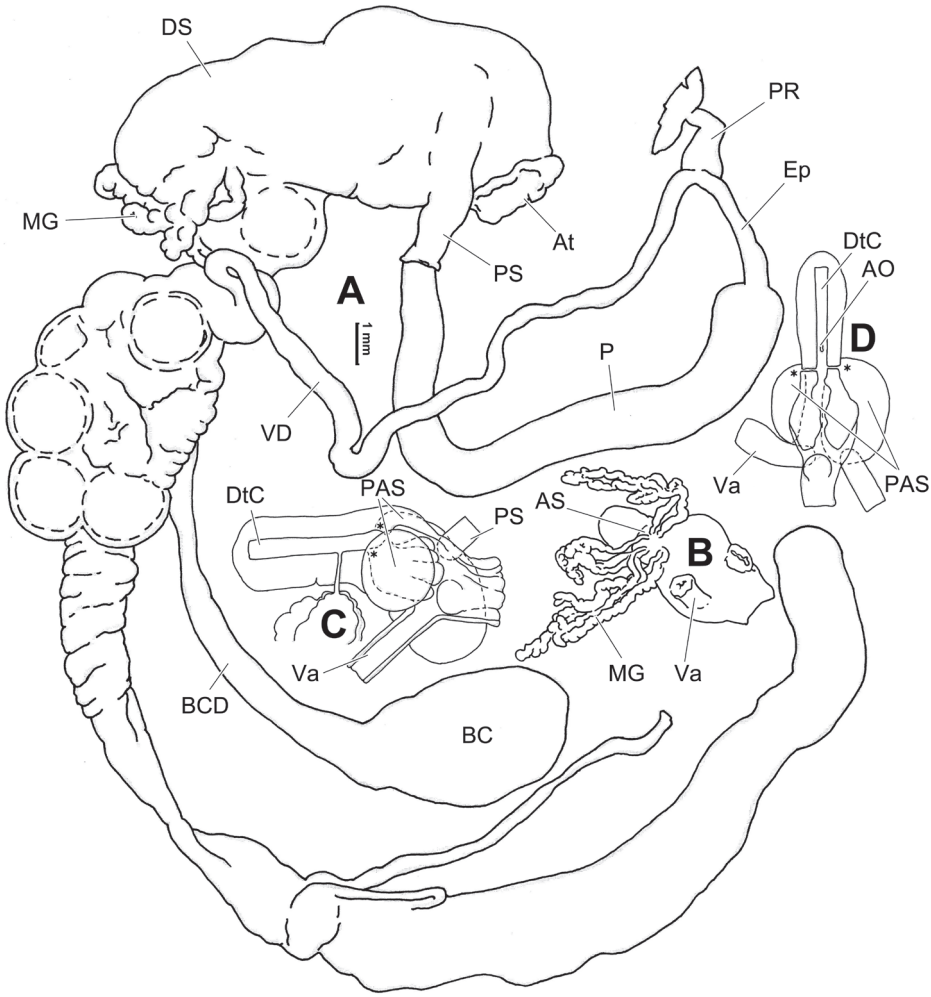

Figure 16. Genital anatomy of *Laeocathaica distinguenda* Möllendorff, 1899 **A, B** HBUMM05436 **C, D** HBUMM05417 **A** general view **B–D** ventral, left, and apical views of dart sac apparatus. Abbreviations: AO – opening of accessory sac leading to dart chamber; AS – accessory sac; At – atrium; BC – bursa copulatrix; BCD – bursa copulatrix duct; DS – dart sac; DtC – a chamber containing love dart; Ep – epiphallus; MG – mucous glands; P – penis; PAS – proximal accessory sac; PO – opening of proximal accessory sac leading to dart chamber; PR – penial retractor muscle; PS – penial sheath; Va – vagina; VD – vas deferens. Asterisk * indicates the opening of proximal accessory sac.

New material. HBUMM00069, 6 fma, 3 fma dissected; Kangding,Sichuan Province, near 29.995149°N, 101.967008°E, 1964-VII-16, coll. Chen, D.-N. HBUMM08439, Manai [马耐], Badixiang [巴底乡], Danbaxian (= Danba), Sichuan Province, 31.11276N 101.885295E, 2008-VII-18, coll. Di, Zhi-Yong [邸智勇].

Distribution. Sichuan: Kangding, Danbaxian (type locality: Rumichangu).

Additional information of shell. The shell is covered with radially arranged low scales of variable length (~ 25 – ~ 300 μm long) everywhere. The size (esp. length) of scales increase from protoconch to body whorl. Spiral grooves are absent throughout the shell.

General anatomy. Eversible head wart present but not prominent. Jaw arcuate, with 3–6 projecting ribs.

Anatomy of genital organs. Penial sheath covering ~ 1/4–1/3 of penis. Penis short, thick, distally expanded. Inside penis, two thick and prominent pilasters fusing into one Y-shaped fork at proximal 1/3–1/2 penis, accompanied with ~ 6 narrower or equally thick pilasters nearby. Pilasters on distal end of penis not merging into thick folds. Vas deferens narrow throughout. Vagina between atrium and dart sac not elongated. Vagina between dart sac and insertion of bursa copulatrix duct ~ 1/2 length of dart sac. Dart sac approximately as long as penis. Love dart ~ 5 mm long, apically with cross-section rhombic. Accessory sac small, internally empty, inserting into dart sac at middle part, opening to distal dart chamber. Mucous glands two (HBUMM00069-spec.1–3), each complicatedly branched. Proximal accessory sac one, large, on right side of dart sac, with an opening leading to dart chamber near its opening. Bursa copulatrix duct basally slightly expanded. Bursa copulatrix elongate, ovate.

Remarks. In *Laeocathaica*, *Laeocathaica dolani* is the only species with only one proximal accessory sac. In addition, this species is unique in the genus that it keeps periostracum scales throughout its lifetime.

Laeocathaica filippina (Heude, 1882)

Figs 2A, 17, 18, 41C, 48G, 48H, 51; Tables 1, 3

Helix filippina Heude, 1882: 23, pl. 20, fig. 19; – Möllendorff 1884: 340, 352; – Ancey 1885: 114; – Standen: 231.
Helix (*Plectopylis*) *subchristinae* Ancey, 1882: 44.
Helix (*Plectotropis*) *subchristinae* – Ancey 1883: 8.
Helix subchristinae – Möllendorff 1884: 340, 352; – Ancey 1885: 114.
Helix subsimilis var. *filippina* – Gredler 1884: 264.
Helix (*Cathaica*) *filippina* – Pilsbry 1892: 214, pl. 49, figs 34, 35.
Laeocathaica subchristinae – Gude 1902: 6.
Laeocathaica filippina – Möllendorff 1899: 88; – Gude 1902: 6; – Yen 1935: 44; – Páll-Gergely et al. 2022: 59, fig. 19.
Laeocathaica subsimilis filippina – Yen 1939: 148, pl. 15, fig. 29.
Laeocathaica (*Laeocathaica*) *christinae filippina* – Zilch 1968: 173; – Richardson 1983: 79.

Museum material. SMF 24266b, four fms; Badung, Hubei, China. SMF 24226, three fms; W-Hupei, China; Slg. K. Hashagen. SMF 24257, two fms; Changyang [长阳], Sytchuan, China; ex B. Schmacker, 1893, Slg. O. Böttger. SMF 95118, five fms; Badung, Hubei, China; Slg. C. R. Böttger, 1904. SMF 24266a, three fms; Badung,

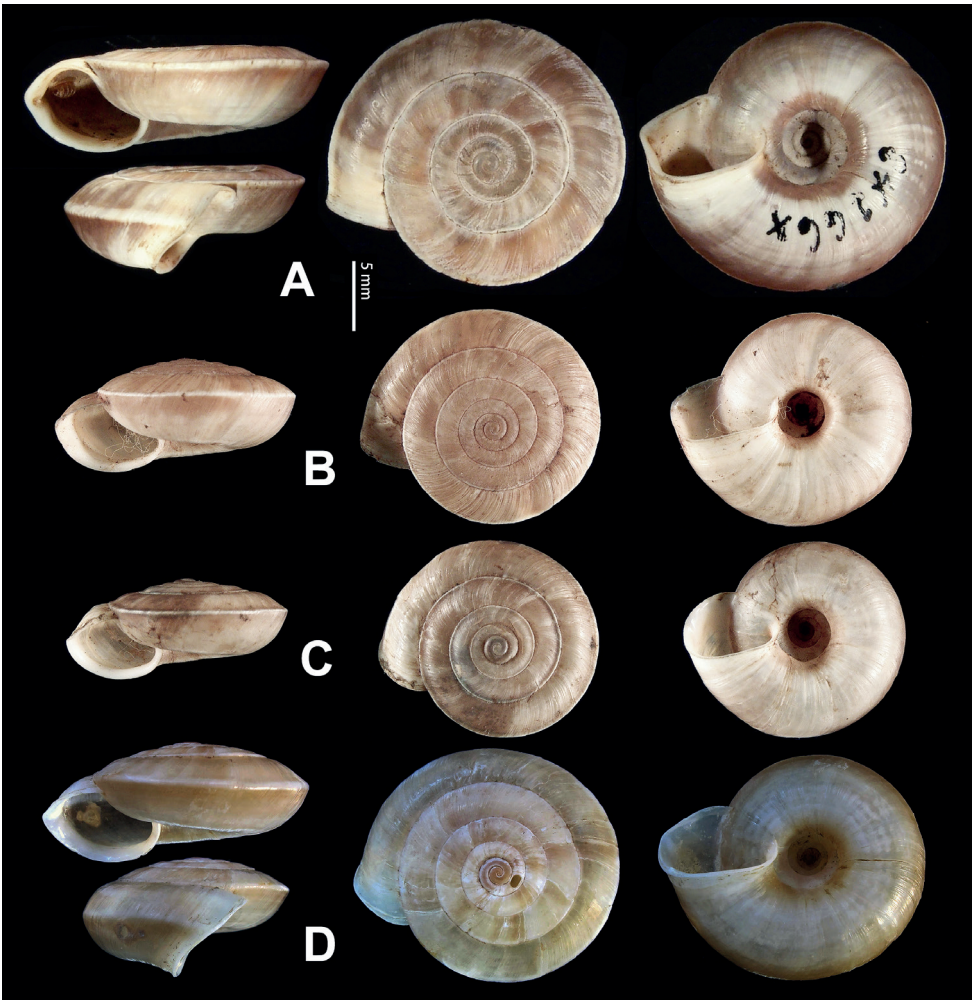

Figure 17. *Laeocathaica filippina* (Heude, 1882) **A** SMF 24266b **B, C** NHMUK ex Salisburg Acc. No. 2044 **D** HBUMM04166-spec.1.

Hubei, China; ex Möllendorff, Slg. W. Kobelt. SMF 294296, three fms; Changyang, China; Slg. C. Bosch, ex Sowerby+Fulton. SMF 294295, one fms; Changyang, China; Slg. Ehrmann, ex Sowerby+Fulton. SMF 24227, one fms (labeled with *L. subsimilis*); China; ex? SMF 294292, one fms (*L. filippina*) and two juvs (*L. carinifera*); Sytshuan, China; Slg. C. Bosch ex H. Rolle. NHMUK ex Salisburg Acc. No. 2044.

New material. HBUMM01256b, Fuhusi, Emei [峨嵋], Sichuan; sandstone, humid; 2003-VII-26, coll. Wu, M.; DNA voucher HBUMM01256b. HBUMM04166, numerous fma, 5 fma dissected; Baidicheng, Fengjie County, Chongqing, two kilometers away from the point (241 m a.s.l., 31.020194°N, 109.472833°E); mixed rocks of slate and sandy stones, woods with shrubs and trees, humid; 2004-VII-20, coll. Wu, M; DNA voucher HBUMM05097.

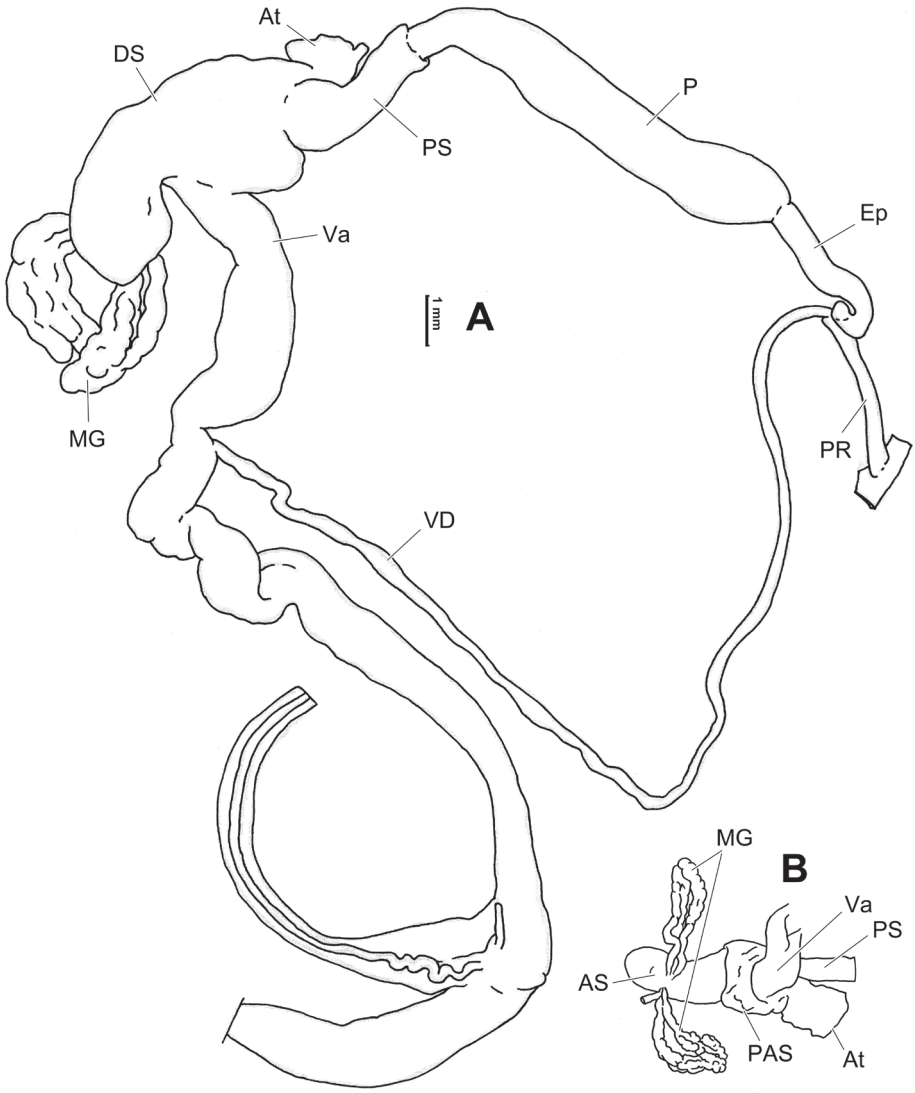

Figure 18. Genital anatomy of *Laeocathaica filippina* (Heude, 1882), HBUMM04166-spec.1 **A** general view **B** ventral view of dart sac apparatus. Abbreviations: AS – accessory sac; At – atrium; DS – dart sac; Ep – epiphallus; MG – mucous glands; P – penis; PAS – proximal accessory sac; PR – penial retractor muscle; PS – penial sheath; Va – vagina; VD – vas deferens.

Distribution. Hubei: Badong (type locality), Yichang (Changyang); Sichuan (Emei); Chongqing: Fengjie.

Additional information of shell. Sculpture on the protoconch was present but indistinct because of erosion or weathering. Spiral grooves are absent throughout the shell.

General anatomy. Eversible head wart low. Jaw arcuate, with four or five projecting ribs.

Anatomy of genital organs. Penial sheath moderately long, covering ~ 1/4–1/3 of penis. Penis slightly expanded distally. A pair of penial internal pilasters fusing into one Y-shaped fork at proximal 1/3; ~ 2 larger pilasters present nearby. Distally inside penis, numerous fine pilasters merging into 6 to 8 short but thick folds near opening of epiphallus. Vas deferens narrow throughout. Vagina between atrium and dart sac not elongated. Vagina between dart sac and insertion of bursa copulatrix duct approximately equal to or slightly shorter than 2/3 length of dart sac. Dart sac ~ 1/2 length of penis. Love dart ~ 2 mm long. Accessory sac spherical, internally almost solid, inserting into dart sac medially, opening to distal dart chamber. Mucous glands 5–7, each complicatedly branched. Proximal accessory sacs two, symmetrical, dorsally separated and ventrally touching, with a few internal pilasters, each with an opening leading to proximal dart chamber. Bursa copulatrix duct of even diameter. Bursa copulatrix ovate, small.

Remarks. This species has a spire of variable height, from flatness to dome shape. The umbilicus of this species is obviously narrower than that of *Laeocathaica christinae*. Furthermore, this species has a pair of ventrally touching proximal accessory sacs instead of ventrally separated ones, which are observed in *L. christinae*.

Laeocathaica hisanoi Páll-Gergely, 2022

Laeocathaica hisanoi Páll-Gergely in Páll-Gergely et al. 2022: 68, fig. 20D.

Examined specimens. None.

Distribution. S Gansu (type locality).

Laeocathaica leucorhaphe Möllendorff, 1899

Fig. 19A

Laeocathaica leucorhaphe Möllendorff, 1899: 95, pl. 6, fig. 2; – Gude 1902: 6; – Yen 1939: 149, pl. 15, fig. 36; – Chen and Zhang 2004: 323, fig. 312; – Páll-Gergely et al. 2022: 63, fig. 18B.
Cathaica leucorhaphe – Yen, 1938: 446.
Laeocathaica (*Laeocathaica*) *leucorhaphe* – Zilch 1968: 174; – Richardson 1983: 78.

Museum material. SMF 9073, lectotype; Sm Tung-ho [铜河 = Daduhe River 大渡河], W-Sytshuan; ex Potanin 312b, Slg. O. v. Möllendorff.

Distribution. W Sichuan (type locality: Daduhe River).

Additional information of shell. The protoconch is finely granulate. Growth lines are indistinct. Spiral grooves are only more distinct on umbilicus side near aperture. Bottom-umbilicus transition changes gently. Peristome is somewhat sinuate.

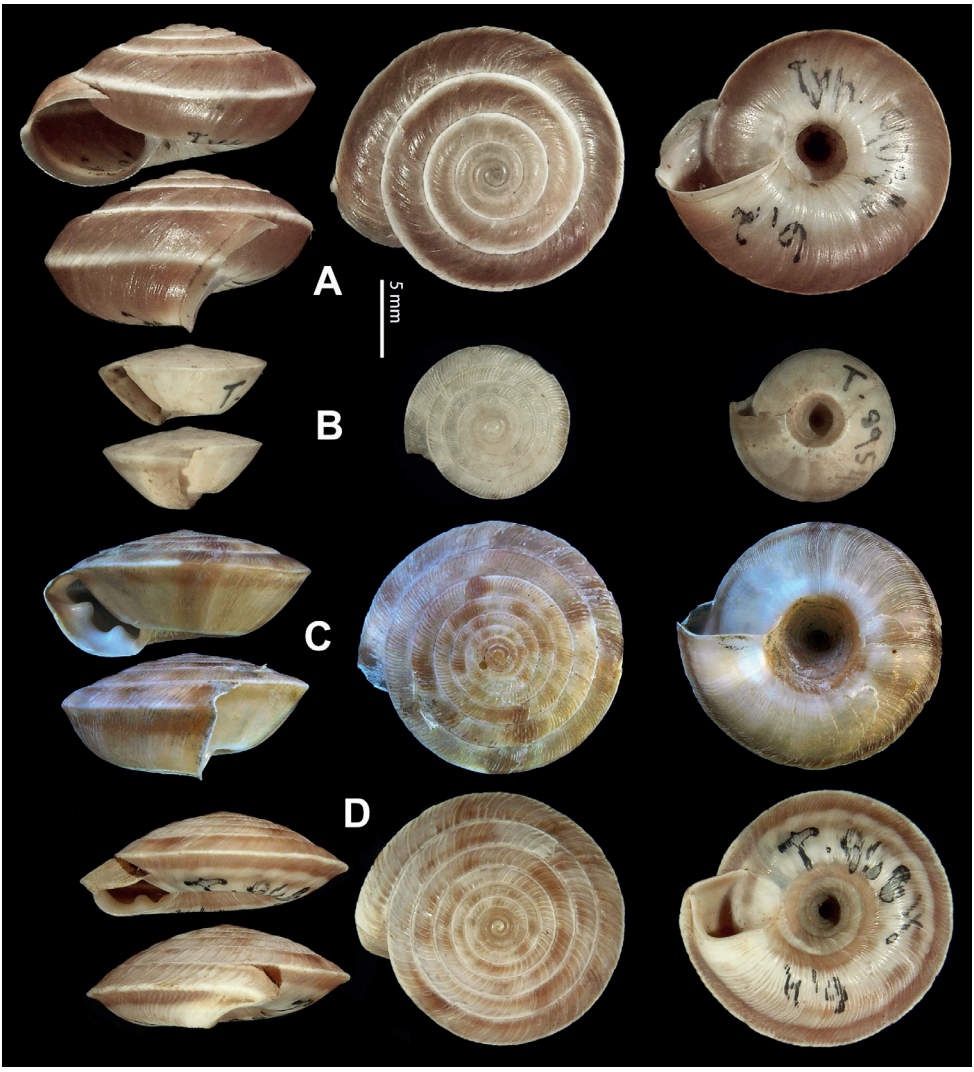

Figure 19. A *Laeocathaica leucorhaphe* Möllendorff, 1899, SMF 9073, lectotype **B, C** *L. odophora* Möllendorff, 1899 **B** SMF 8954, holotype **C** HBUMM08430-spec.1 **D** *L. pewzowi* Möllendorff, 1899, SMF 9084, lectotype.

Laeocathaica minwui Páll-Gergely, 2022

Figs 2A, 11A

Laeocathaica minwui Páll-Gergely in Páll-Gergely et al. 2022: 64, fig. 21.

Museum material. SMF 95019, holotype, one fms; Prov. Sze-chuan, West China; Slg. C. R. Böttger ex Möllendorff ex L. Fuchs. SMF 24255a, five fms; O. Sy-tshuan. Ex. L.

Fuchs, Slg. O. v. Möllendorff. The following lots of specimens labeled with *L. subsimilis*: SMF 6920: one fms; Sy-tshuan, W-China; Ex. Möllendorff, Slg. W. Kobelt. SMF 24263, one fms; Kao-cha-hien; Ex. B. Schmacker 1893, Slg. O. Böttger. SMF 42563, two fms; Chang-yang, China; ex B. Schmacker, Slg. O. Böttger.

Distribution. Sichuan (type locality); Hubei (type locality).

Additional information of shell. The protoconch is finely granulate. Spiral grooves are very weakly present. Bottom-umbilicus transition changes gently. Peristome is somewhat sinuate.

Laeocathaica odophora Möllendorff, 1899

Figs 2A, 3, 19B, 19C, 20, 42E, 47A, 47B, 51; Tables 1, 3

Laeocathaica odophora Möllendorff, 1899: 97, pl. 6, fig. 6; – Yen 1939: 149, pl. 15, fig. 39; – Chen and Zhang 2004: 328, fig. 318; – Páll-Gergely et al. 2022: 63, fig. 18B.
Laeocathaica (*Laeocathaica*) *odophora* – Zilch 1968: 174; – Richardson 1983: 78.
Laeocathaica (*Laeocathaica*) *odontophora* – Richardson 1983: 78.

Museum material. SMF 8954, holotype, juv; Dshie-dshou [阶州= Wudu], S-Gansu. Slg. O. v. Möllendorff.

New material. HBUMM00566a, 5 juvs; Luotuoxiang [骆驼巷], Bikou [碧口], Wenxian, Gansu Province, 32.827686°N, 105.064656°E; 1998-IV-25, coll. Chen, D.-N. and Zhang, G.-Q. HBUMM04612, 1 fma and 1 juv; 650 m away from Bikou Bridge, Wenxian, Gansu Province; 1998-VI-24, coll. Zhang, Xue-Zhong [张学忠]. HBUMM08158, 3 juvs; slope near river, Wenxian, Gansu Province, 807 m, 32.847111°N, 104.88775°E; grass and a few shrubs, on branches and rock cliff; 2017-VIII-6, coll. Sheng, X.-F., etc.; DNA voucher HBUMM08158a. HBUMM08430, 1 fma, 1fms, 1 juv; 1 fma dissected; near Fengjiaba [冯家坝], national road 212, Wenxian, Gansu Province, near point (33.08672°N, 104.826572°E), on slope, 2019-X-12, coll. Li, Q.-M.; DNA voucher HBUMM08430a.

Distribution. Gansu: Wudu (type locality), Wenxian.

Additional information of shell. The protoconch is smooth except some fine threads at the beginning and the end of the whorls. Spiral grooves are absent. On teleoconch between two adjacent ribs there are several indistinct fine threads.

General anatomy. Eversible head wart present but not prominent. Jaw arcuate, with seven projecting ribs.

Anatomy of genital organs. Penial sheath short, covering ~ 1/6 of penis. Penis tubular and equally thick. Inside penis, ~ 5 low pilasters present proximally, two high pilasters fusing into one Y-shaped fork at proximal 1/4. Fine pilasters on distal end of penis not merging into thick folds. Vas deferens narrow throughout. Vagina between atrium and dart sac not elongated. Vagina between dart sac and insertion of bursa copulatrix duct ~ 1/2 length of dart sac. Dart sac ~ 1/2 length of penis. Love dart ~ 4.5 mm long, apically 2-bladed. Accessory sac small but externally distinguishable,

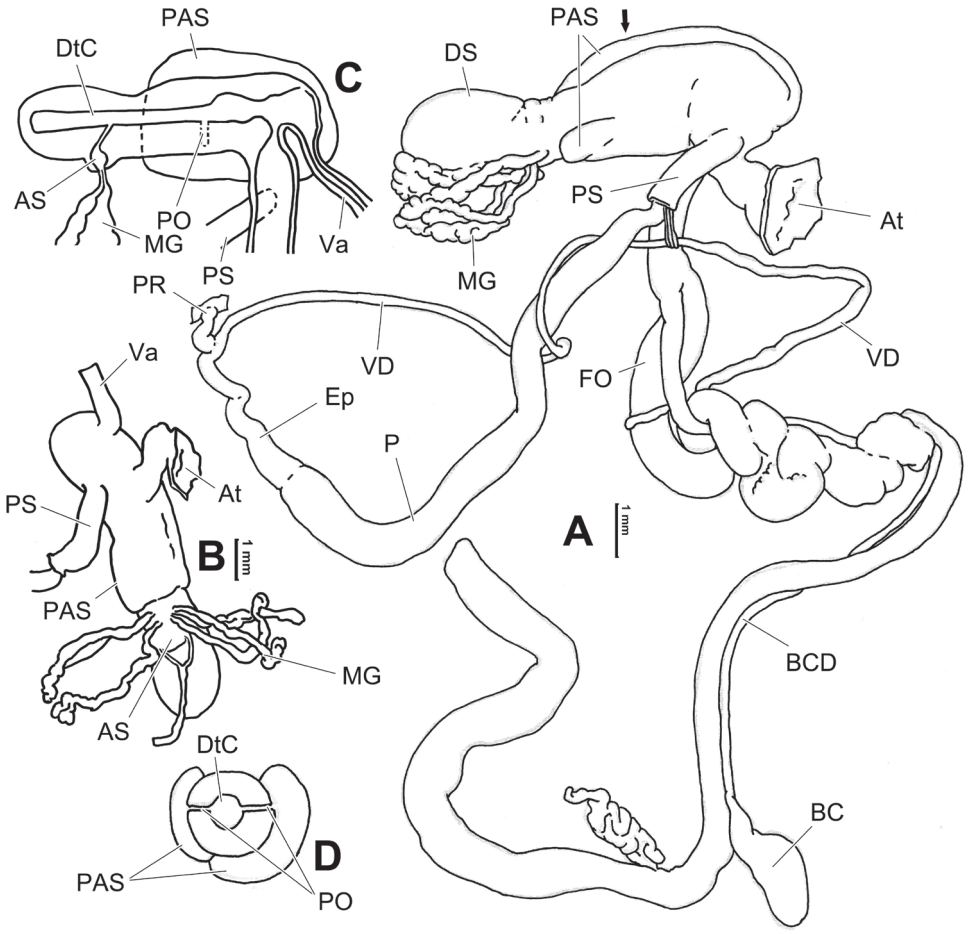

Figure 20. Genital anatomy of *Laeocathaica odophora* Möllendorff, 1899, HBUMM08430-spec.1 **A** general view **B** ventral view of dart sac apparatus **C** left view of dart sac apparatus **D** cross-section of dart sac at the position arrowed in (**A**). Abbreviations: AS – accessory sac; At – atrium; BC – bursa copulatrix; BCD – bursa copulatrix duct; DS – dart sac; DtC – a chamber containing love dart; Ep – epiphallus; FO – free oviduct; MG – mucous glands; P – penis; PAS – proximal accessory sac; PO – opening of proximal accessory sac leading to dart chamber; PR – penial retractor muscle; PS – penial sheath; Va – vagina; VD – vas deferens.

internally solid, inserting into dart sac at distal 1/3, opening to dart chamber. Mucous glands 5 (HBUMM08430-spec.1), each singly tubular or simply branched. Proximal accessory sacs two, asymmetrical with the right one distinctly larger, apically separated and ventrally touching, each centrally with an opening (rounded, diameter ~ 0.2 mm) leading to proximal dart chamber. Bursa copulatrix duct of even diameter. Bursa copulatrix ovate, small.

Remarks. This species has a pair of asymmetrical and ventrally touching proximal accessory sacs that is rarely observed in the genus. In comparison, its conchologically

similar species *Laeocathaica zhengpingliui* Wu, sp. nov. has a pair of symmetrical proximal accessory sacs that are ventrally separated from each other.

For more comments, see *Laeocathaica zhengpingliui* Wu, sp. nov.

Laeocathaica pewzowi Möllendorff, 1899

Figs 2A, 3, 19D, 21, 42F, 47G, H; Table 1

Laeocathaica pewzowi Möllendorff, 1899: 98, pl. 6, fig. 4, 4a; – Sturany 1900: 22, pl. 2, figs 25–28; – Wiegmann 1900: 115, pl. 3, fig. 104; – Möllendorff 1901: 302; – Gude 1902: 6; – Yen 1939: 150, pl. 15, fig. 40; – Schileyko 2004: 1686, fig. 2174A; – Chen and Gao 2004: 329, fig. 320 (an erroneous figure that should be a *Laeocathaica odophora*); – Páll-Gergely et al. 2022: 67, fig. 23C, D.
Laeocathaica (*Laeocathaica*) *pewzowi* – Zilch 1968: 174; – Richardson 1983: 78.

Museum material. SMF 9084, lectotype; Wen-hsien, S-Gansu; Potanin 248, 661, 793, Slg. O. v. Möllendorff. SMF 9085, paratypes, four fms; same data as lectotype. SMF 24268, Hung-dan (= Hengdan) b. Wen-hsien; Slg. O. v. Möllendorff, ex Berezowski. ZIN RAS No. 4, "*Aegista pewzowi* Schalf." 2 fma, locality unknown, coll. Potanin, 1885-IX-8, det. Möllendorff.

New material. HBUMM08452, 1 fms and 4 juvs, Shangdezhen [尚德镇], Wenxian, Gansu Province, near point (32.907414°N, 104.76994°E); 2020-VIII, coll. Chen, Z.-G.

Distribution. Gansu: Wenxian (type locality).

Additional information of shell. Protoconch is smooth and has no granules, perhaps caused by erosion or weathering. Teleoconch has rough ribs between which fine threads are present. Spiral grooves are absent throughout.

General anatomy. Head with flat but distinct eversible head wart. Jaw arcuate, with four projecting ribs.

Anatomy of genital organs. Penial sheath covering ~ 1/9 of penis. Penis tubular and distally thicker. Inside penis, ~ 4 high parallel pilasters on proximal 2/3, at proximal ~ 1/4 two weak pilasters fusing into one Y-shaped fork. Fine pilasters on distal end of penis merging into ~ 7 thin or thick folds. Vas deferens narrow throughout. Vagina between atrium and dart sac not elongated. Vagina between dart sac and insertion of bursa copulatrix duct ~ 1/2 length of dart sac. Dart sac ~ 2/5 length of penis. Accessory sac tiny, internally solid, inserting into dart sac at middle part, opening to dart chamber. Mucous glands four, each singly tubular or simply branched. Proximal accessory sacs two, of similar size and symmetrical, apically separated and ventrally touching, each distally with an opening leading to proximal dart chamber. Bursa copulatrix duct of even diameter. Bursa copulatrix long-ovate.

Remarks. The species has the most common pattern of the dart sac apparatus of the genus, i.e., two equally- sized and ventrally touching proximal accessory sacs, each with an opening leading to the dart chamber; this has been observed in ten of the 21 species anatomically studied herein. This species can be immediately recognized by its particular shell morphology.

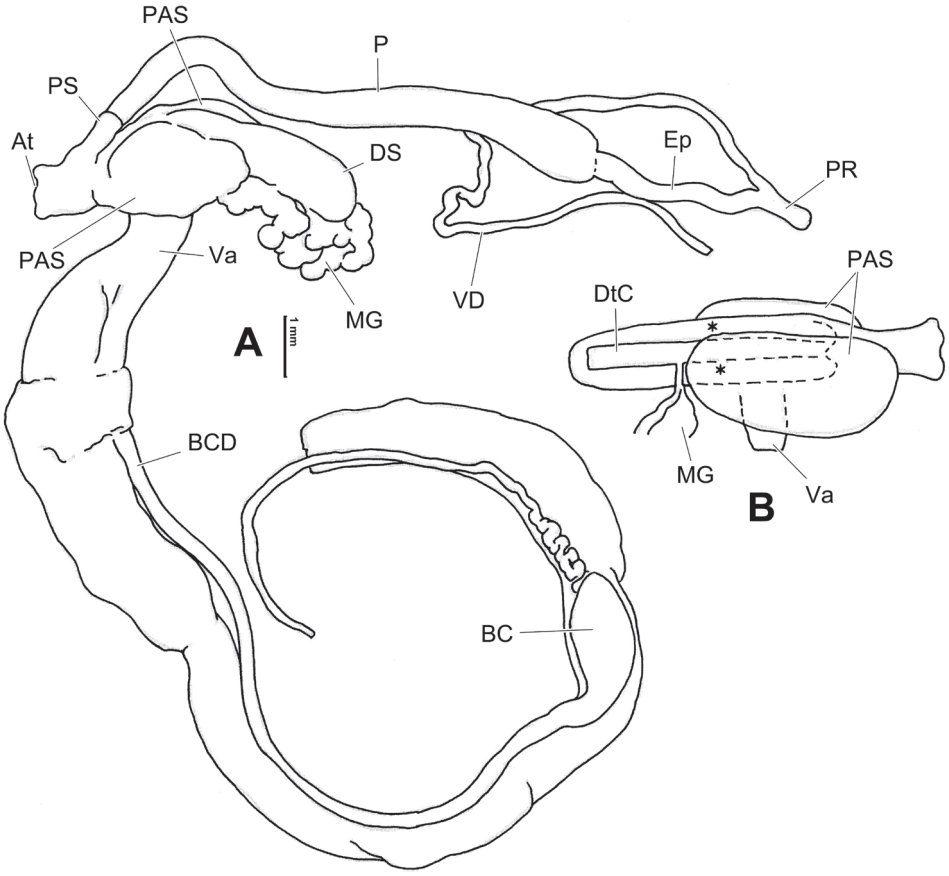

Figure 21. Genital anatomy of *Laeocathaica pewzowi* Möllendorff, 1899, ZIN RAS No. 4, "*Aegista pewzowi* Schalf." **A** general view **B** left view of dart sac apparatus. Abbreviations: AS – accessory sac; At – atrium; BC – bursa copulatrix; BCD – bursa copulatrix duct; DS – dart sac; DtC – a chamber containing love dart; Ep – epiphallus; MG – mucous glands; P – penis; PAS – proximal accessory sac; PR – penial retractor muscle; PS – penial sheath; Va – vagina; VD – vas deferens. Asterisk * indicates the opening of proximal accessory sac.

Laeocathaica phaeomphala Möllendorff, 1899

Figs 2A, 3, 22, 23, 42D, 48E, F, 51, 52D; Tables 1, 3

Laeocathaica phaeomphala Möllendorff, 1899: 96, pl. 6, fig. 3; – Wiegmann 1900: 111, pl. 3, figs 101–103; – Gude 1902: 6; – Yen 1939: 149, pl. 15, fig. 37; – Chen and Zhang 2004: 325, fig. 314; – Páll-Gergely et al. 2022: 67, fig. 18C.
Laeocathaica (*Laeocathaica*) *phaeomphala* – Zilch 1968: 174; – Richardson 1983: 78.

Museum material. SMF 9089, lectotype; Wenhsien, S-Gansu; Potanin 51b, 72, 741, Slg. O. v. Möllendorff. SMF 9090, paratypes, four fms; the same data as lectotype. ZIN RAS No. 4, 1 fma and 1 subadult, Wen-Xian, 1885-IX-8, coll. Potanin, det. Möllendorff.

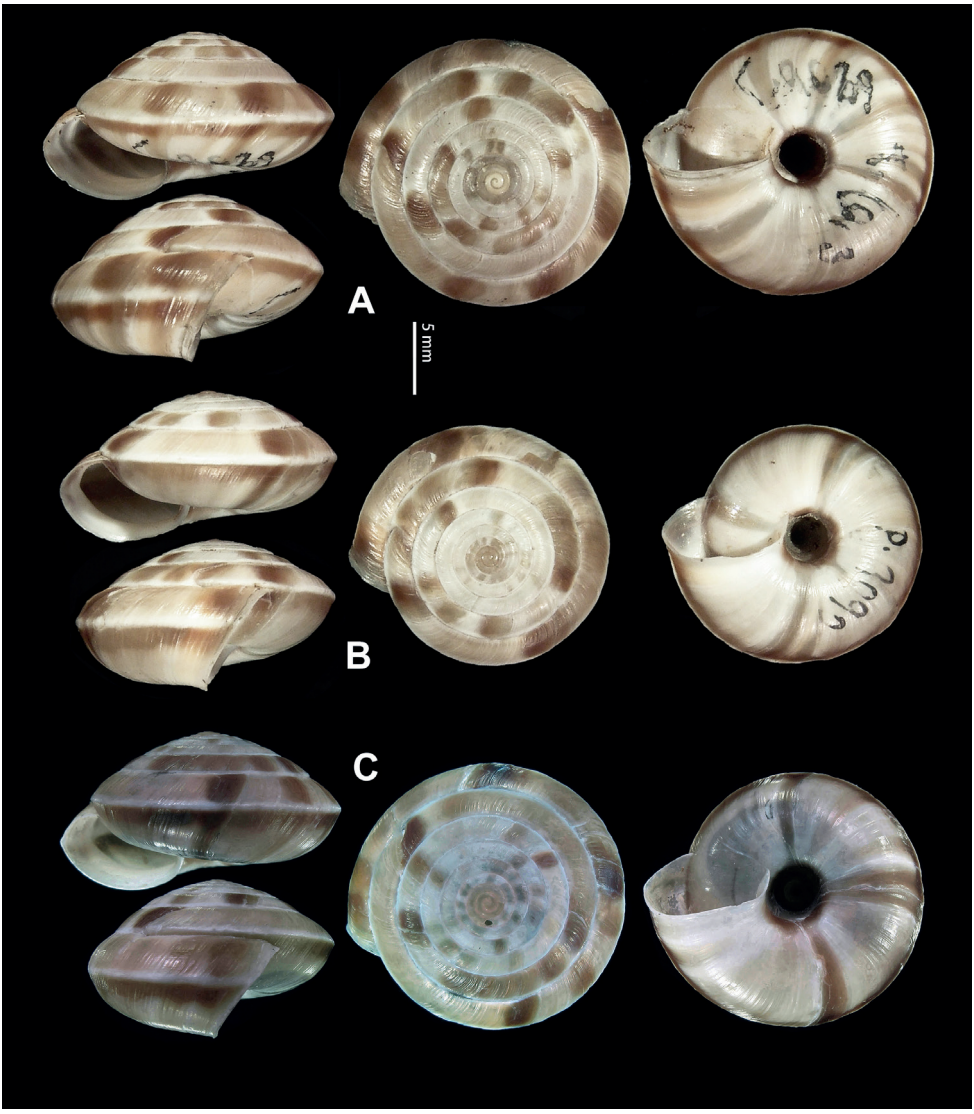

Figure 22. *Laeocathaica phaeomphala* Möllendorff, 1899 **A** SMF 9089, lectotype **B** SMF 9090, paratype **C** HBUMM05433a-spec.6.

New material. HBUMM05433, 2 fma, 1 fms, and many juvs, all fma dissected; Yuxushan, Wenxian, Gansu Province, 32.957259°N, 104.689152°E, shrubs and slate, 2006-IX-27, coll. Wu, M., Liu, J.-M., Zheng, W. and Gao, L.-H. HBUMM05477, numerous fma; Jidushan nearby Baishuijiang, Wenxian, Gansu Province; limestone and broad-leaved woods; 2006-IX-27; coll. Wu, M., Liu, J.-M., Zheng, W. and Gao, L.-H. HBUMM08424, slope near Wenzhoulu [文州路], Wenxian, Gansu Province, near 32.943151°N, 104.692505°E, on slope; 2019-X-12, coll. Li, Q.-M.; DNA voucher HBUMM08424a. CZG202008-w3, 9 subadults, Shangdezhen, Wenxian, Gansu Province, 2020-VIII, coll. Chen, Z.-G.

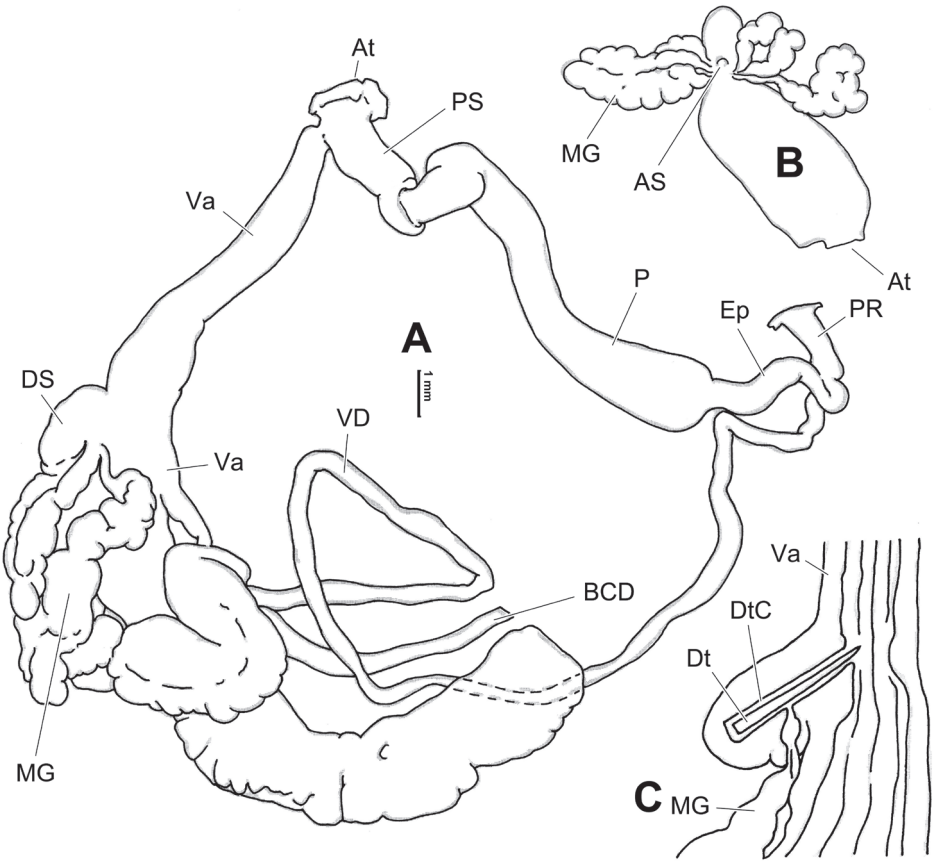

Figure 23. Genital anatomy of *Laeocathaica phaeomphala* Möllendorff, 1899, HBUMM05433a-spec.6 **A** general view **B, C** ventral and left views of dart sac apparatus. Abbreviations: AS – accessory sac; At – atrium; BCD – bursa copulatrix duct; DS – dart sac; DtC – a chamber containing love dart; Ep – epiphallus; MG – mucous glands; P – penis; PR – penial retractor muscle; PS – penial sheath; Va – vagina; VD – vas deferens.

Distribution. Gansu: Wenxian (type locality).

Additional information of shell. The first $1^{1}/_{4}$ protoconch whorls are almost smooth, and the subsequent 1/4 whorls have dense radially arranged fine threads. Spiral grooves are regularly present throughout body whorl.

General anatomy. Head with flat but distinct eversible head wart. Jaw arcuate, with 5–7 projecting ribs.

Anatomy of genital organs. Penial sheath covering ~ 1/5 of penis. Penis tubular and distally thicker. Inside penis, ~ 7 high parallel pilasters on proximal 1/2, no pilasters fusing into Y-shaped fork. Fine pilasters on distal end of penis merging into 9–12 thin or thick folds. Vas deferens narrow throughout. Vagina between atrium and dart sac extremely elongated, ~ 4× longer than dart sac. Vagina between dart sac and insertion of bursa copulatrix duct approximately as long as dart sac. Dart sac ~ 1/6 length of penis. Love dart ~ 1.5 mm long, apically 2-bladed. Accessory sac tiny, internally

empty, inserting into dart sac at middle part, opening to dart chamber. Mucous glands eight, each singly tubular or simply branched. Proximal accessory sac absent. Bursa copulatrix duct equally thick.

Remarks. This species is one of the three species that do not have proximal accessory sac on dart sac apparatus. However, the shell morphology of *Laeocathaica phaeomphala* differs greatly from that of the other two species *L. polytyla* and *L. tropidorhaphe*.

Laeocathaica polytyla Möllendorff, 1899

Figs 2A, 3, 24A, B, 26, 43A, B, 45K, L, 51; Tables 1, 3

Laeocathaica polytyla Möllendorff, 1899: 98, pl. 6, fig. 7; – Wiegmann 1900: 118, pl. 3, figs 105–107; – Gude 1902: 6; – Yen 1939: 150, pl. 15, fig. 41; – Schileyko 2004: 1686, fig. 2174B–D; – Chen and Zhang 2004: 331, fig. 322; – Páll-Gergely et al. 2022: 68, fig. 20A–C.

Laeocathaica (*Laeocathaica*) *polytyla* – Zilch 1968: 174; – Richardson 1983: 78.

Museum material. SMF 9098, lectotype; Nanping, Sung-pan. SMF 9099, paratypes; six fms; Nanping, Sung-pan. Other SMF material see in Yen 1939 (150).

New material. HBUMM00506, 13 fma, 1 dissected; Anchanghexiang [安昌河乡], Wenxian, Gansu Province, 1200 m, near point (33.066003°N, 104.460018°E); 1998-V-19, coll. Chen, D.-N. and Zhang, G.-Q. HBUMM00513, a subadult; Shuanghexiang [双河乡], Jiuzhaigouxian, Sichuan Province, 1100 m, near (33.179715°N, 104.264968°E); 1998-V-18, coll. Chen, D.-N. and Zhang, G.-Q. HBUMM00579, many fms; Jiuzhaigouxian, Sichuan Province; 1998-V-18, coll. Chen D. and Zhang, G.-Q. HBUMM05419, 1 fms; hill foot of Yuxushan, Wenxian, Gansu Province; slate and shrubs, dry; 2006-IX-27, coll. Wu, M., Liu, J.-M., Zheng, W. and Gao, L.-H. HBUMM06490, many fms; Yuxushan, Wenxian, Gansu Province, 1070 m a.s.l., 32.959861°N, 104.678222°E, shrubs and slate, 2011-VIII-07, coll. Wu, M., Xu, Q. and Budha, P. HBUMM06523, many fms and juvs; town of Wenxian, Gansu Province, 1024 m a.s.l., 32.941111°N, 104.668889°E; 2011-VIII-08, coll. Wu, M., Xu, Q. and Budha, P. HBUMM08454, 23 fms, east of the town of Jiuzhaigouxian, Sichuan Province, 2020-VIII, coll. Chen, Z.-G. CZG202008-w6, 1 subadult; Shangdezhen, Wenxian, Gansu Province, near point (32.907414°N, 104.76994°E); 2020-VIII, coll. Chen, Z.-G. CZG202008-w11, 2 fms, near point (32.94936°N, 104.693006°E), town of Wenxian, Gansu Province, 2020-VIII, coll. Chen, Z.-G. HBUMM05437, many fma; 1 fma dissected; Yuxushan, Wenxian, Gansu Province, 32.957259°N, 104.689152°E, shrubs and slate, 2006-IX-27, coll. Wu, M., Liu, J.-M., Zheng, W. and Gao, L.-H.; DNA voucher HBUMM05411. HBUMM06753, 3 fma, 7 fms; Eastern bank of Baishuijiang, Lihuacun, Jiuzhaigouxian, Sichuan Province, 1425 m, 33.267222°N, 104.234722°E; 2011-VI-14, coll. Wu, M., Xu, Q. and Buhda, P.

Distribution. Gansu: Wenxian. Sichuan: Jiuzhaigouxian (type locality).

Additional information of shell. Tiny elongate granules on protoconch, which can be only observed in juvenile shells, are densely and radially arranged. The granules

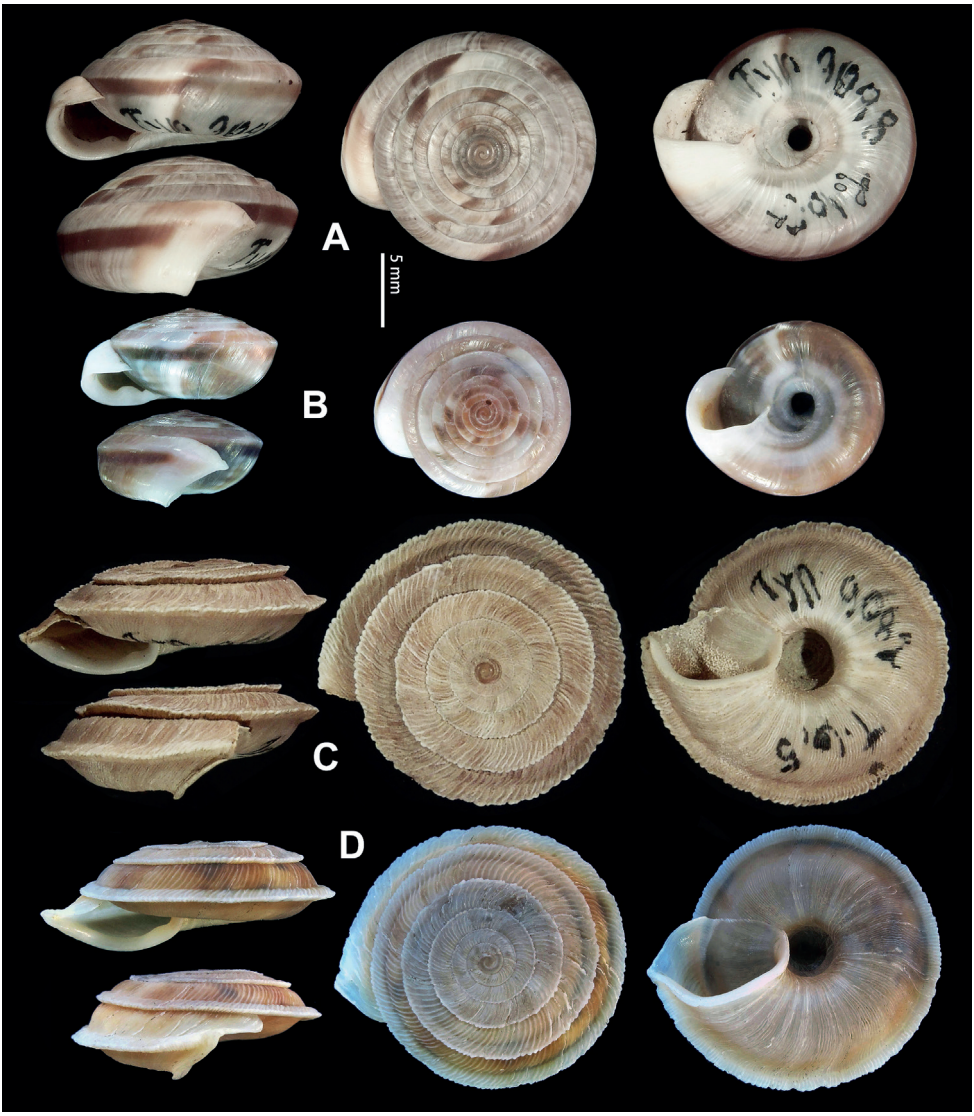

Figure 24. A, B *Laeocathaica polytyla* Möllendorff, 1899 **A** SMF 9098, lectotype **B** HBUMM05437-spec.1 **C, D** *L. potanini* Möllendorff, 1899 **C** SMF 9082, paratype **D** HBUMM00633-spec.1.

on protoconch are absent in adult shell because of erosion or weathering. On teleoconch the growth lines are indistinct. Spiral grooves are absent throughout.

General anatomy. Eversible head wart prominent. Jaw arcuate, with three projecting ribs.

Anatomy of genital organs. Penial sheath covering ~ 1/4 of penis. Penis proximately tubular and distally expanded. Inside penis, two pilasters fusing into one Y-shaped fork at proximal 1/5, two more pilasters of similar thickness also present. Fine pilasters on distal end of penis merging into ~ 8 thick folds. Vas deferens narrow

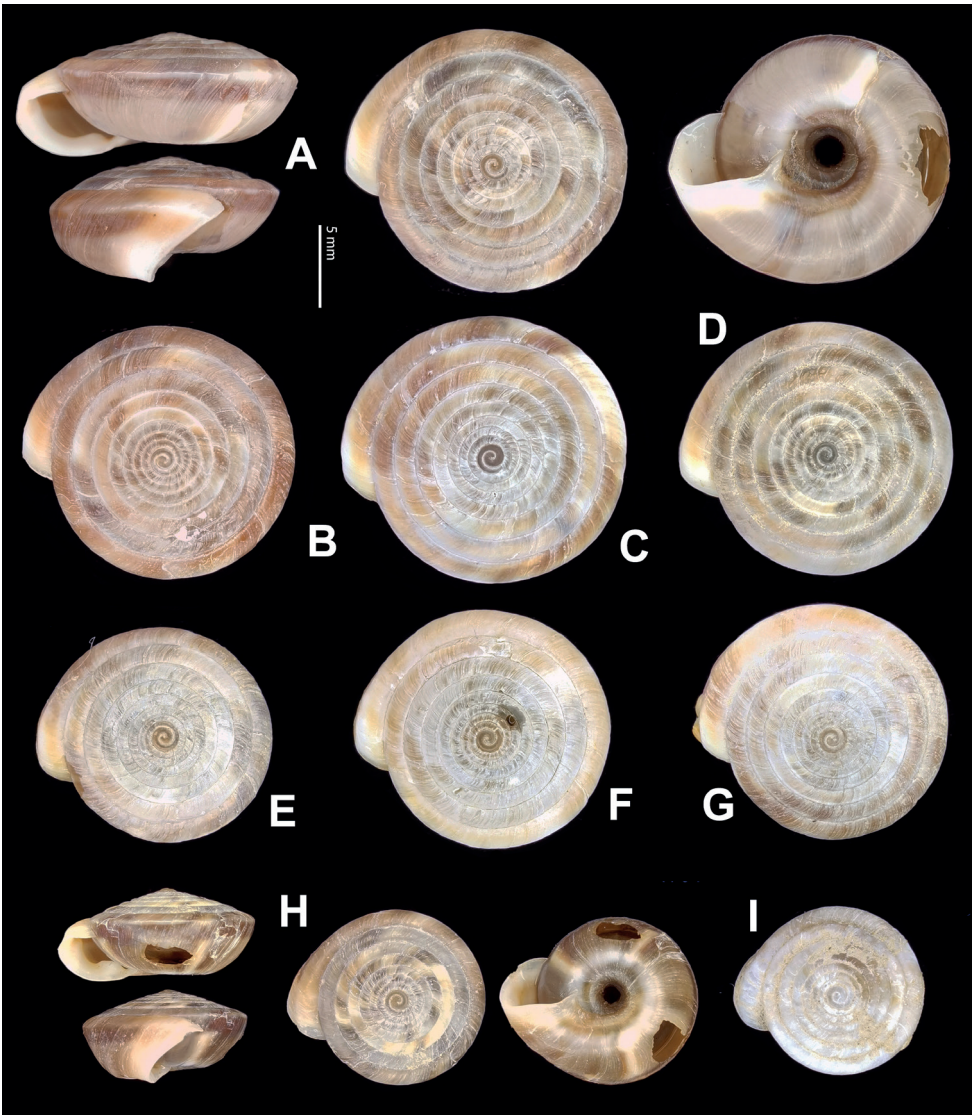

Figure 25. *Laeocathaica parapolytyla* Wu, sp. nov. **A–E** paratypes HBUMM06640-spec.2–6 **F** holotype, HBUMM06640-spec.1 **G–I** paratypes HBUMM06640-spec.7–9. Both **A, H** show four views **B–G, I** show apical view only.

throughout. Vagina between atrium and dart sac not elongated. Vagina between dart sac and insertion of bursa copulatrix duct ~ 1/2 length of dart sac. Dart sac ~ 1/2 length of penis. Love dart ~ 1 mm long, apically 2-bladed. Accessory sac small but externally distinguishable, internally solid, inserting into dart sac at distal 1/3, opening to dart sac chamber. Mucous glands four or five, each singly tubular or simply branched. Proximal accessory sac absent. Bursa copulatrix duct equally thick.

Remarks. See *Laeocathaica parapolytyla* Wu, sp. nov.

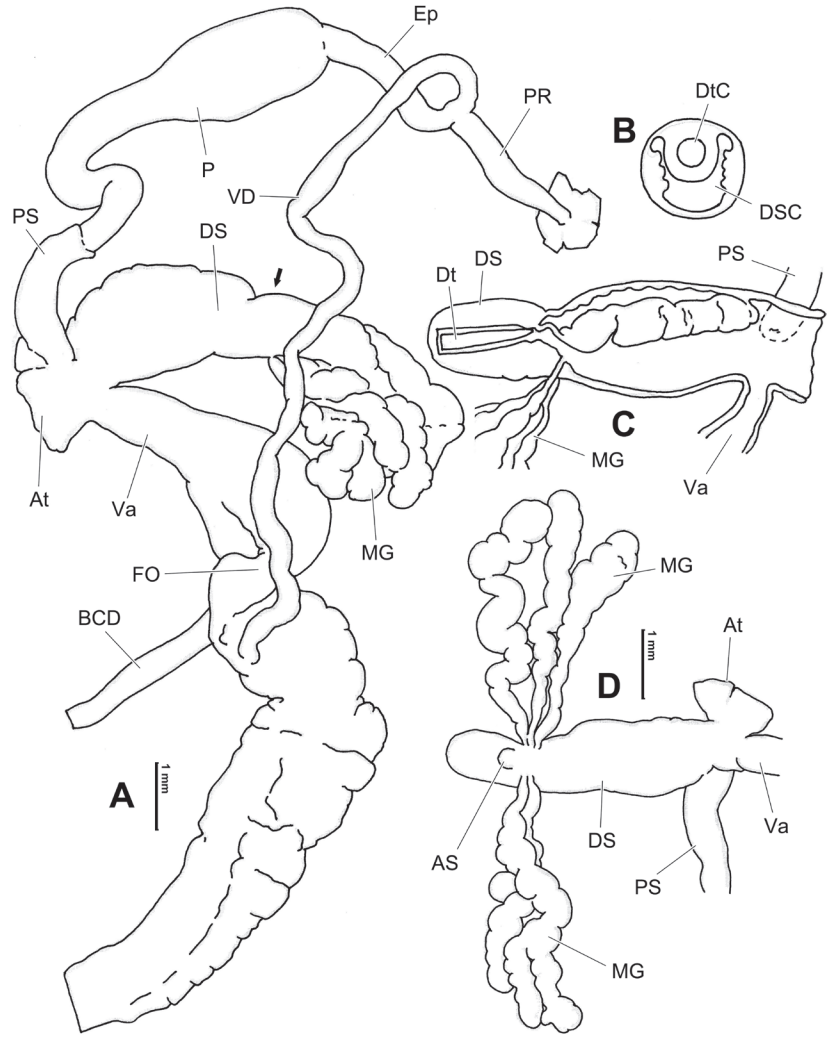

Figure 26. Genital anatomy of *Laeocathaica polytyla* Möllendorff, 1899, HBUMM05437-spec.1 **A** general view **B** cross-section of dart sac at the position arrowed in (**A**) **C, D** left and ventral side of dart sac apparatus. Abbreviations: AS – accessory sac; At – atrium; BCD – bursa copulatrix duct; DS – dart sac; DSC – dart sac chamber; DtC – a chamber containing love dart; Ep – epiphallus; FO – free oviduct; MG – mucous glands; P – penis; PR – penial retractor muscle; PS – penial sheath; Va – vagina; VD – vas deferens.

Laeocathaica potanini Möllendorff, 1899

Figs 2A, 3, 24C, D, 28, 43C, 45A, B, 51; Tables 1, 3

Laeocathaica potanini Möllendorff, 1899: 96, pl. 6, fig. 5; – Wiegmann 1900: 109, pl. 3, figs 98–100; – Gude 1902: 6; – Yen 1939: 149, pl. 15, fig. 38; – Yen 1942: 284; – Chen and Zhang 2004: 326, fig. 316; – Páll-Gergely et al. 2022: 70, fig. 23A, B.
Laeocathaica (*Laeocathaica*) *potanini* – Zilch 1968: 174; – Richardson 1983: 79.

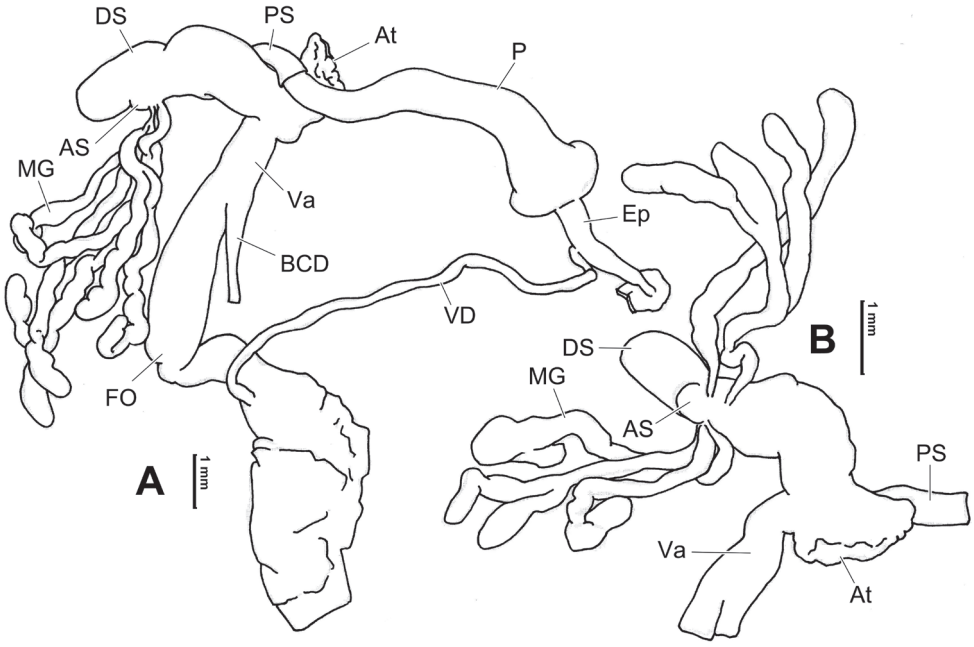

Figure 27. Genital anatomy of *Laeocathaica parapolytyla* Wu, sp. nov., HBUMM06640-spec.1, holotype **A** general view **B** ventral view of dart sac apparatus. Abbreviations: AS – accessory sac; At – atrium; BCD – bursa copulatrix duct; DS – dart sac; Ep – epiphallus; FO – free oviduct; MG – mucous glands; P – penis; PR – penial retractor muscle; PS – penial sheath; Va – vagina; VD – vas deferens.

Museum material. SMF 9082, lectotype; Wenhsien, S-Gansu; Potanin 251, 587, 734, Slg. O. v. Möllendorff. SMF 9083, paratypes, three fms; Same data as lectotype. SMF 8960, paratype; Hungdan (= Hengdan) b. Wen-hsien, S-Gansu; ex Beresowski, Slg. O. v. Möllendorff.

New material. HBUMM00633, many fma; 4 fma dissected; Yuxushan, Wenxian, Gansu Province, 1000 m a.s.l., near 32.957259°N, 104.689152°E, shrubs and slate, 1998-V-17, coll. Chen, D.-N. and Zhang, G.-Q. HBUMM00700, 5 fma and 2 juvs; Hejiaping [何家坪], Wenxian, Gansu Province, near 32.844062°N, 105.021857°E; 1998-IV-24, coll. Chen, D.-N. and Zhang, G.-Q. HBUMM05423, 4 juvs; hill foot of Yuxushan, Wenxian, Gansu Province; slate and shrubs, dry; 2006-IX-27, coll. Wu, M., Liu, J.-M., Zheng, W. and Gao, L.-H. HBUMM05427, many fma and fms; DNA voucher HBUMM05409. HBUMM05438, 4 fma, 7 fms, 7 juvs: Yuxushan, Wenxian, Gansu Province, 32.957259°N, 104.689152°E, shrubs and slate, 2006- IX-27, coll. Wu, M., Liu, J.-M., Zheng, W. and Gao, L.-H. HBUMM06483, Yuxushan, Wenxian, Gansu Province, 1070 m a.s.l., 32.959861°N, 104.678222°E; shrubs and slate; 2011-VIII-07, coll. Wu, M., Xu, Q. and Budha, P. (not dissected); DNA voucher HBUMM06482. HBUMM06520, 3 fms and 2 juvs; town of Wenxian, Gansu Province, 1024 m a.s.l., 32.941111°N, 104.668889°E; 2011-VIII-08, coll. Wu, M., Xu, Q. and Budha, P. HBUMM08427, slope near X496, Wenxian, Gansu Province, near 32.474345°N, 104.915976°E, on slope; 2019-X-13, coll. Li, Q.-M. (not dissected);

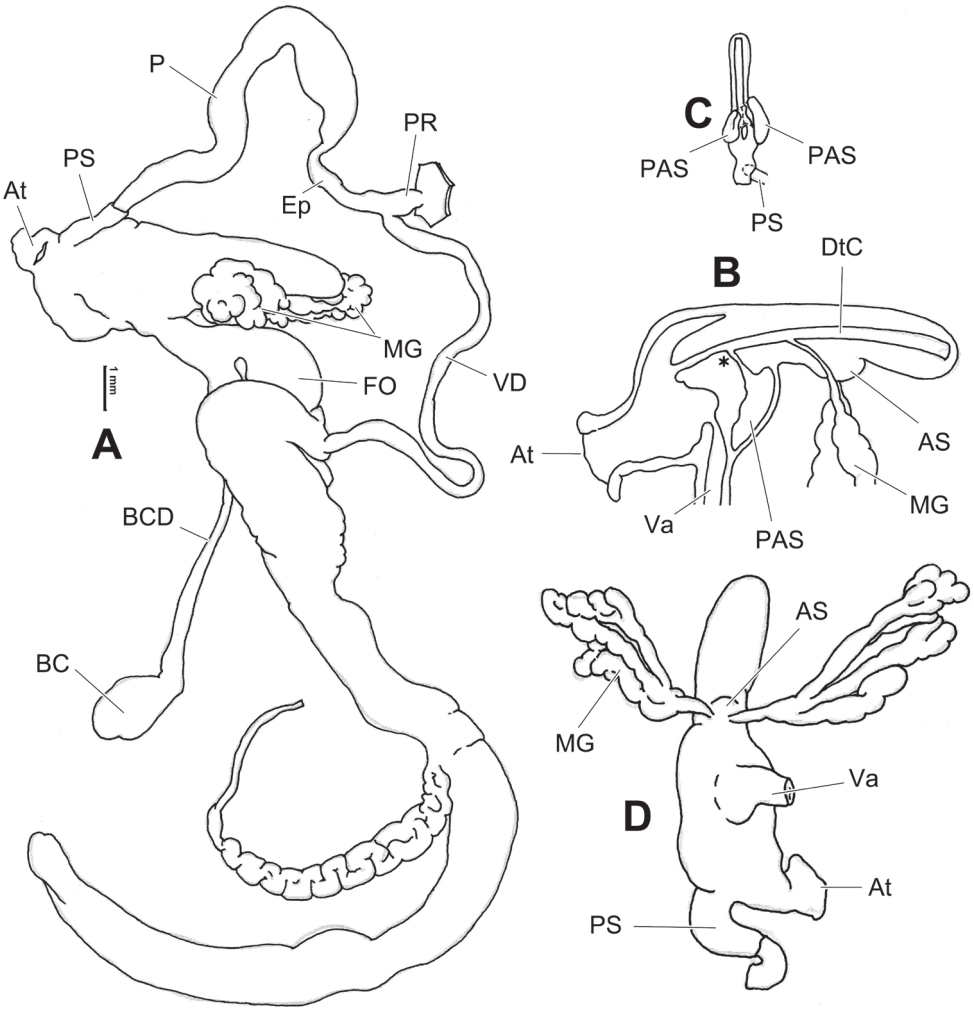

Figure 28. Genital anatomy of *Laeocathaica potanini* Möllendorff, 1899, HBUMM00633-spec.1 **A** general view **B–D** right, apical, and ventral views of dart sac apparatus. Abbreviations: AS – accessory sac; At – atrium; BC – bursa copulatrix; BCD – bursa copulatrix duct; DS – dart sac; DtC – a chamber containing love dart; Ep – epiphallus; FO – free oviduct; MG – mucous glands; P – penis; PAS – proximal accessory sac; PR – penial retractor muscle; PS – penial sheath; Va – vagina; VD – vas deferens. Asterisk * indicates the opening of proximal accessory sac.

DNA voucher HBUMM08427a. CZG202008-w1, 7 fms and many juvs, town of Wenxian, Gansu Province, 2020-VIII, coll. Chen, Z.-G.

Distribution. Gansu: Wenxian (type locality).

Additional information of shell. Granules on protoconch can only be unclearly and partially observed near suture because of erosion or weathering in adults. Granules are short (~ 20 μm long) on fine threads. Spiral grooves are absent throughout. On teleoconch whorls, fine threads are present between every two adjacent ribs.

General anatomy. Eversible head wart present. Jaw arcuate, with five projecting ribs.

Anatomy of genital organs. Penial sheath short, covering ~ 1/6 of penis. Penis tubular, somewhat expanded distally. Inside penis, ~ 5 low pilasters present proximally, another two high pilasters fusing into one Y-shaped fork at proximal 1/2. Fine pilasters on distal end of penis merging into ~ 4 thick folds. Vas deferens narrow throughout. Vagina between atrium and dart sac not elongated. Vagina between dart sac and insertion of bursa copulatrix duct ~ 1/2 length of dart sac. Dart sac ~ 1/2 length of penis. Love dart ~ 6 mm long, apically rhombic in cross-section, subsequently 2-bladed. Accessory sac small but externally distinguishable, internally solid, inserting into dart sac at middle part, opening to dart chamber. Mucous glands two (n = 3) or three (n = 1), each complicatedly branched. Proximal accessory sacs two, symmetrical, apically separated and ventrally touching, each distally with an opening leading to proximal dart chamber. Bursa copulatrix duct basally thick. Bursa copulatrix ovate, small.

Laeocathaica prionotropis Möllendorff, 1899

Figs 2A, 3, 29, 30, 43D, 44E, F, 51; Tables 1, 3

Laeocathaica prionotropis Möllendorff, 1899: 94, pl. 6, fig. 1, 1a; – Wiegmann 1900: 106, pl. 3, figs 94–97; – Gude 1902: 6; – Yen 1939: 149, pl. 15, fig. 34; – Chen and Zhang 2004: 320, fig. 309; – Páll-Gergely et al. 2022: 70, figs 25, 26.

Laeocathaica prionotropis albocincta Möllendorff, 1899: 95; – Gude 1902: 6; – Yen 1939: 149, pl. 15, fig. 35.

Cathaica prionotropis albocincta – Yen 1938: 446.

Laeocathaica (*Laeocathaica*) *prionotropis* – Zilch 1968: 174; – Richardson 1983: 79.

Laeocathaica (*Laeocathaica*) *prionotropis albocincta* – Zilch 1968: 175; – Richardson 1983: 79.

Museum material. ZIN RAS No. 7, 2 subadults with soft parts, Wen-Xian, coll. Potanin, 1885-IX-6–8, det. Möllendorff. SMF 9078, lectotype. SMF 9079, 2 paratypes. *Laeocathaica prionotropis albocincta* Möllendorff, 1899: SMF 9080, lectotype; Tungho, W-Sy-tshuan; ex Potanin 312a, Slg. O. v. Möllendorff. SMF 9081, paratype, juv; ex Potanin 312b, Slg. O. v. Möllendorff.

New material. HBUMM00422, 3 fms; Yanwuba [演武坝], Wenxian, Gansu Province, 1200 m a.s.l., 32.936494°N, 104.557695°E; 1998-IV-23, coll. Chen, D.-N. and Zhang, G.-Q. HBUMM00687, Shanggou [上垢], Shawanxiang [沙湾乡], Dangchangxian, Gansu Province, near 33.625712°N, 104.570162°E; 1998-V-6, coll. Chen, D.-N. and Zhang, G.-Q. HBUMM05165, 3 fma, 2 fms; Yuxushan, Wenxian, Gansu Province, near 32.957259°N, 104.689152°E, shrubs and slate, 1998-V-17, coll. Chen, D.-N. and Zhang, G.-Q. HBUMM05496, numerous fma and juvs, 1 dissected; 5 km away from Hejiawan [何家湾] Bridge, along the road to Bikou, Wenxian, Gansu Province, near point (32.769664°N, 105.22781°E), shrubs, limestones, loess, near farmland, 2006- IX-28, coll. Wu, M., Liu, J.-M., Zheng, W. and Gao, L.-H. HBUMM05549, many fma and juvs; Hengdan, Wenxian, Gansu Province; north side

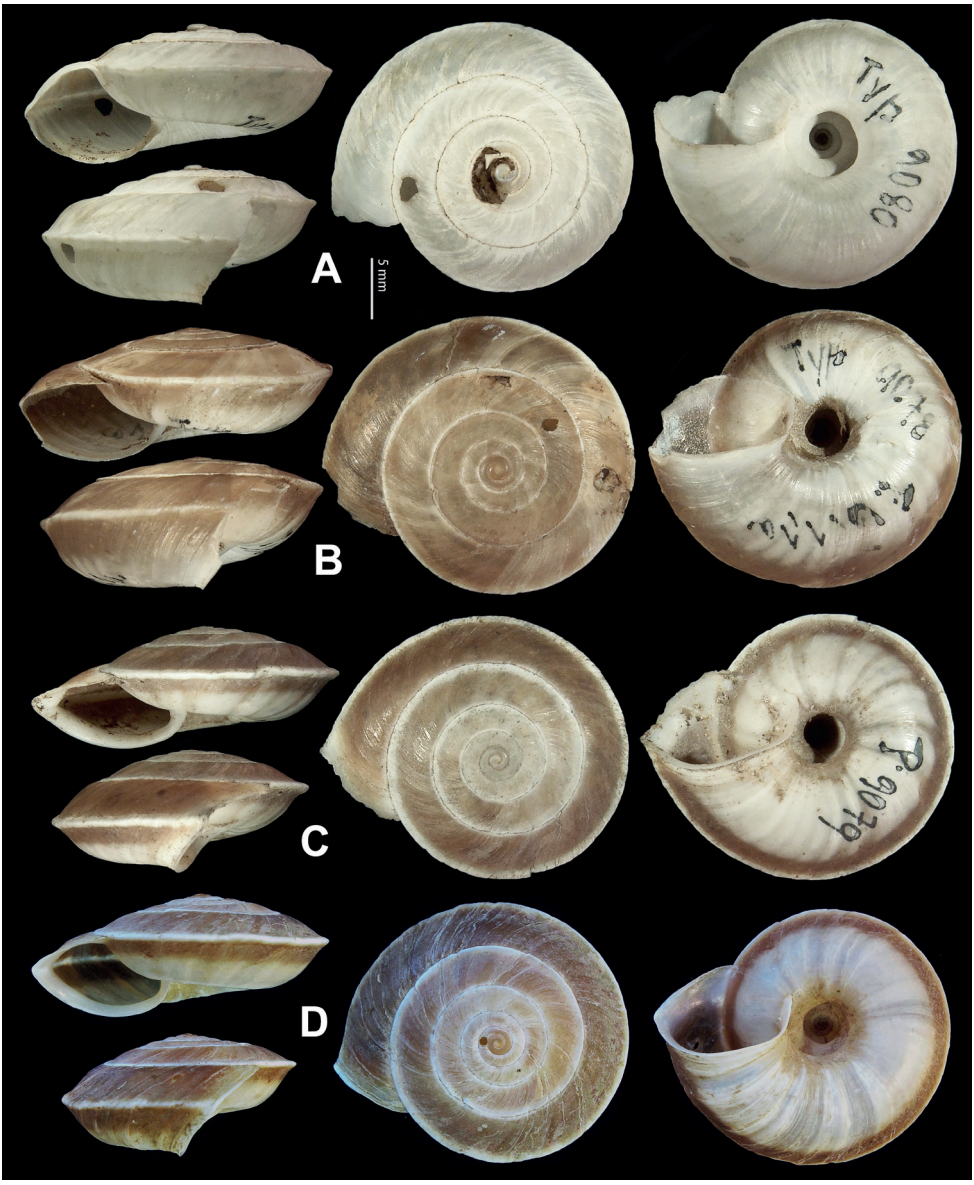

Figure 29. *Laeocathaica prionotropis* Möllendorff, 1899 **A** SMF 9080, lectotype of *L. prionotropis albocincta* Möllendorff, 1899 **B** SMF 9078, lectotype **C** SMF 9079, paratype **D** HBUMM05549-spec.1.

of Baishuijiang River, along 212 Guodao, near point (32.864025°N, 104.859517°E); hillside, bushes; 2006-IX-29; coll. Wu, M., Liu, J.-M., Zheng, W. and Gao, L.-H. HBUMM05559, many fma; HBUMM05777, 7 fma and 2 juvs, 1 dissected; same data as HBUMM05549. HBUMM05756, juvs; Zhouquxian [舟曲县], Gansu Province, near point (33.797295°N, 104.38151°E); limestone, broad-leaved trees and

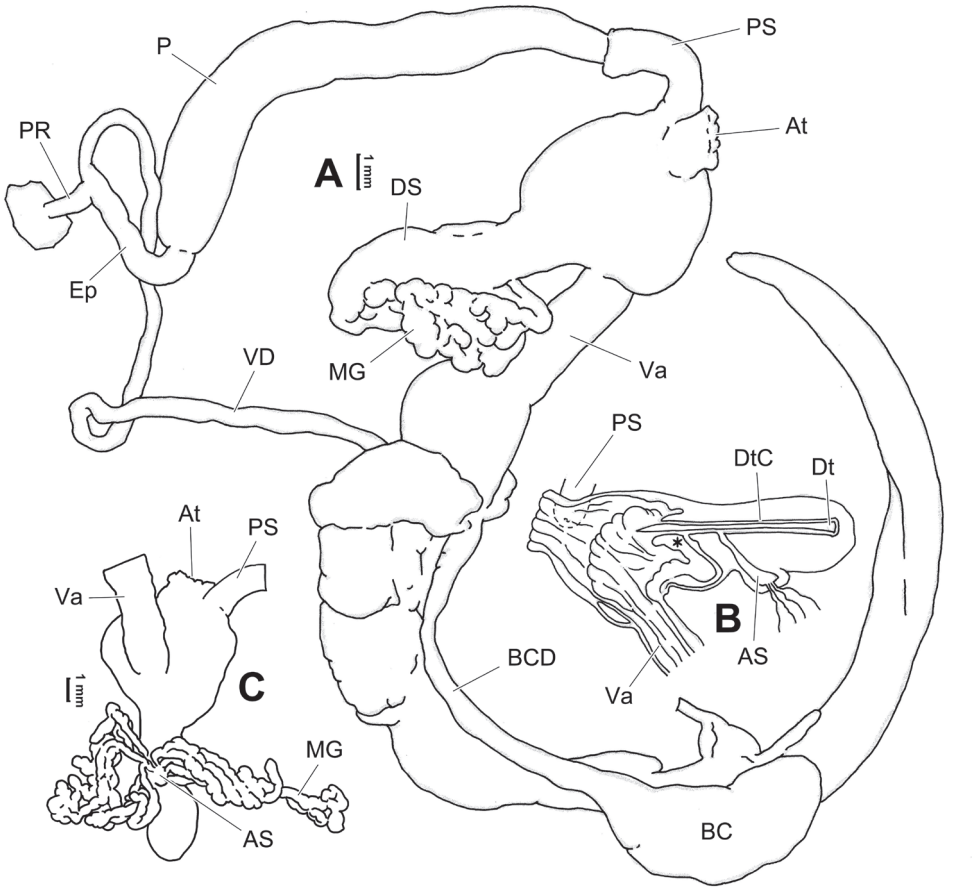

Figure 30. *Laeocathaica prionotropis* Möllendorff, 1899, HBUMM05549-spec.1 **A** general view **B** right view of dart sac apparatus **C** ventral view of dart sac apparatus. Abbreviations: AS – accessory sac; At – atrium; BC – bursa copulatrix; BCD – bursa copulatrix duct; DS – dart sac; DtC – a chamber containing love dart; Ep – epiphallus; MG – mucous glands; P – penis; PR – penial retractor muscle; PS – penial sheath; Va – vagina; VD – vas deferens. Asterisk * indicates the opening of proximal accessory sac.

shrubs; 2006-X-5, coll. Zheng, W. and Liu, J.; 5742. HBUMM05564, many fma and juvs; Hengdan, Wenxian, Gansu Province; north side of Baishuijiang River, along 212 Guodao, near point (32.864025°N, 104.859517°E); top of hill, bushes; 2006-IX-29; coll. Wu, M., Liu, J.-M., Zheng, W. and Gao, L.-H. HBUMM05689, Guantingzhen, Dangchangxian, Gansu Province, near point (33.82428°N, 104.538282°E); limestone hills, along 212 Guodao; 2006-X-3, coll. Zheng, W. and Liu, J.-M. HBUMM05765, many fma and juvs; HBUMM05764b, 1 fma and 1 fms: Bikou, along the road from Datang Hydropower Station to Hejiawan Bridge; 2006-IX-28, coll. Liu, J.-M. and Zheng, W. HBUMM05766, many fma; same data as HBUMM05765. HBUMM05774, 5 fma, 4 juvs; same data as HBUMM05765. HBUMM06533,

1 fma; town of Wenxian, Gansu Province, 1024 m a.s.l., 32.941111°N, 104.668889°E, 2011-VIII-08, coll. Wu, M., Xu, Q. and Budha, P.; DNA voucher HBUMM06534. HBUMM08120, many juvs; Zhuantangzhen [篆塘镇], 2 juv shells, Chongqing, near point (28.898641°N, 106.675179°E); 2014-X-10, coll. Du, Li [杜莉] and Lai, Yi-tong [来益同]. HBUMM08150, slope near river, Wenxian, Gansu Province, 807 m, 32.847111°N, 104.88775°E; grass and a few shrubs, on branches and rock cliff; 2017-VIII-6, coll. Sheng, X.-F., etc.; DNA voucher HBUMM08150a. HBUMM08299, 5 fma and 1 juv, 1 dissected; Bikou, Wenxian, Gansu Province; 2019-IV, coll. Li, Q.-S. HBUMM05549, many fma; 1 fma dissected; Hengdan, along national road 212, Wenxian, Gansu Province, near 32.855948°N, 104.865229°E, shrubs on hill slope, 2006-IX-29, coll. Wu, M., Liu, J.-M., Zheng, W. and Gao, L.-H. HBUMM05469, many fma; 1 fma dissected; bank of Baishuijiang, Wenxian, Gansu Province, 32.946383°N, 104.685343°E, limestone and loess, broad-leaved woods, 2006-IX-27, coll. Wu, M., Liu, J.-M., Zheng, W. and Gao, L.-H.; DNA voucher HBUMM05440. HBUMM08366, 1 fma dissected; Gansu Province, 2019, coll. Li, Q.-S.; DNA voucher HBUMM08366a. HBUMM08423, 1 fma dissected; slope near Wenzhoulu, Wenxian, Gansu Province, near 32.943151°N, 104.692505°E, on slope, 2019-X-12, coll. Li, Q.-M.; DNA voucher HBUMM08423a. HBUMM08421, 1 fma dissected; slope near X496, Wenxian, Gansu Province, near 32.474345°N, 104.915976°E, on slope, 2019-X-13, coll. Li, Q.-M.; DNA voucher HBUMM08421a. CZG202008-w4, 2 fms, Yuleixiang [玉垒乡], Wenxian, Gansu Province, near point (32.83335°N, 105.036382°E); 2020-VIII, coll. Chen, Z.-G. CZG202008-w7, 1 subadult, town of Jiuzhaigouxian, Sichuan Province, near point (33.260369°N, 104.248974°E); 2020-VIII, coll. Chen, Z.-G. CZG202008-w8, 1 fms, roadside, from Longnan to Wenxian, Gansu Province, 2020-VIII, coll. Chen, Z.-G.

Distribution. Chongqing. Gansu: Dangchangxian, Wenxian (type locality), Zhouquxian. Sichuan: Jiuzhaigouxian.

Additional information of shell. Tiny granules (~ 25 – ~ 40 μm) on the protoconch are regularly and densely arranged. Each granule is like a hump deposited in a shallow socket. On adult shell the protoconch granules are not clear, perhaps because of erosion. On teleoconch, tiny ear-shaped scales are arranged along growth lines. On umbilical side, scale scars are regularly arranged. Spiral grooves are only present on apical side of body whorl. The shell of specimens HBUMM08366 and HBUMM08421 are not typical because the periphery is angular rather than sharply carinate.

General anatomy. Eversible head wart of normal size. Jaw arcuate, with five projecting ribs (HBUMM05469).

Anatomy of genital organs. Penial sheath short, proximally covering ~ 1/5 penis. Penis tubular, slightly expanded distally. Inside penis, three or four low pilasters present proximally, two fusing into one Y-shaped fork at proximal 1/2, another two high pilasters fusing into one Y-shaped fork at proximal 1/3 with cross expanded to be a large lump (~ 1 × 1 × 2 mm^3). Fine pilasters on distal end of penis merging into more than eight thick but short folds. Vas deferens narrow throughout. Vagina between atrium and dart sac not elongated. Vagina between dart sac and insertion of bursa copulatrix duct ~ 1/3–1

length of dart sac. Dart sac ~ 1/2 (HBUMM05469) to 2/3 (HBUMM05549) length of penis. Love dart ~ 8 mm long, apically rhombic in cross-section. Accessory sac small but externally distinguishable, internally solid, inserting into dart sac at distal 1/3, opening to dart chamber. Mucous glands three (HBUMM08423), four (HBUMM05469, HBUMM08421), or eight (HBUMM05549), each simply or complicatedly branched. Proximal accessory sacs two, symmetrical, apically separated and ventrally touching, internally with a few low pilasters, each with a distal opening leading to proximal dart chamber. Bursa copulatrix duct of even diameter. Bursa copulatrix ovate, small.

Remarks. The most distinctive character of the genitalia of *Laeocathaica prionotropis* is the lump formed by the fusing pilasters in the penis.

The undetermined juvenile specimens from Chongqing (HBUMM08120) conchologically resemble *Laeocathaica prionotropis*. However, their locality is far from the distribution area of *L. prionotropis* on the South Gansu Plateau [甘南高原].

Laeocathaica stenochone Möllendorff, 1899

Figs 2A, C, 31, 32, 43E, F, 46C, D, 50B, 51; Tables 1, 3

Laeocathaica stenochone Möllendorff, 1899: 91, pl. 5, fig. 4; – Wiegmann 1900: 100, pl. 3, figs 89,90; – Gude 1902: 6; – Yen 1939: 148, pl. 15, fig. 30; – Yen 1942: 283; – Chen and Zhang 2004: 314, fig. 301.
Laeocathaica subsimilis – Sturany 1900: 21 (Möllendorff 1901: 302).
Laeocathaica (*Laeocathaica*) *stenochone* – Zilch 1968: 175; – Richardson 1983: 79.
Laeocathaica carinifera – Páll-Gergely et al. 2022: 50, fig. 12D.

Museum material. ZIN RAS No. 5, *Laeocathaica stenochone* Möllendorff., 1 fully mature soft part and 1 subadult, Zwischen dem Dorf Yu-Lin-guan und der Stadt Wenhsien, 1885-IX-6–8, coll. Potanin, det. Möllendorff. SMF 9071, lectotype; Hsi-gu-tsheng (= town of Zhouquxian) [西固城], SO-Gansu, China; ex Potanin 577, Slg. O. v. Möllendorff. SMF 8951, paratype; Zw. Yue-ling-guan u. Wen-hsien; Slg. O. v. Möllendorff, ex potanin 730. SMF 9072, paratype, A shell with immature aperture; same data as lectotype. SMF 24270, paratype, not full matured at aperture; ?Sy-tshuan; ex Beresowski 908c, Slg. O. v. Möllendorff.

New material. HBUMM05495, many fma; 1 fma dissected; 5 km away from Hejiawan Bridge, along the road to Bikou, Wenxian, Gansu Province, near point (32.769664°N, 105.22781°E), shrubs, limestones, loess, near farmland, 2006-IX-28, coll. Wu, M., Liu, J.-M., Zheng, W. and Gao, L.-H.; DNA voucher HBUMM05492. HBUMM05764, HBUMM05764a, HBUMM05767, HBUMM05769, HBUMM05772, HBUMM05774c: many fma and juvs; Bikou, along the road from Datang Hydropower Station to Hejiawan Bridge; 2006-IX-28, coll. Liu, J.-M. and Zheng, W. HBUMM08431, 1 fma dissected; near Shichuanba [石川坝], Wenxian, Gansu Province, near 33.17534°N, 105.019362°E; 2019-X-12, coll. Li, Q.-M.; DNA voucher HBUMM08431a.

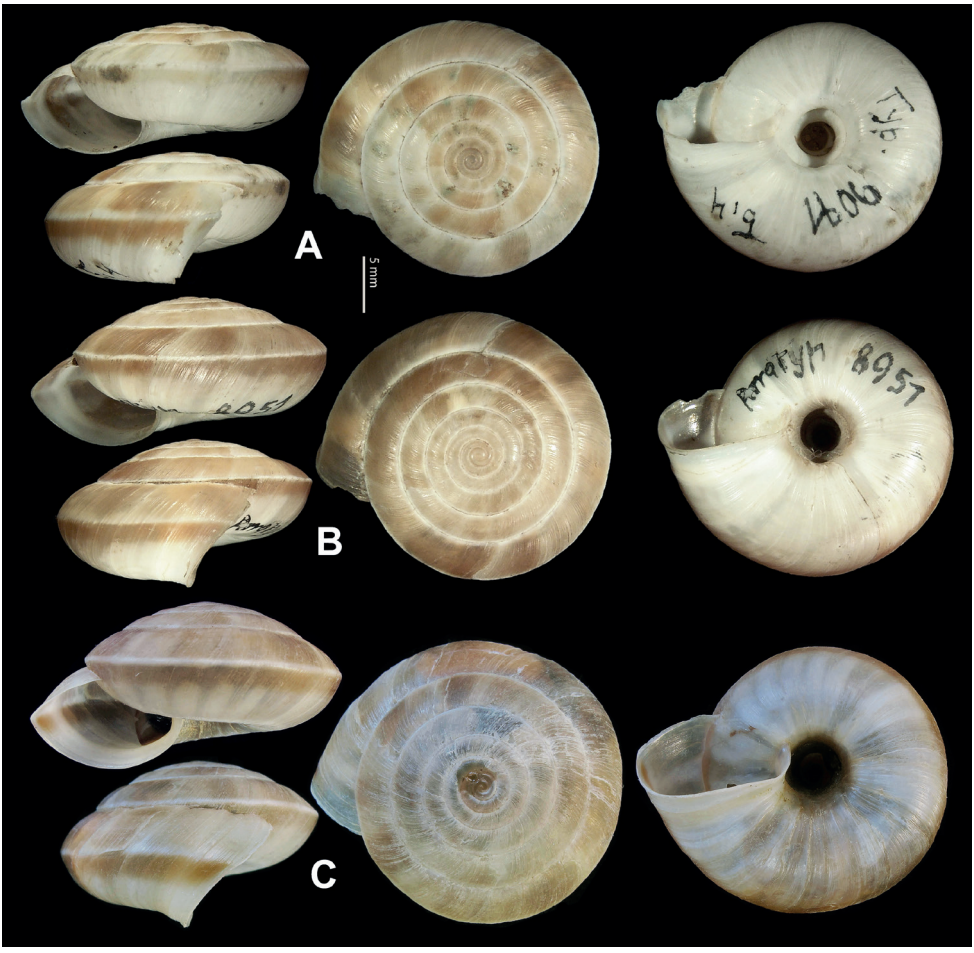

Figure 31. *Laeocathaica stenochone* Möllendorff, 1899 **A** SMF 9071, lectotype **B** SMF 8951, paratype **C** HBUMM05495-spec.1.

Distribution. Gansu: Huixian [徽县], Wenxian, Wudu, Zhouqu (type locality).

Additional information of shell. The protoconch is radially and regularly covered with dense thick granules (~ 25 – ~ 55 µm long) on the first $1^{1}/_{4}$ whorls. On the remaining protoconch whorls granules are indistinct and replaced by crowded radial threads. Spiral grooves are only indistinctly present on the apical side of body whorl.

General anatomy. Eversible head wart indistinct. Jaw arcuate, with three projecting ribs.

Anatomy of genital organs. Penial sheath very short, covering ~ 1/10 of penis. Penis tubular, equally thick. Inside penis, two high pilasters forming one Y-shaped fork at proximal 1/5, besides with two pilasters parallelly merging into one thickest pilaster. Fine pilasters on distal end of penis merging into ~ 6 thick folds, among which one is thicker than the others. Vas deferens narrow throughout. Vagina between atrium and

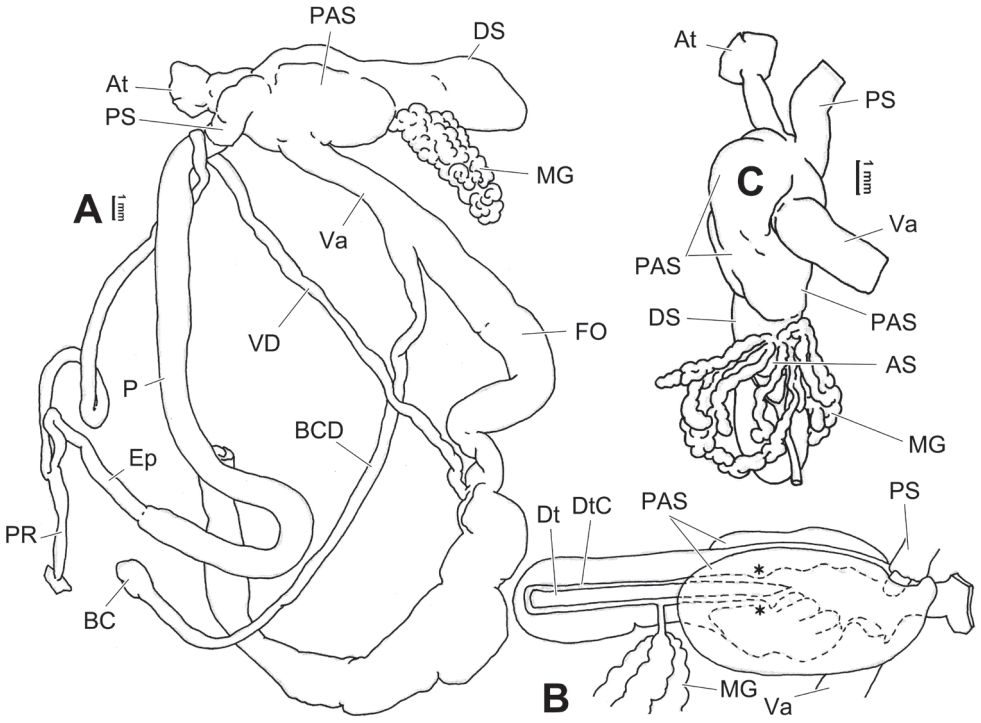

Figure 32. Genital anatomy of *Laeocathaica stenochone* Möllendorff, 1899, HBUMM05495-spec.1 **A** general view **B** left view of dart sac apparatus **C** ventral view of dart apparatus. Abbreviations: AS – accessory sac; At – atrium; BC – bursa copulatrix; BCD – bursa copulatrix duct; DS – dart sac; Dt – love dart; DtC – a chamber containing love dart; Ep – epiphallus; FO – free oviduct; MG – mucous glands; P – penis; PAS – proximal accessory sac; PR – penial retractor muscle; PS – penial sheath; Va – vagina; VD – vas deferens. Asterisk * indicates the opening of proximal accessory sac.

dart sac not elongated. Vagina between dart sac and insertion of bursa copulatrix duct ~ 1/2 length of dart sac. Dart sac ~ 1/2 length of penis. Love dart ~ 9 mm long, apically 2-bladed, subsequently rounded. Accessory sac small, internally solid, inserting into dart sac at middle part, opening to dart chamber. Mucous glands ~ 5, each complicatedly branched. Proximal accessory sacs two, symmetrical, separated apically and touching ventrally, each with an opening leading to proximal dart chamber near dart chamber opening. Bursa copulatrix duct of even diameter. Bursa copulatrix ovate, very small.

Remarks. Geographically, the distribution of *Laeocathaica carinifera* in the Yangtze valley in Chongqing and Sichuan does not overlap those of *L. stenochone* and *L. qingchuanensis* Wu, sp. nov., both of which occur along the Bailongjiang River (Fig. 2C). In terms of shell morphology, *Laeocathaica stenochone* close to *L. carinifera* and *L. qingchuanensis* Wu, sp. nov. can be distinguished (Fig. 50B). *Laeocathaica stenochone* shows a particular protoconch and teleoconch sculpture (Fig. 46C, D), which is completely different from those of *L. carinifera* (Fig. 45I, J). In molecular analysis based on present combination of 16S + ITS2 sequences (Fig. 51),

Laeocathaica stenochone (voucher HBUMM08431a) cannot be distinguished from *L. carinifera* (voucher HBUMM05103, HBUMM05131) because they share the same ITS2 sequence and show only 3-site difference in 16S sequence, suggesting they are possibly genetically very close species. However, *L. stenochone* and *L. carinifera* cannot be treated as one species (see Discussion).

Compared to *Laeocathaica carinifera*, *L. stenochone* has a symmetrical dart sac apparatus, short penial sheath, and significantly longer and evenly slender penis (Fig. 32), in which the Y-shaped fork is present more proximally (Fig. 43E, F).

The specimens HBUMM08433 (8 fma, Wufengxi [五凤溪], Jintang County [金堂县], Chengdu [成都], Sichuan Province; coll. Li, Q.-M., 2019-XI; DNA voucher HBUMM08433a) that show a very similar shell to *Laeocathaica stenochone* could represent a different species to *L. carinifera* and *L. stenochone* due to a different genital trait.

Laeocathaica tropidorhaphe Möllendorff, 1899

Figs 2A, D, 33, 34, 44A, B, 46I, J, 50A, 51; Tables 1, 3

Laeocathaica tropidorhaphe Möllendorff, 1899: 94, pl. 5, fig. 7; – Gude 1902: 6; – Yen 1939: 149, pl. 15, fig. 33; – Yen 1942: 284; – Chen and Zhang 2004: 319, fig. 307.
Laeocathaica (*Laeocathaica*) *tropidorhaphe* – Zilch 1968: 175; – Richardson 1983: 79.
Laeocathaica dangchangensis Chen & Zhang, 2004: 339, 443, fig. 332.
Laeocathaica amdoana – Páll-Gergely et al. 2022: 38, fig. 7A, B, D.

Museum material. SMF 9074, lectotype; Zw. Li-dshia-pu u. Hsi-gu-tsheng, S. O. Gansu; ex Potanin 923, Slg. O. v. Möllendorff. SMF 9075, paratypes, four fms; Tan-tshang (= Dangchang), SO-Gansu; ex Potanin 545, 623, 808b. SMF 9076, paratype, one fms; Dshie-dshou; ex Potanin 119, Slg. O. v. Möllendorff. SMF 9077, paratypes, two fms; the same data as lectotype. SMF 95126, paratype, one fms; SO-Gansu, NW-China; Slg. C. R. Böttger 1904 (ex Möllendorff!). SMF 24269, one fms labeled with "*L. stenochone*"; Tan-tschan; Slg. O. v. Möllendorff.

New material. HBUMM00486, 3 fma; Daigusicun, Diebuxian, Gansu Province, 2000 m a.s.l., near 34.004644°N, 103.939651°E; 1998-V-10, coll. Chen, D.-N. and Zhang, G.-Q. HBUMM00519, 2 fma, 1 fms; Jinpingxiang [锦屏乡], Wudu, Gansu Province, 33.411281°N, 104.793036°E; 1998-V-11, coll. Chen, D.-N. and Zhang, G.-Q. HBUMM00526, 2 fma; Lijiexiang [立节乡], Zhouquxian, Gansu Province, 33.901549°N, 104.076052°E; 1998-V-10, coll. Chen, D.-N. and Zhang, G.-Q. HBUMM00527; 2 fma; Shanggou, Shawanxiang, Dangchangxian, Gansu Province, near 33.625712°N, 104.570162°E; 1998-V-6, coll. Chen, D.-N. and Zhang, G.-Q. HBUMM00693, 12 fma, 1 fma dissected: Wangguanxiang [望关乡], Kangxian [康县], Gansu Province, near point (33.461266°N, 105.378423°E); 1998-V-5, coll. Chen, D.-N. and Zhang, G.-Q. HBUMM05664, many fma, 1 fma dissected; east bank of Bailongjiang, Lianghekou, Dangchang, Gansu Province, near 33.695553°N, 104.496612°E, limestone, 2006-X-02, coll. Liu, J.-M. and Zheng, W. HBUMM05619, many fma, 1 fma dissected; Foyazhen [佛崖镇], Wudu, Gansu

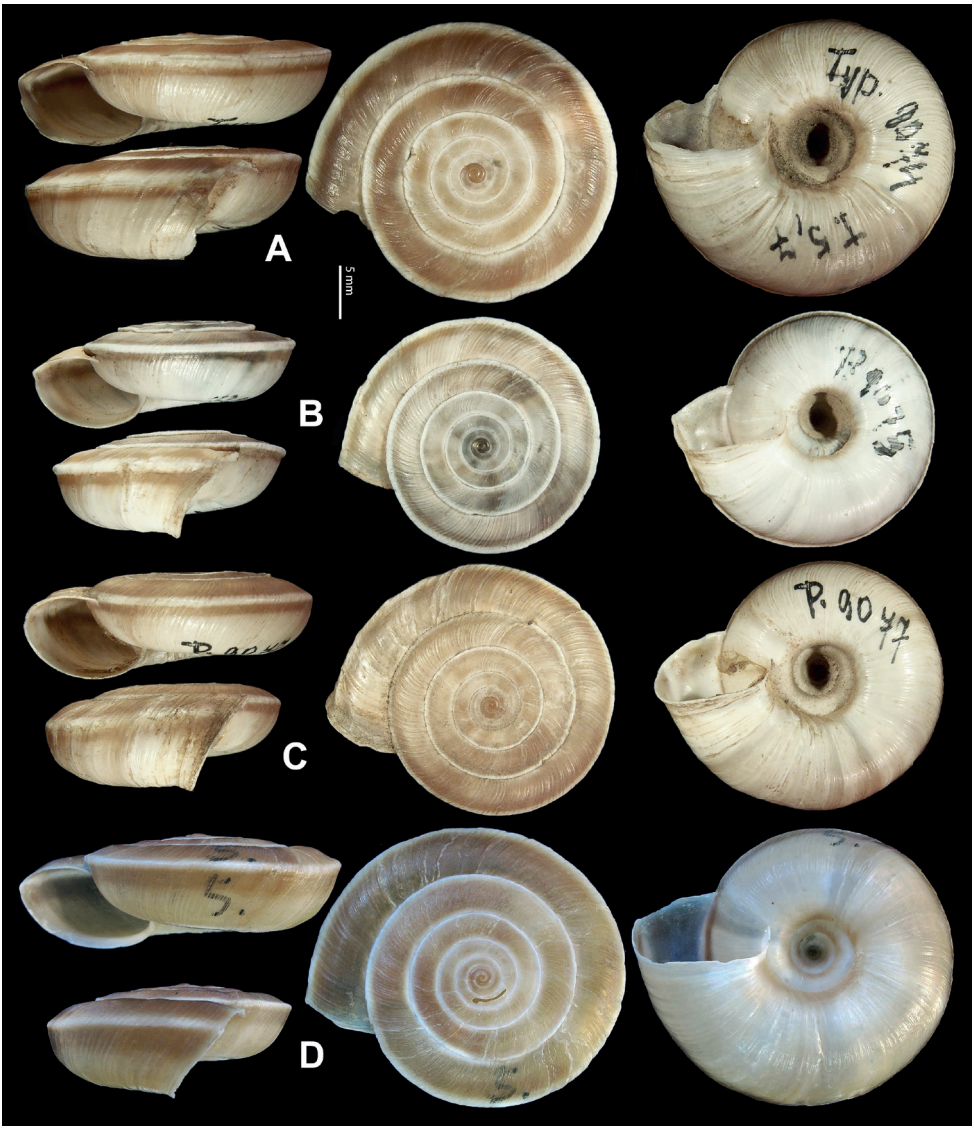

Figure 33. *Laeocathaica tropidorhaphe* Möllendorff, 1899 **A** SMF 9074, lectotype **B** SMF 9075, paratype **C** SMF 9077, paratype **D** HBUMM05664.

Province, 33.44°N, 105.27°E, limestone hill with thick shrubs and broad-leaved woods, 2006-X-02, coll. Liu, J.-M. and Zheng, W.; DNA voucher HBUMM05617. HBUMM06621, 2 fma; near Zhangzhazhen, Jiuzhaigouxian, Sichuan Province, 2100 m a.s.l., 33.299167°N, 103.859444°E; 2011-VIII-11, coll.Wu, M., Xu, Q. and Buhda, P.; DNA voucher HBUMM06620. HBUMM08425, 1 fma dissected; near Yangshanwan No. 2 Bridge, along the national road 212, Gansu Province, on slope, 2019-X-11, coll. Li, Q.-M.; DNA voucher HBUMM08425a. HBUMM05621, nu-

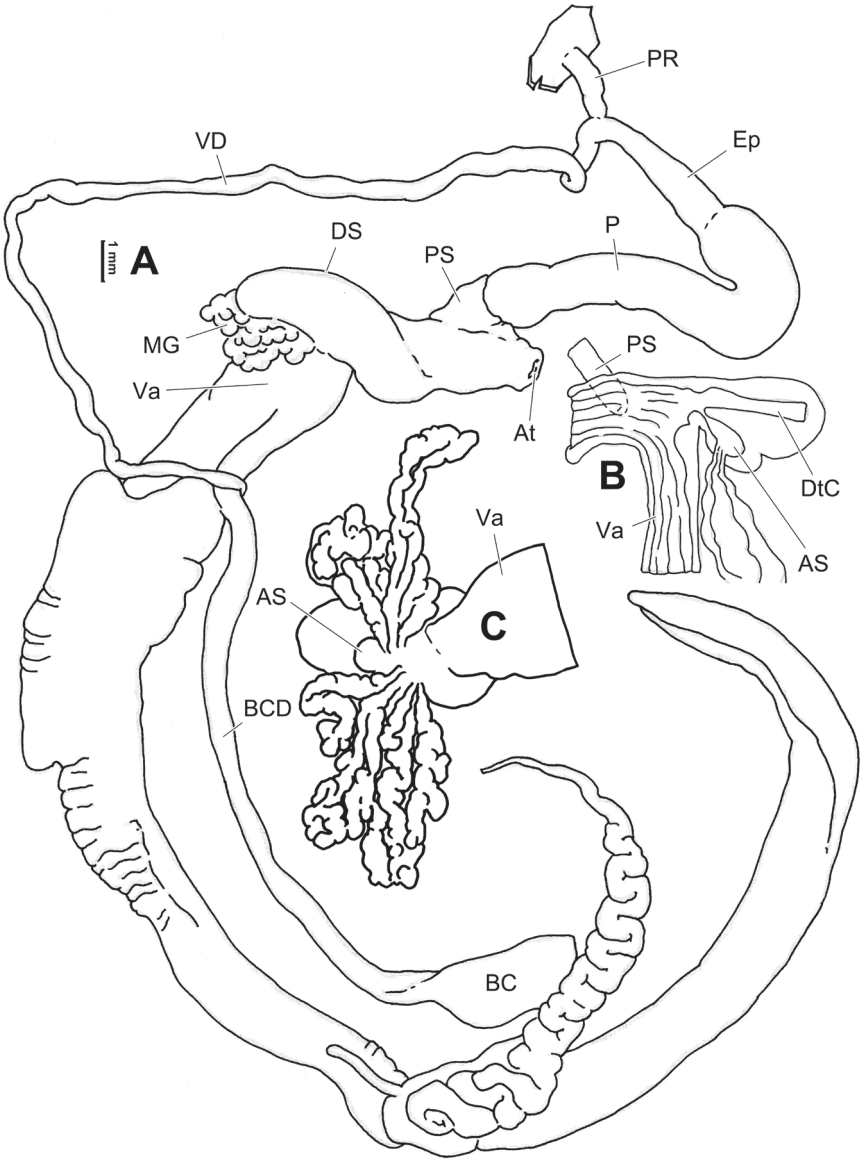

Figure 34. Genital anatomy of *Laeocathaica tropidorhaphe* Möllendorff, 1899 **A** general view **B** right view of dart sac apparatus, HBUMM05664-spec.1 **C** ventral view of dart apparatus **A, C** HBUMM05619-spec.1. Abbreviations: AS – accessory sac; At – atrium; BC – bursa copulatrix; BCD – bursa copulatrix duct; DS – dart sac; DtC – a chamber containing love dart; Ep – epiphallus; MG – mucous glands; P – penis; PR – penial retractor muscle; PS – penial sheath; Va – vagina; VD – vas deferens.

merous fma, 1 fma dissected; Foyazhen, Wudu, Gansu Province, 33.44°N, 105.27°E, limestone hill with thick shrubs and broad-leaved woods, 2006-X-02, coll. Liu, J.-M. and Zheng, W. HBUMM05719, numerous fma, 1 fma dissected; Dangchang, Gansu

Province, 2006-X-04, coll. Liu, J.-M. and Zheng, W.; DNA voucher HBUMM05716. HBUMM00450 (3 fma), HBUMM05664 (many fma, 1 fma dissected), Wangguanxiang, Kangxian, Gansu Province; 1998-V-1, coll. Chen, D.-N. and Zhang, G.-Q. HBUMM00508, 4 fma, 1 dissected; Xinglongcun, Zhongzhaixiang, Wenxian, Gansu Province; 1998-V-19, coll. Chen, D.-N. and Zhang, G.-Q. HBUMM00625, 1 fms and 2 shells of subadult, Erlangshan [二郎山], Zhouquxian, Gansu Province; 1998-V-9, coll. Chen, D.-N. and Zhang, G.-Q. HBUMM05166, 2 fma and 2 juvs; Zhongzhaixiang, Wenxian, Gansu Province; 1998-V-19, coll. Chen, D.-N. and Zhang, G.-Q. HBUMM05600, many fma and juvs; southern slope of Beishan, Wudu, Gansu Province, limestone hill with sparse shrubs; 2006-X-02, coll. Liu, J.-M. and Zheng, W. HBUMM05608, numerous fma; northern slope of Beishan, Wudu, Gansu Province, limestone hill with sparse shrubs; 2006-IX-IX-30, coll. Liu, J.-M. and Zheng, W. HBUMM05664, HBUMM05669, HBUMM05684 (many fma, 8 dissected): eastern bank of Bailongjiang, Lianghekou, Dangchangxian, Gansu Province, near point (33.697332°N, 104.493015°E); limestone; 2006-X-02, coll. Zheng, W. and Liu, J. HBUMM05691, HBUMM05692, HBUMM05693b, HBUMM05694: Guantingzhen, Dangchangxian, Gansu Province, near point (33.82428°N, 104.538282°E); limestone hills, along 212 Guodao; 2006-X-3, coll. Zheng, W. and Liu, J.-M.; DNA voucher HBUMM05688. HBUMM08369, 4 subadults; Gansu Province, 2019, coll. Li, Q.-S. CZG202008-w2, 4 subadults Shangdezhen, Wenxian, Gansu Province, near point (32.907414°N, 104.76994°E), 2020-VIII, coll. Chen, Z.-G. CZG202107-w1, 12 fms and 8 subadults, east of the town of Jiuzhaigouxian, Sichuan Province, near point (33.259523°N, 104.245884°E); 2021-VII, coll. Chen, Z.-G.

Distribution. Gansu: Dangchangxian (type locality), Diebuxian, Kangxian, Wenxian, Wuduxian, Zhouquxian (type locality). Sichuan: Jiuzhaigouxian.

Additional information of shell. Protoconch has regularly arranged fine granules (each ~ 30 μm long) and fine radial threads, both of which are usually obscured by erosion or weathering. Apical and umbilical sides of body whorl have densely and regularly arranged spiral grooves.

General anatomy. Eversible head wart present. Jaw arcuate, with five projecting ribs.

Anatomy of genital organs. Penial sheath covering ~ 1/6–1/5 of penis. Penis tubular, slightly thick distally. Inside penis, two adjacent pairs of pilasters forming two Y-shaped forks at proximal 1/4. Fine pilasters on distal end of penis merging into ~ 9 more or less thick short folds. Vas deferens narrow throughout. Vagina between atrium and dart sac elongated. Vagina between dart sac and insertion of bursa copulatrix duct ~ $^{1}/_{2}$–1 length of dart sac. Dart sac ~ 1/3 length of penis. Love dart ~ 3 mm long, apically rhombic in cross-section. Accessory sac small, internally empty, inserting into dart sac proximally, opening to dart chamber. Mucous glands 7 (HBUMM05664) – 10 (HBUMM05619), each simply or complicatedly branched. Proximal accessory sacs absent. Bursa copulatrix duct of even diameter. Bursa copulatrix ovate, small.

Remarks. In terms of shell shape, this species has an obviously depressed spire and more or less sharp carina or angulation above periphery compared to the sympatric (Fig. 2D) *Laeocathaica amdoana* and *L. distinguenda*. Their shell differences are

also indicated by the average shapes showed in Fig. 50A. The aperture of *Laeocathaica tropidorhaphe*, more or less stretched outwards, is narrower than that of *L. distinguenda* (Fig. 50A). *Laeocathaica dangchangensis* Chen & Zhang, 2004 shows a typical shell of *L. tropidorhaphe* (Fig. 50A).

The systematic affinity between *Laeocathaica amdoana*, *L. distinguenda* and *L. tropidorhaphe* is supported by the phylogeny resulting from the present analyses (Fig. 51), which also indicates that the character state of the presence of proximal accessory sacs may have repeated on different branches of Clade M (*Laeocathaica*) (Fig. 51).

For more comments, see *Laeocathaica amdoana*.

New taxa of *Laeocathaica*

Laeocathaica parapolytyla Wu, sp. nov.

https://zoobank.org/C78DF85F-7C31-47A3-921D-BE2D72DF128A
Figs 2A, B, 25, 27, 42G, H, 48I, J; Tables 1, 2
[近多结射带蜗牛]

Type material. ***Holotype*** HBUMM06640-spec.1, 1 dissected; town of Wenxian, Gansu Province, 1269 m a.s.l., near point (32.944391°N, 104.685604°E); 2011-VIII-09, coll. Wu, M., Xu, Q. and Budha, P.; DNA voucher HBUMM06639. ***Paratypes*** HBUMM06640-spec.2–9 (apex of spec.9 was removed for SEM observation), same data as holotype. HBUMM00532, Xinglongcun, Zhongzhaixiang, Wenxian, Gansu Province, near point (33.232415°N, 104.419075°E); 1998-V-19, coll. Chen, D.-N. and Zhang, G.-Q.

Measurement of holotype. Shell height 6.9 mm, maximum diameter 15.6 mm, aperture height 3.9 mm, aperture breadth 5.8 mm, umbilicus diameter 5.0 mm, protoconch whorls $1^{1}/_{2}$, whorls $8^{7}/_{8}$.

Diagnosis. Protoconch with dense radially-arranged threads, visible through umbilicus. Beneath carina a clear chestnut band present. Mucous glands four or five. Penis with two pairs of pilasters fusing into two Y-shaped forks. Vagina between atrium and dart sac not elongated. Proximal accessory sac absent.

Description of shell. Sinistral, depressed, thin but somewhat solid. Shell with $8^{1}/_{8}$–$9^{3}/_{8}$ fairly flat whorls. Suture impressed. Protoconch $1^{1}/_{2}$–$1^{3}/_{4}$ whorls, with densely arranged radial threads that may be invisible because of weathering or erosion. Periphery distinctly angulate. Growth lines indistinct. Spiral grooves are absent throughout. Aperture oblique, roundly square, descending in front. Peristome not expanded and indistinctly reflexed at lower part. Within aperture a ring-like thickening present, basally with a flat tooth. Columella oblique. Umbilicus abruptly broadened after penultimate whorl, ~ 1/4 of maximum diameter. Protoconch visible through umbilicus. Shell apically in intermittent yellowish white and pale chestnut patches except white carina. In umbilical view shell distinctly paler in greyish yellow, just beneath carina a clear chestnut band present, umbilical region brownish.

General anatomy. Eversible head wart prominent. Jaw arcuate, with four projecting ribs.

Anatomy of genital organs. Penial sheath covering ~ 1/5 of penis. Penis distally fairly expanded. Inside penis, two high pilasters fusing into one Y-shaped fork at proximal 1/4, another pair of pilasters fusing into one Y-shaped fork at middle part. Fine pilasters on distal end of penis merging into ~ 7 thick and short folds. Epiphallic papilla absent. Vas deferens narrow throughout. Vagina between atrium and dart sac not elongated. Vagina between dart sac and insertion of bursa copulatrix duct ~ 1/2 length of dart sac. Dart sac ~ 1/2 length of penis. Accessory sac small but externally distinguishable, internally solid, ventrally inserting into dart sac at distal 1/3, together with mucous glands opening to dart chamber. Mucous glands four or five, each singly tubular or bifurcated. Proximal accessory sac absent. Bursa copulatrix duct equally thick.

Etymology. The name of this new species is made up of *para-* meaning similar to and *polytyla* from *Laeocathaica polytyla* Möllendorff, 1899, which is conchologically close to the new species.

Ecology. On rocks of local hill.

Distribution. Only known from the type locality.

Remarks. The new species exhibits a large intraspecific change in size (Fig. 25), which is also showed in *Laeocathaica polytyla* (Fig. 24A, B). *Laeocathaica parapolytyla* Wu, sp. nov. looks like a flattened and sharply carinate *L. polytyla*, but has slightly different coloring and coarser growth lines. The terminal genitalia of these two species are similar, but in the new species the penis internally has two pairs of pilasters that fuse into two Y-shaped forks, while in *Laeocathaica polytya* the penis has only one Y-shaped fork formed by adjacent pilasters.

Laeocathaica qishilii Wu, sp. nov.

https://zoobank.org/DE713AA0-C437-4118-ABD7-97941F207D7D
Figs 2A, B, 4, 35A, B, 36, 44C, 48A, B, 49A, B; Tables 1, 2
[奇石射带蜗牛]

Type material. ***Holotype*** HBUMM08298-spec.1, fma, border of Jiuzhaigou County and Wen County, near point (33.14376°N, 104.246674°E); 2019-IV, coll. Li, Q.-S. ***Paratypes*** HBUMM08298-spec.2–8, 7 fma, 3 fma dissected; same data as holotype. HBUMM06779 and HBUMM06778, 2 fma and 1 fms, 1 fma dissected; Shijiba, Wen County, 1193 m a.s.l., 33.102222°N, 104.335556°E, 2011-VIII-10, coll. Wu, M., Xu, Q. and Budha, P.

Measurement of holotype. Shell height 8.1 mm, maximum diameter 23.7 mm, aperture height 5.6 mm, aperture breadth 10.6 mm, umbilicus diameter 5.6 mm, protoconch whorls $1^{1}/_{2}$, whorls $5^{5}/_{8}$.

Diagnosis. Protoconch with decussate radial and spiral threads. Umbilicus broad and deep, through which protoconch is visible. A bright band present between carina and suture. Beneath carina a dark chestnut band present. Mucous glands two. Penis with two proximal thick internal pilasters fusing into a Y-shaped fork at proximal 1/3. Vagina between atrium and dart sac not elongated. Two proximal accessory sacs on both sides of dart sac, with two pores leading to opening of dart chamber.

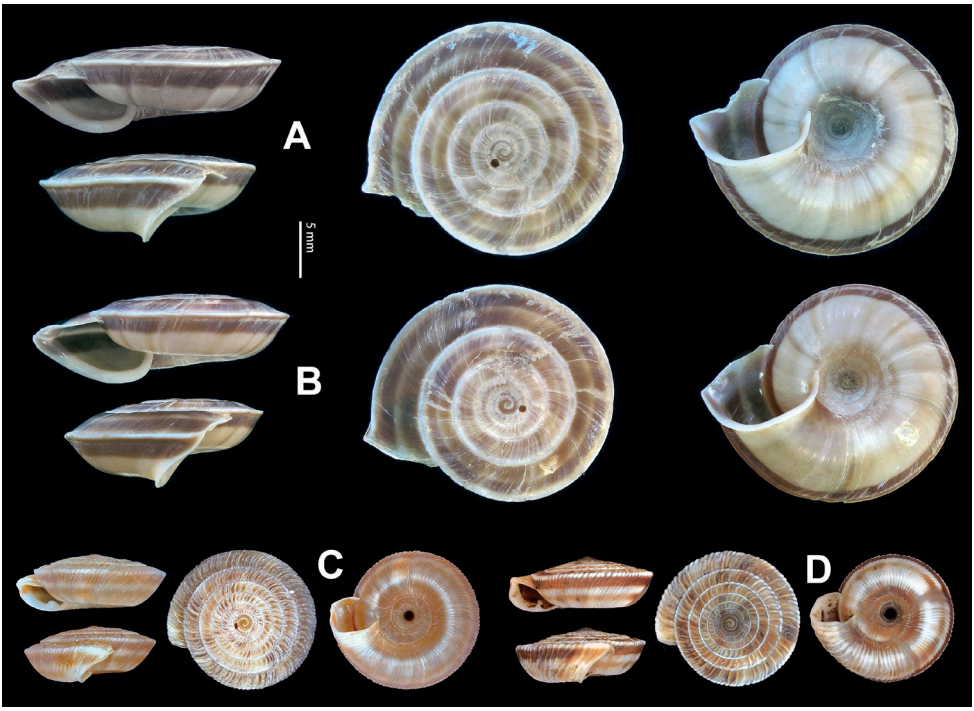

Figure 35. A, B *Laeocathaica qishilii* Wu, sp. nov. **A** holotype, HBUMM08298-spec.1 **B** paratype, HBUMM08298-spec.2 **C, D** *L. qiminglii* Wu, sp. nov. **C** holotype, HBUMM08422-spec.1 **D** paratype, HBUMM08448-spec.1.

Table 2. Shell measurements (range, mean ± s.d.) of the new species of *Laeocathaica* Möllendorff, 1899 described in this work (length in mm).

Species	*n*	Shell height	Maximum diameter	Aperture height	Aperture breadth	Umbilicus diameter	Protoconch whorls	Whorls
L. parapolytyla Wu, sp. nov.	8	5.5–8.4 7.2±1.05	11.4–17.2 15.1±2.23	2.8–4.6 3.9±0.66	4.2–6.8 5.8±0.95	3.0–5.0 4.1±0.65	1.500–1.750 1.594±0.1108	8.125–9.375 8.875±0.4432
L. qiminglii Wu, sp. nov.	2	5.2–5.3 5.2±0.03	12.6–13.2 12.9±0.44	2.0–2.4 2.2±0.28	3.9–4.2 4.0±0.24	5.2–5.4 5.3±0.13	1.500	7.625–7.750 7.688±0.0883
L. zhengpingliui Wu, sp. nov.	10	7.9–10.0 9.2±0.77	17.2–20.1 19.0±1.1	4.6–6.8 5.8±0.61	5.9–8.1 7.2±0.67	6.0–7.9 6.7±0.56	1.500–1.750 1.600±0.0986	8.625–9.250 8.838±0.2361
L. cheni Wu, sp. nov.	9	8.6–10.4 9.3±0.56	16.5–19.7 18.7±1.05	5.0–6.5 6.0±0.48	6.0–8.1 7.3±0.62	4.8–7.1 6.2±0.72	1.500–1.625 1.609±0.0442	9.000–9.625 9.219±0.0.2086
L. qingchuanensis Wu, sp. nov.	6	10.7–13.9 12.3±1.19	20.7–27.5 24.5±2.10	6.2–8.5 7.6±0.78	9.0–11.9 10.7±0.99	4.1–6.4 5.1±0.59	1.500–1.625 1.510±0.0347	6.125–7.000 6.500±0.2447
L. qishilii Wu, sp. nov.	8	7.4–8.2 7.9±0.31	21.3–23.7 22.8±0.79	5.6–6.9 6.2±0.49	9.8–11.4 10.5±0.47	5.0–6.1 5.6±0.35	1.500–1.625 1.516±0.0442	5.500–5.875 5.703±0.1325
L. nordsiecki Wu, sp. nov.	5	3.6–3.8 3.7±0.08	10.3–10.8 10.5±0.18	2.2–3.0 2.7±0.31	2.9–3.3 3.1±0.16	4.6–5.0 4.8±0.13	1.500–1.625 1.600±0.0560	5.000–5.125 5.100±0.0559

Description of shell. Sinistral, depressed, thin but somewhat solid. Shell with $5^{1}/_{2}$–$5^{7}/_{8}$ fairly flat whorls. Suture impressed. Protoconch $1^{1}/_{2}$–$1^{5}/_{8}$ whorls, with decussate radial and spiral threads, on the first whorl of which may be invisible

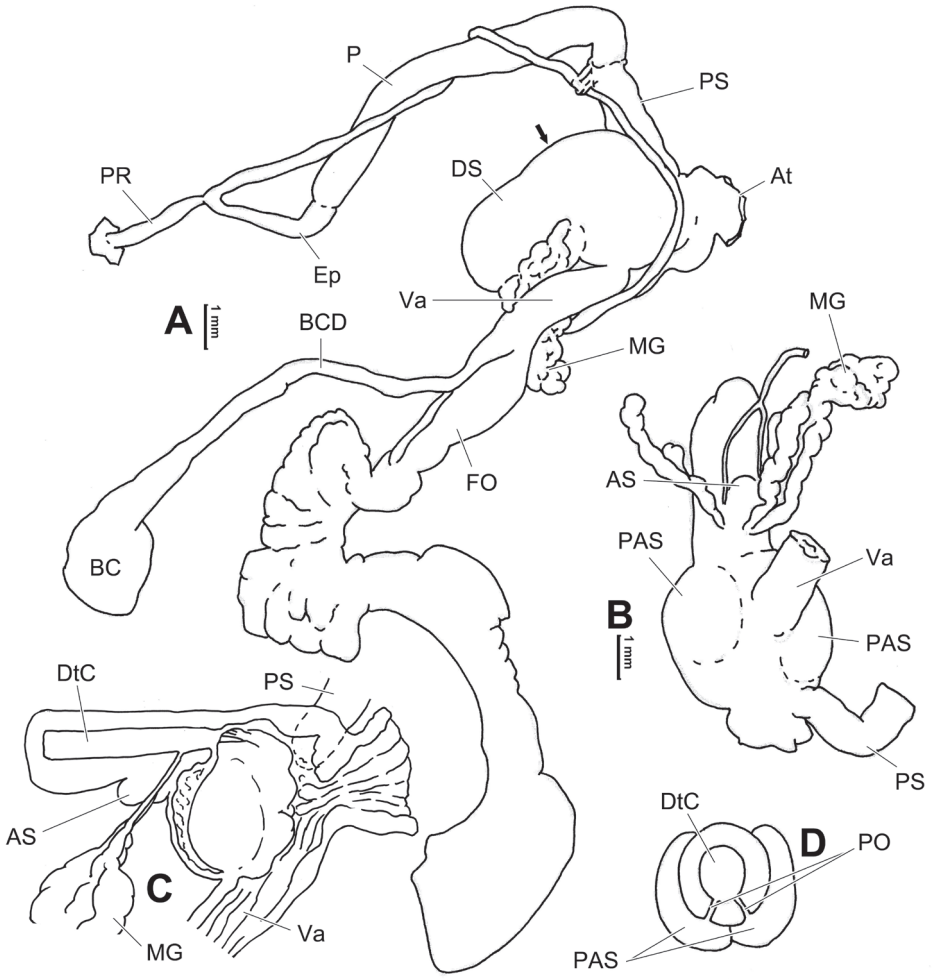

Figure 36. Genital anatomy of *Laeocathaica qishilii* Wu, sp. nov., HBUMM08298-spec.1, holotype **A** general view **B** ventral view of dart sac apparatus **C** left view of dart sac apparatus **D** cross-section of dart sac at the position arrowed in (**A**). Abbreviations: AS – accessory sac; At – atrium; BC – bursa copulatrix; BCD – bursa copulatrix duct; DS – dart sac; DtC – a chamber containing love dart; Ep – epiphallus; FO – free oviduct; MG – mucous glands; P – penis; PAS – proximal accessory sac; PO – opening of proximal accessory sac leading to dart chamber; PR – penial retractor muscle; PS – penial sheath; Va – vagina; VD – vas deferens.

because of weathering or erosion. Growth lines fine, more or less clear. Aperture oblique, peach-shaped, descending. Peristome expanded and reflexed at lower part. Columella oblique. Umbilicus broad, ~ $^{1}/_{3}$ of maximum diameter. Protoconch visible through umbilicus. Shell apically in chestnut except white carina, after the first three or four whorls a bright band present between carina and adjacent suture. In umbilical view shell distinctly paler in greyish yellow and just beneath carina a chestnut band present.

General anatomy. Eversible head wart present. At mantle edge leaf-shaped appendage absent. On internal body wall of head region between ommatophorous insertions with neither glands nor tiny pits. Body greyish brown, central dorsum with pale longitudinal stripes. Sole dirty white. Jaw arcuate, with 3–5 more or less projecting ribs.

Anatomy of genital organs. Penial sheath short but well developed. Penis of equal thickness, externally simple. Inside penis, two very thick longitudinal pilasters fusing into a Y-shaped fork at proximal 1/3, accompanied with another two thick pilasters, these plasters then change into numerous fine pilasters that distally merge into three short but thick folds near opening of epiphallus. Epiphallic papilla absent. Vas deferens narrow throughout. Vagina between atrium and dart sac not elongated. Accessory sac spherical, solid, inserting into dart sac medially, opening to distal dart chamber. Mucous glands two, each complicatedly branched. Proximal accessory sacs two, symmetrical, dorsally separated and ventrally touching, each with a pore leading to proximal dart chamber. Love dart ~ 6 mm long, apically 2-bladed, medially round-hexagonal. Bursa copulatrix duct equally narrow. Bursa copulatrix pear-shaped.

Etymology. This new species is named after Mr Li, Qi-Shi, who made this work possible with his field work.

Ecology. This species is found under rotten wood.

Distribution. Only known from the type locality.

Remarks. This new species has a unique protoconch on which decussate radial and spiral threads are present compared to the granulation on this part in the other *Laeocathaica* species. The new species is conchologically close to *Laeocathaica prionotropis*, but the former species is apically more depressed, more broadly umbilicate, has a more expanded peristome, a more elongated aperture due to the more prominent carina, is apically evenly brown, and has a smooth shell surface instead of the finely scaly surface in the latter species. The new species shares the inner structure of the dart sac with *L. prionotropis*. However, they differ in the internal structure of penis: in *L. prionotropis*, partial pilasters merge into a tubercle, which is missing in the new species. They also differ in the number of tubes of the mucous glands.

***Laeocathaica qiminglii* Wu, sp. nov.**

https://zoobank.org/F7DA5306-7753-4358-BFBC-815547FB064F

Figs 2A, B, 35C, D, 48C, D, 49D, 51, Tables 1–3

[启明射带蜗牛]

Type material. ***Holotype*** HBUMM08422-spec.1, fms, a slope near X496 (32.969442°N, 104.654191°E), Wenxian, Gansu Province; 2019-X-13; coll. Li, Q.-M.; DNA voucher HBUMM08422a. ***Paratypes*** HBUMM08422-spec.2, 1 animal with mature shell but immature genitalia, dissected; same data as holotype. HBUMM08448, 7 fms, east of town of Wenxian, 2020-VIII, coll. Chen, Z.-G.

Measurement of holotype. Shell height 5.2 mm, maximum diameter 13.2 mm, aperture height 2.0 mm, aperture breadth 4.2 mm, umbilicus diameter 5.4 mm, protoconch whorls $1^{1}/_{2}$, whorls $7^{5}/_{8}$.

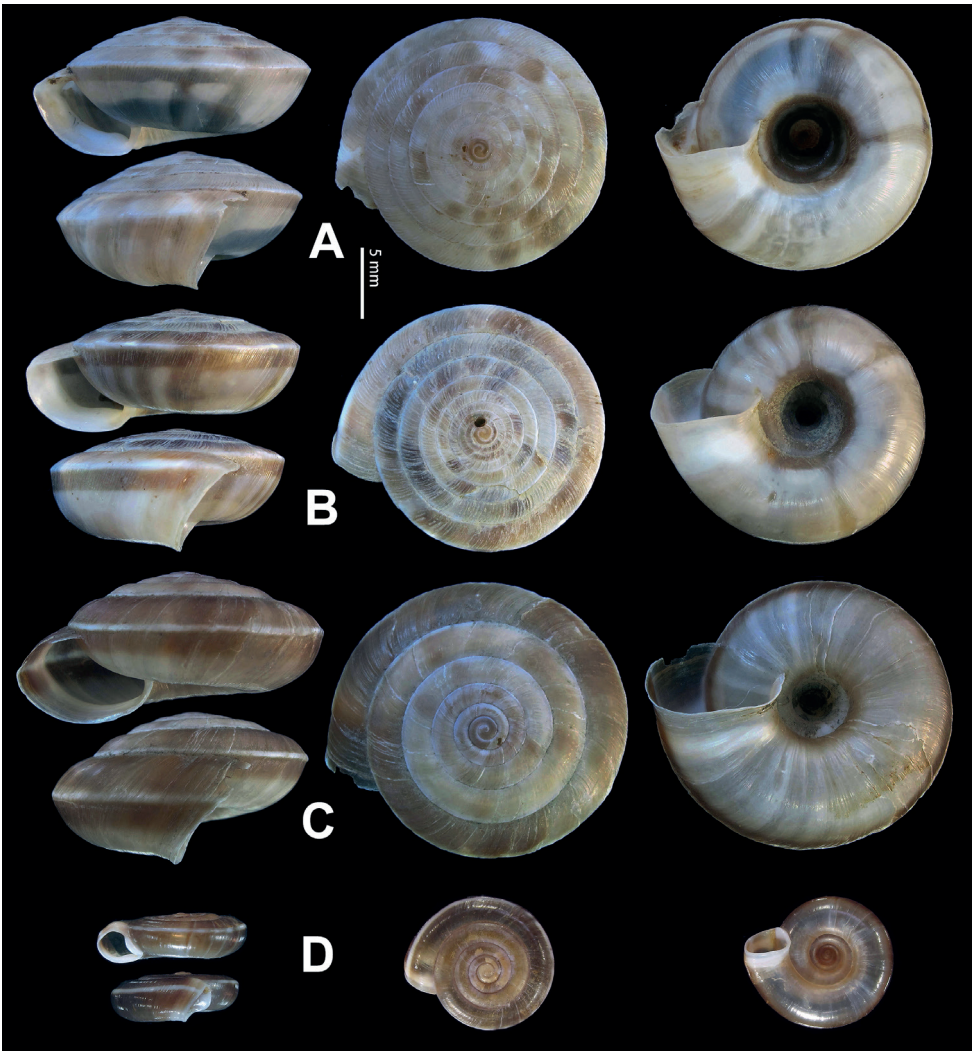

Figure 37. A *Laeocathaica zhengpingliui* Wu, sp. nov., HBUMM05553-spec.1, holotype **B** *L. cheni* Wu, sp. nov., HBUMM05553b-spec.1, holotype **C** *L. qingchuanensis* Wu, sp. nov., HBUMM01179a-spec.1, holotype **D** *L. nordsiecki* Wu, sp. nov., HBUMM08446-spec.1, holotype.

Diagnosis. Protoconch without granules. Umbilicus extremely broad, ~ $^{1}/_{2}$ of maximum diameter. Shell evenly pale brown with umbilicus side paler.

Description of shell. Sinistral, fairly depressed, solid. Shell with $7^{5}/_{8}$–$7^{3}/_{4}$ fairly flat whorls. Suture impressed. Spire depressed-cone-shaped. Protoconch $1^{1}/_{2}$ whorls, smooth on the first whorl where sculpture may be erased by weathering or erosion, followed by sparse radial threads. Protoconch visible through umbilicus. Growth lines unclear. Spiral grooves absent. After ~ $2^{1}/_{2}$ whorls, with regularly spaced thick ribs between which are many fine threads. Aperture oblique, peach-shaped, descending in front. Body whorl sharply carinate above periphery. Peristome seldom expanded and

only slightly reflexed at lower part. Columella very oblique. Umbilicus very broad, ~ 1/2 of maximum diameter. Shell evenly pale brown with umbilicus side paler.

General anatomy. Eversible head wart small but prominent. At mantle edge leaf-shaped appendage absent. On internal body wall of head region between ommatophorous insertions with neither glands nor tiny pits. Body greyish brown, central dorsum with pale longitudinal stripes. Sole dirty white. Jaw arcuate, with five projecting ribs.

Anatomy of genital organs. Penial sheath present. Vagina between atrium and dart sac not elongate. Mucous glands four (observations of the genitalia of this species are only based on the paratype HBUMM08422-spec.2).

Etymology. This new species is named after the collector Mr. Qiming Li.

Ecology. In October, this species was found in the crevices of broken stones on dry slope.

Distribution. Only known from the type locality.

Remarks. This species has the strongest ribs on the shell surface and the broadest umbilicus of all species of *Laeocathaica*.

***Laeocathaica zhengpingliui* Wu, sp. nov.**

https://zoobank.org/3F6DC3CB-8F91-4E64-93F6-96174797F396

Figs 2A, 2B, 37A, 38, 44D, 47K, 47L; Tables 1, 2

[正平射带蜗牛]

Type material. ***Holotype*** HBUMM05553-spec.1, fma, Hengdan, Wenxian, Gansu Province; north side of Baishuijiang River, along 212 Guodao, near point (32.864025°N, 104.859517°E); hillside, bushes; 2006-IX-29; coll. Wu, M., Liu, J.-M., Zheng, W. and Gao, L.-H.; DNA voucher HBUMM05527. ***Paratypes*** HBUMM05553-spec.2–49, 49 shells including 3 fms (1 broken), 15 juvs and 41 fma, same data as holotype. Ten shells randomly selected from 43 fully mature shells were measured. 2 fma dissected (anatomy no. sp2). HBUMM05565b, 1 fms without protoconch, 9 juvs; Hengdan, Wenxian, Gansu Province; north side of Baishuijiang River, along 212 Guodao, top of hill; 2006-IX-29, Wu, M., Liu, J.-M., Zheng, W. and Gao, L.-H. HBUMM05576c, 1 fma with partially broken shell, dissected; same data as HBUMM05565b.

Measurement of holotype. Shell height 10.0 mm, maximum diameter 19.6 mm, aperture height 5.6 mm, aperture breadth 7.5 mm, umbilicus diameter 7.0 mm, protoconch whorls 1 5/8, whorls 9 1/4.

Diagnosis. Protoconch without granules. Umbilicus more than 1/3 maximum diameter, through which protoconch is visible. Beneath carina a chestnut band present. Palatal with two blunt teeth. Mucous glands six. Proximal 4/5 of penis with ~ 6 thick internal pilasters. Two adjacent pairs of penial pilasters fusing into two Y-shaped forks at distal 2/3 of penis. Vagina between atrium and dart sac moderately elongated. Proximal accessory sacs two, separate, symmetrical, each with a pore leading to opening of accessory sac.

Description of shell. Sinistral, depressed, thin but somewhat solid. Shell with 8 5/8–9 1/4 fairly flat whorls. Suture impressed. Protoconch 1 1/2–1 3/4 whorls, with very fine axial striae which may be invisible on the first whorl possibly by weathering or erosion.

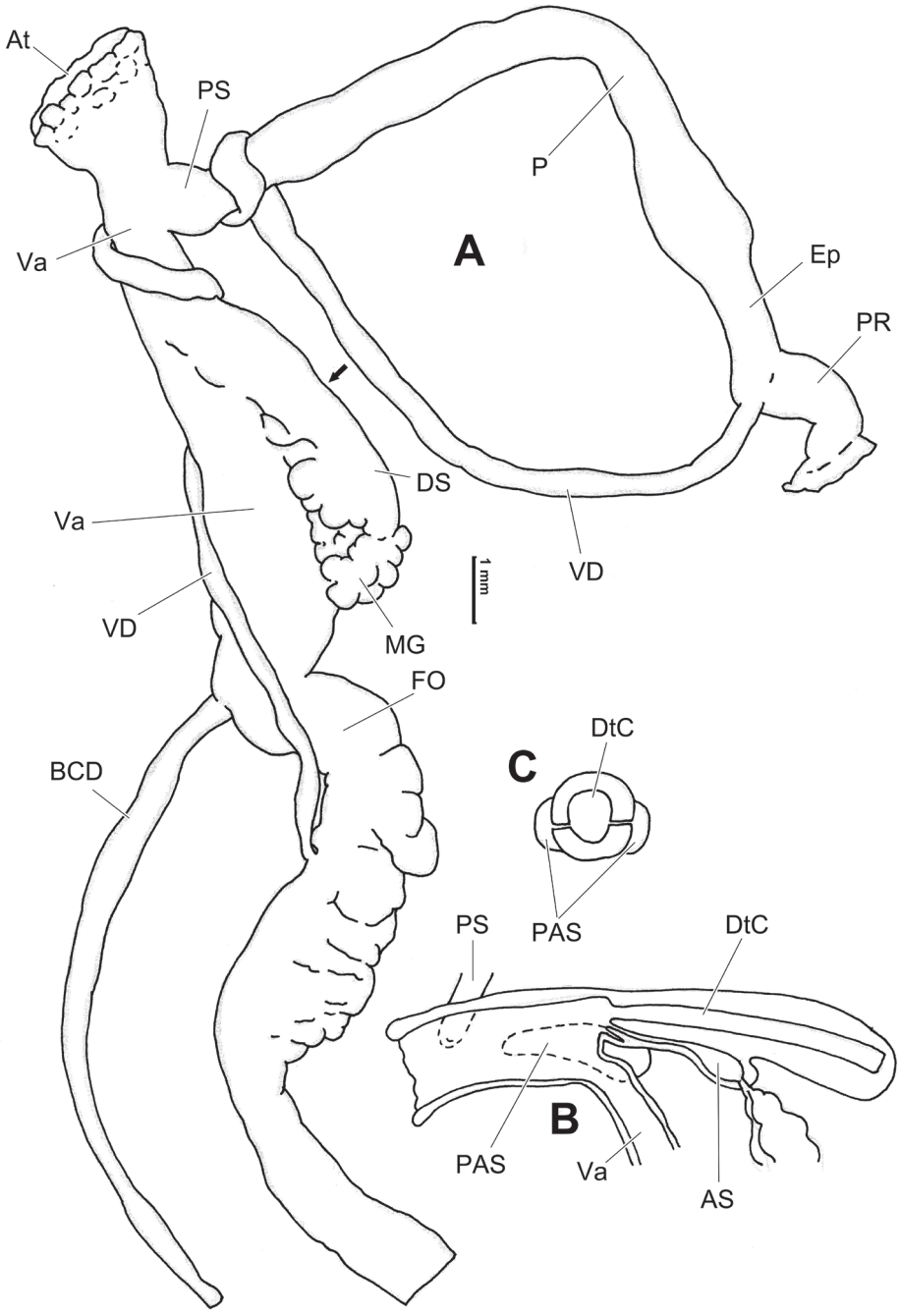

Figure 38. Genital anatomy of *Laeocathaica zhengpingliui* Wu, sp. nov., HBUMM05553-spec.1, holotype **A** general view **B** right view of dart apparatus **C** cross-section of dart sac at the position arrowed in (**A**). Abbreviations: AS – accessory sac; At – atrium; BCD – bursa copulatrix duct; DS – dart sac; DtC – a chamber containing love dart; Ep – epiphallus; FO – free oviduct; MG – mucous glands; P – penis; PAS – proximal accessory sac; PR – penial retractor muscle; PS – penial sheath; Va – vagina; VD – vas deferens.

Growth lines thick or rib-like above but fine beneath carina. Above periphery a sharp whitish carina present. Aperture oblique, peach-shaped, slightly descending in front. On ring-like thickening within aperture, a blunt tooth present near columella and another one near carina. Peristome almost not expanded, just minutely reflexed at lower part. Columella oblique. Umbilicus with a tint of pale brown, broadly conical, more than 1/3 of maximum diameter. Protoconch visible through umbilicus. Whorls apically in yellowish white with intermittent brownish patches. In umbilical view shell yellowish white with several brownish patches, and just beneath carina a chestnut band present.

General anatomy. Eversible head wart lowly present. At mantle edge leaf-shaped appendage absent. On internal body wall of head region between ommatophorous insertions with neither glands nor tiny pits. Body greyish brown, central dorsum with pale longitudinal stripes. Sole dirty white. Jaw arcuate, with ~ 6 more or less projecting ribs.

Anatomy of genital organs. Penial sheath very short. Penis distally slightly expanded, externally simple. Penis of proximal 4/5 internally with ~ 6 thick longitudinal pilasters, two adjacent pairs of which fuse into two Y-shaped forks at distal 2/3; pilasters then branching into fine pilasters that are connected to form network. Epiphallic papilla absent. Vas deferens narrow throughout. Vagina between atrium and dart sac somewhat elongated. Accessory sac spherical, empty, inserting into dart sac at middle part, opening near the opening of dart chamber. Mucous glands six, each a single tube or simply branched. Proximal accessory sacs two, separate, symmetrical, each with a pore leading to opening of accessory sac/dart chamber. Love dart ~ 5 mm long, rounded and bladeless throughout. Bursa copulatrix duct equally narrow.

Etymology. This new species is named after Mr. Liu, Zheng-Ping [刘正平], an amateur Chinese conchologist.

Ecology. This species is found on exposed slate rocks of hill side.

Distribution. This species is only known from the type locality.

Remarks. The new species is conchologically close to *Laeocathaica odophora*; however, its carina is blunter, the aperture has only two weak teeth near the columella instead of two strong apertural teeth in the latter species, and the umbilicus is significantly broader. Regarding genitalia, the new species has two separated proximal accessory sacs of equal size, while in *Laeocathaica odophora* two proximal accessory sacs are ventrally adjacent and separated only by a very thin membrane, and the much smaller right proximal accessory sac makes *L. odophora* have an asymmetrical dart sac.

***Laeocathaica cheni* Wu, sp. nov.**

https://zoobank.org/C1A30E6B-FB66-4BB1-9C24-908CCCCFFA6B

Figs 2A, B, 37B, 39, 44F–H, 46K, L, 49F, 51; Tables 1–3

[陈氏射带蜗牛]

Type material. ***Holotype*** HBUMM05553b-spec.1, fma, dissected; Hengdan, Wenxian, Gansu Province; north side of Baishuijiang River, along 212 Guodao, near point (32.864025°N, 104.859517°E); hillside, bushes; 2006-IX-29; coll. Wu, M., Liu, J.-

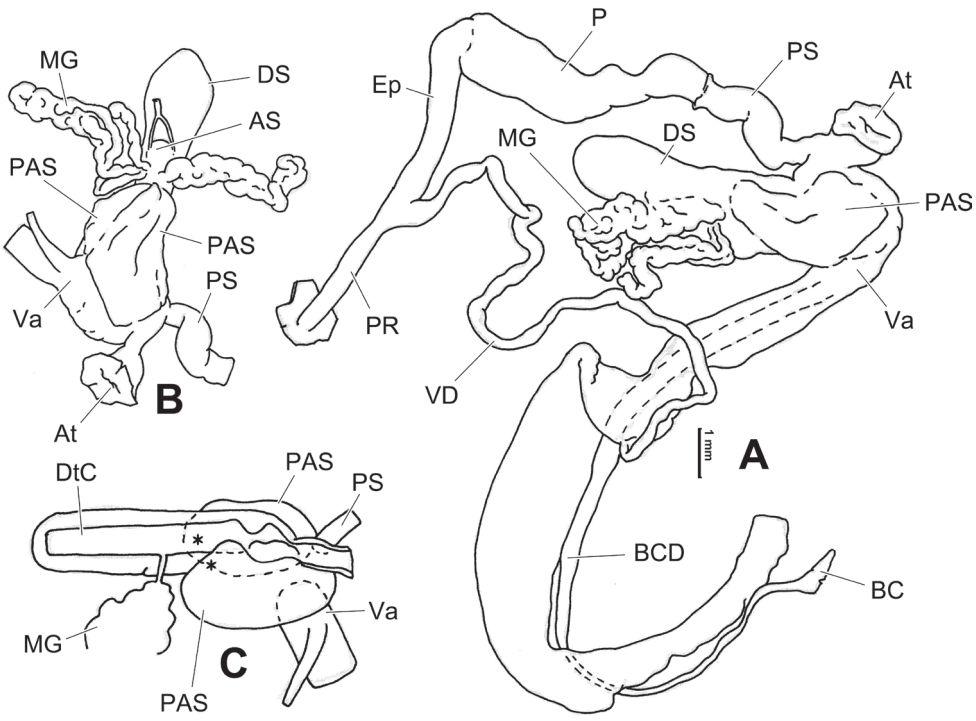

Figure 39. Genital anatomy of *Laeocathaica cheni* Wu, sp. nov., HBUMM05553b-spec.1, holotype **A** general view **B** ventral view of dart apparatus **C** left view of dart sac apparatus. Abbreviations: AS – accessory sac; At – atrium; BC – bursa copulatrix; BCD – bursa copulatrix duct; DS – dart sac; DtC – a chamber containing love dart; Ep – epiphallus; MG – mucous glands; P – penis; PAS – proximal accessory sac; PR – penial retractor muscle; PS – penial sheath; Va – vagina; VD – vas deferens. Asterisk * indicates the opening of proximal accessory sac.

M., Zheng, W. and Gao, L.-H. ***Paratypes*** HBUMM05553b-spec. 2–7, 8 fma, 1 dissected (anatomy no. sp3); same data as holotype. HBUMM05576a- spec. 1–2, 2 fms, South bank of Baishuijiang River, Hengdan, Wenxian, Gansu Province; near point (32.863381°N, 104.854879°E); hilltop, bushes; 2006-IX-29; coll. Wu, M., Liu, J.-M., Zheng, W. and Gao, L.-H. HBUMM08420, 1 fma with fully mature shell but immature genitalia, dissected, a slope near X496 (32.969442°N, 104.654191°E), Wenxian, Gansu Province; 2019-X-13; coll. Li, Q.-M.; DNA voucher HBUMM08420a. HBUMM08428, 3 fma (1 dissected) and 1 juv, same data as HBUMM08420; DNA voucher HBUMM08428a. HBUMM08368, 2 fma and 3 juvs, not dissected; Gansu Province; 2019; coll. Li, Q.-S.; DNA voucher HBUMM08368a.

Measurement of holotype. Shell height 9.0 mm, maximum diameter 19.3 mm, aperture height 5.6 mm, aperture breadth 7.3 mm, umbilicus diameter 7.1 mm, protoconch whorls $1^{5}/_{8}$, whorls $9^{1}/_{8}$.

Diagnosis. Protoconch with elongated granules. Umbilicus suddenly narrowed from penultimate whorl, more than $^{1}/_{3}$ maximum diameter, through which proto-

conch is visible. Beneath carina a chestnut band present. Mucous glands four. Proximal 1/2 of penis with ~ 5 thin internal pilasters, two of them fusing into a Y-shaped fork at middle part. Distal region of penis with tongue-shaped papillae. Vagina between atrium and dart sac not elongated. Proximal accessory sacs two, symmetrical, each with a pore leading to dart chamber.

Description of shell. Sinistral, depressed, somewhat solid. Shell with 9–9$^{5}/_{8}$ fairly flat whorls. Suture impressed. Protoconch 1$^{1}/_{2}$–1$^{5}/_{8}$ whorls, with fine granules (each ~ 20 μm long) almost invisible because of weathering or erosion. Growth lines thick or rib-like above but fine below carina. Above periphery a whitish carina present. Aperture oblique, peach-shaped, descending. On ring-like thickening within aperture, a very blunt tooth present near columella. Peristome almost not expanded, just minutely reflexed at lower part. Columella oblique. Umbilicus brownish, more than 1/3 of maximum diameter, suddenly narrowed from penultimate whorl. Protoconch visible through umbilicus. Whorls apically yellowish brown with intermittent darker brown patches. In umbilical view shell yellowish white with several brownish patches, and just beneath carina a thick chestnut band present.

General anatomy. Eversible head wart weakly present. At mantle edge leaf-shaped appendage absent. On internal body wall of head region between ommatophorous insertions with neither glands nor tiny pits. Body greyish brown, central dorsum with pale longitudinal stripes. Sole dirty white. Jaw arcuate, with ~ 8 more or less projecting ribs.

Anatomy of genital organs. Penial sheath short but well developed. Penis distally expanded, externally simple. Inside penis, proximal 1/2 with ~ 5 internal pilasters, two of which fuse into one Y-shaped fork at middle of penis; distal 1/2 with tongue-shaped (HBUMM05553b) or diamond-shaped papillae (HBUMM08428) that are erect or inclined towards atrium. Fine pilasters on distal end of penis merging into ~ 6 more or less thick short folds. Epiphallic papilla absent. Vas deferens narrow throughout. Vagina between atrium and dart sac not elongated. Accessory sac tiny, internally solid, inserting into dart sac medially, opening to dart chamber. Mucous glands four, each a single tube or simply branched. Proximal accessory sacs two, symmetrical, dorsally separated and ventrally touching each other, each with a ventral pore leading to proximal dart chamber. Love dart ~ 7 mm long, apically 2-bladed or rhombic (HBUMM08428-spec.1) then rounded. Bursa copulatrix duct equally narrow.

Etymology. This new species is named in honor of Prof Chen, De-Niu, who works on land mollusks in the Institute of Zoology, Chinese Academy of Sciences, Beijing.

Ecology. This species is found on exposed slate rocks of the hill side.

Distribution. Only known from the type locality.

Remarks. The new species is conchologically close to *L. zhengpingliui* Wu, sp. nov., but the new species has a much more depressed spire and relatively much larger aperture. In the genitalia, the middle part of penis, i.e., the distal 1/2 of the penis of the new species is occupied with regular tongue/diamond-shaped papillae (Fig. 44F, H), while in *L. zhengpingliui* Wu, sp. nov., the middle part is clearly short (only ~ 1/6 of the penis length) and does not have such tongue/diamond-shaped papillae (Fig. 44D).

***Laeocathaica qingchuanensis* Wu, sp. nov.**
https://zoobank.org/771F6786-2918-4B14-8591-1614D3C2699C
Figs 2A, C, 37C, 40, 44E, 45E, F, 49E, 50B, Tables 1, 2
[青川射带蜗牛]

Type material. ***Holotype*** HBUMM01179a-spec.1, fma, Dagou [大沟] Nature Reserve, Qingchuan County [青川县], Guangyuan, Sichuan Province; limestone and slate, hill foot along stream, from point A (837 m a.s.l., 32.594°N, 105.230638°E) to point B (941 m a.s.l., 32.600888°N, 105.217806°E); 2003-VII-13; coll. Wu, M. ***Paratypes*** HBUMM01179a-spec. 2–12, 6 fma (1 protoconch lost) and 5 juvs, 3 fma dissected (anatomy no. sp5); same data as holotype. HBUMM03001, 2 fma and 8 juvs, not measured and not dissected; same coll. data as holotype. HBUMM08195, 1 dissected, Qingchuan, Guangyuan, Sichuan Province, 490 m (SC-QC-040), 32.525556°N, 105.591472°E; near roots of grasses and on rocks, treeless; 2017-VIII-6, coll. Sheng, X.-F. etc.; DNA voucher HBUMM08195a. HBUMM08196, 6 fma and 3 fms,coll. data as HBUMM08195; DNA voucher HBUMM08196a. HBUMM08200, 12 fma and 1 subadult, not dissected, not measured; Qingchuan, Guangyuan, Sichuan Province, 511 m (SC-GY-043), 32.238889°N, 106.08525°E; on rocks and grass leaves, very thin litter layer; 2017-VIII-6, coll. Sheng, X.-F. etc.

Measurement of holotype. Shell height 10.8 mm, maximum diameter 21.7 mm, aperture height 6.1 mm, aperture breadth 9.2 mm, umbilicus diameter 5.1 mm, protoconch whorls $1^{1}/_{2}$, whorls $6^{1}/_{4}$.

Diagnosis. Protoconch with fine granules. Umbilicus moderately broad, through which protoconch is visible. Bluntly carinate slightly above periphery. Beneath carina a brown band present. Mucous glands 6–8. Approximately 1/2 of penis with three proximal thick internal pilasters, Y-shaped fork formed by adjacent pilasters absent. Vagina between atrium and dart sac moderately elongated. Proximal accessory sacs two, dorsally separated and ventrally touching, each with a pore leading to dart sac chamber near entrance of dart chamber.

Description of shell. Sinistral, depressed, thin but somewhat solid. Shell with $6^{1}/_{8}$–7 slightly convex whorls. Suture impressed. Protoconch $1^{1}/_{2}$–$1^{5}/_{8}$ whorls, fine granules (each ~ 30 – ~ 50 μm long) distinctly present. Growth lines fine and unclear. Aperture oblique, peach-shaped, descending. Within aperture with a white thickening. Peristome expanded and reflexed at lower part. Columella oblique. Umbilicus moderately broad, ~ $^{1}/_{4}$ of maximum diameter. Protoconch visible through umbilicus. Shell apically in pale brown with some intermittent darker patches. Carina slightly above periphery, blunt, white; beneath which a brown band present. Whorls apically in yellowish white with intermittent brownish patches. In umbilical view shell yellowish white with several white radial striations.

General anatomy. Eversible head wart lowly present. At mantle edge leaf-shaped appendage absent. On internal body wall of head region between ommatophorous insertions with neither glands nor tiny pits. Body greyish brown, central dorsum with pale longitudinal stripes. Sole dirty white. Jaw arcuate, with 4–6 projecting ribs.

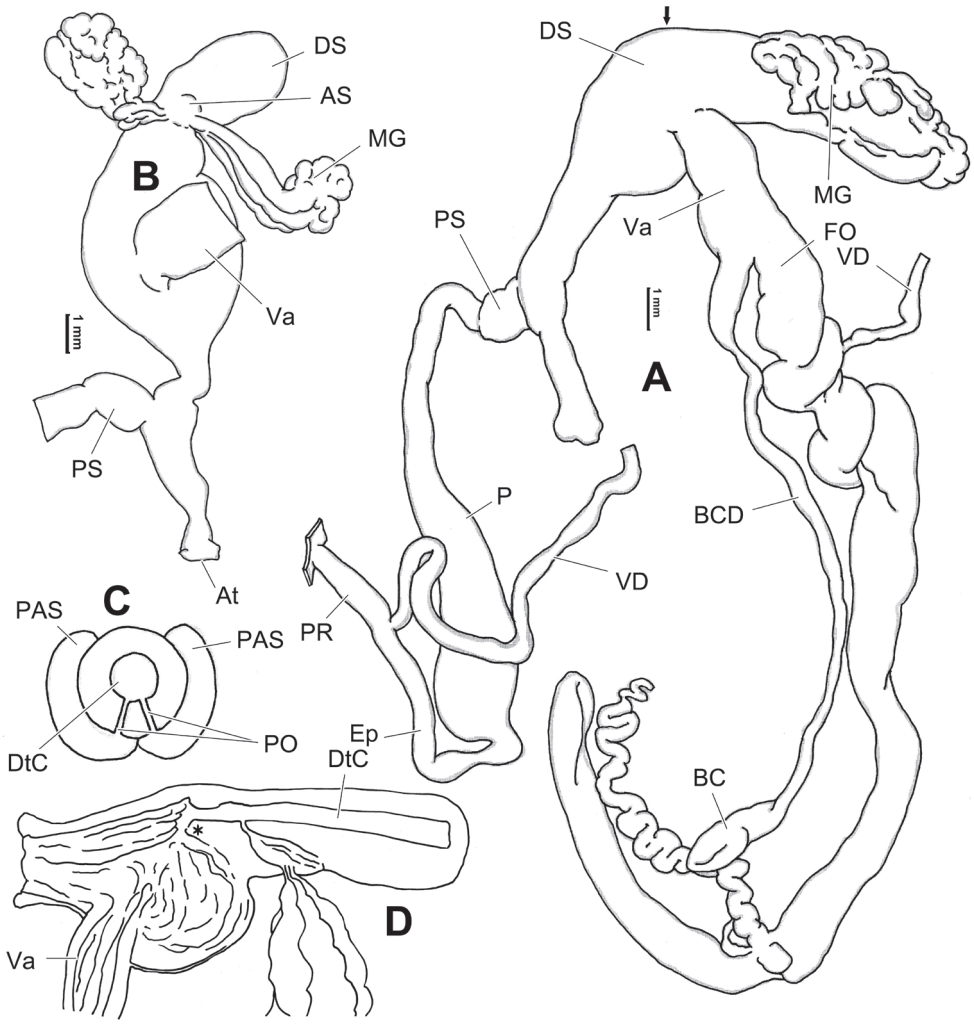

Figure 40. Genital anatomy of *Laeocathaica qingchuanensis* Wu, sp. nov., HBUMM01179a-spec.1, holotype **A** general view **B** ventral view of dart apparatus **C** cross-section of dart sac at the position arrowed in (**A**) **D** right view of dart sac apparatus. Abbreviations: AS – accessory sac; At – atrium; BC – bursa copulatrix; BCD – bursa copulatrix duct; DS – dart sac; DtC – a chamber containing love dart; Ep – epiphallus; FO – free oviduct; MG – mucous glands; P – penis; PAS – proximal accessory sac; PO – opening of proximal accessory sac leading to dart chamber; PR – penial retractor muscle; PS – penial sheath; Va – vagina; VD – vas deferens. Asterisk * indicates the opening of proximal accessory sac.

Anatomy of genital organs. Penial sheath short. Penis distally swollen, externally simple. Proximal 1/2 penis with four thick internal pilasters which do not fusing, pilasters then branching into numerous fine pilasters that merge into ~ 6 short but thick (thickest in the genus) folds near opening of epiphallus. Vas deferens narrow throughout. Vagina between atrium and dart sac moderately elongated. Accessory sac

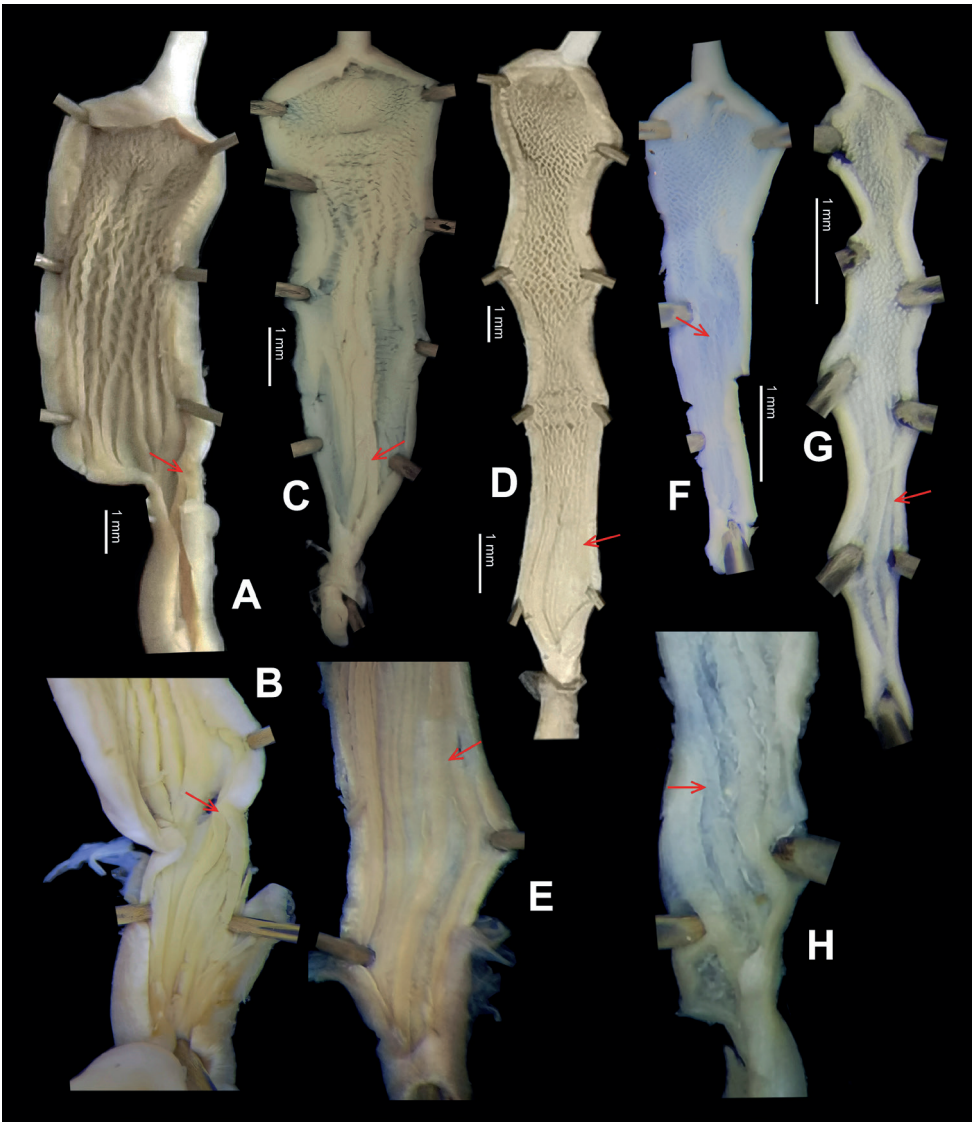

Figure 41. Internal view of penis **A, B** *Laeocathaica amdoana* Möllendorff, 1899, HBUMM05640-spec.1 **A** general view **B** proximal penis **C** *L. filippina* (Heude, 1882), HBUMM04166-spec.1, general view **D, E** *L. distinguenda* Möllendorff, 1899, HBUMM05436-spec.1 **D** general view **E** proximal penis **F** *L. carinalis* Chen & Zhang, 2004, HBUMM08300-spec.1, general view **G, H** *L. dityla* Möllendorff, 1899, HBUMM00698-spec.1 **G** general view **H** proximal penis. Arrows indicate the position where two penial internal pilasters fuse into one distal pilaster.

spherical, internally with high pilasters and fairly solid inside, inserting into dart sac medially, opening to distal dart chamber. Mucous glands 6–8, each single tube or simply branched. PAS two, dorsally separated and ventrally touching, each with a pore

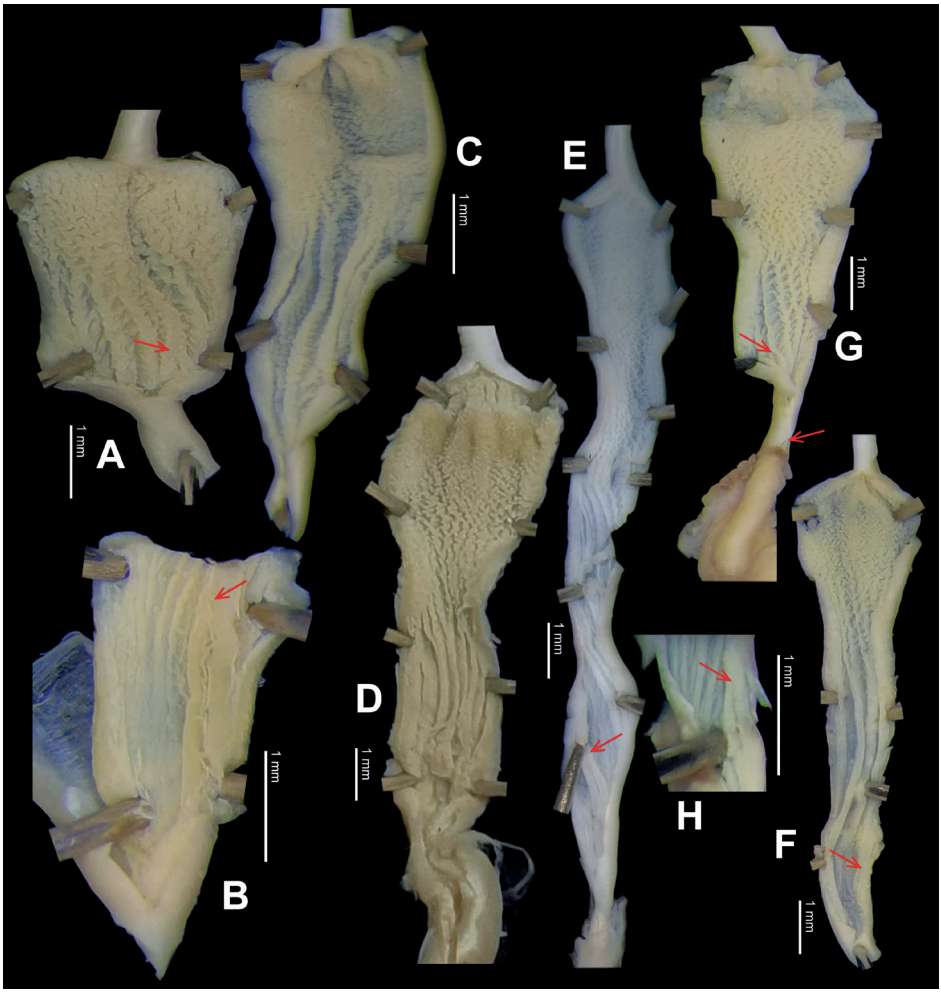

Figure 42. Internal view of penis **A, B** *Laeocathaica dolani* (Pilsbry, 1934), HBUMM00069-spec.1 **A** general view **B** proximal penis **C** *L. christinae* (H. Adams, 1870), HBUMM01251a-spec.1, general view **D** *L. phaeomphala* Möllendorff, 1899, HBUMM05433-spec.1 **E** *L. odophora* Möllendorff, 1899, HBUMM08430-spec.1 **F** *L. pewzowi* Möllendorff, 1899, ZIN RAS No. 4, "*Aegista pewzowi* Schalf." **G, H** *L. parapolytyla* Wu, sp. nov., HBUMM06640-spec.1, holotype **G** general view **H** proximal part. Arrows indicate the position where two penial internal pilasters fuse into one distal pilaster.

leading to dart chamber near dart chamber opening. Proximal bursa copulatrix duct slightly expanded. Bursa copulatrix elongate ovate.

Etymology. This new species is named after name of the type locality Qingchuan, Sichuan Province.

Ecology. This species is found on slate rocks covered with mosses in a humid mountainous environment.

Distribution. Only known from the type locality.

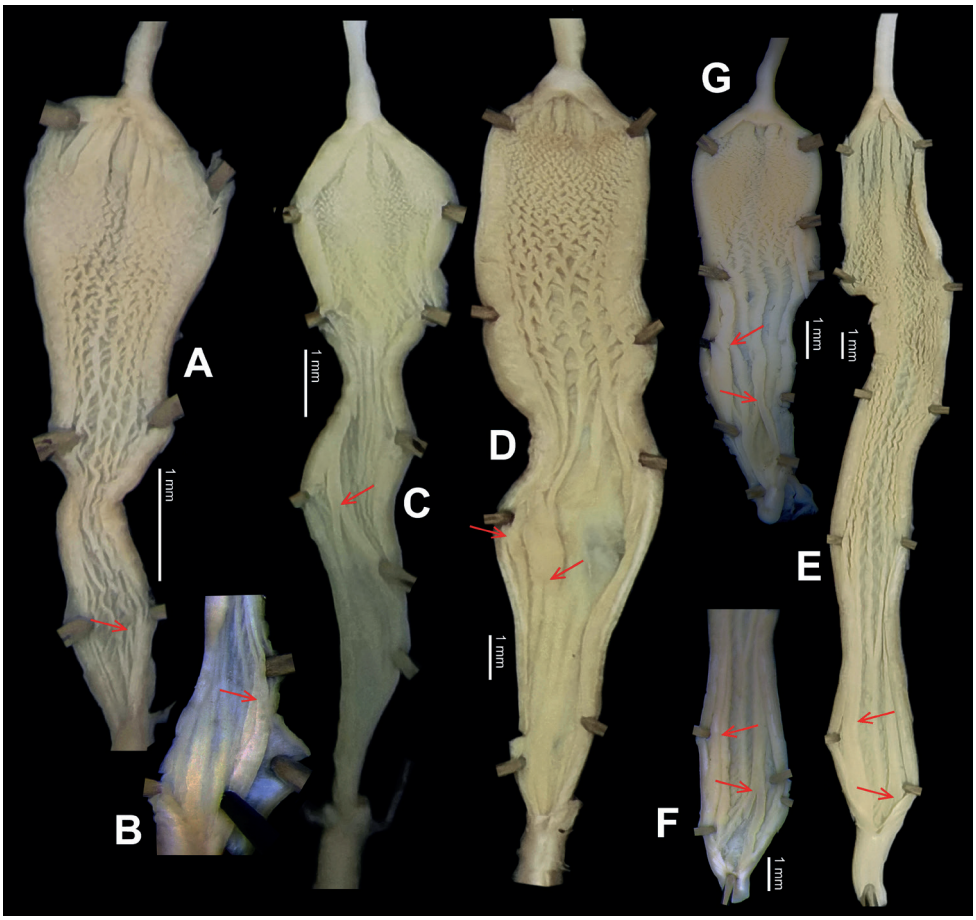

Figure 43. Internal view of penis **A, B** *Laeocathaica polytyla* Möllendorff, 1899, HBUMM05437-spec.1 **A** general view **B** proximal penis **C** *L. potanini* Möllendorff, 1899, HBUMM00633-spec.1, general view **D** *L. prionotropis* Möllendorff, 1899, HBUMM05549-spec.1, general view **E, F** *L. stenochone* Möllendorff, 1899, HBUMM05495-spec.1 **E** general view **F** proximal penis **G** *L. carinifera* (H. Adams, 1870), HBUMM08443-spec.2, general view. Arrows indicate the position where two penial internal pilasters fuse into one distal pilaster.

Remarks. *Laeocathaica qingchuanensis* Wu, sp. nov. is close to *L. stenochone* and *L. carinifera* in general shell shape, aperture shape and coloration, but the new species has a relatively higher shell (Fig. 50B) and the slimmest protoconch granules (Fig. 45E). The new species differs from *Laeocathaica stenochone* and *L. carinifera* in that it has both a long vaginal section above the dart sac and the inner structures of penis, where proximal parallel penial pilasters do not form the Y-shaped fork (Fig. 44E). In addition, compared to *Laeocathaica carinifera* (Fig. 10), the new species has a very short penial sheath and a pair of symmetrical proximal accessory sac (Fig. 40). Among the aforementioned three species, *Laeocathaica stenochone* has a relatively longer penis.

Table 3. Voucher information and the GenBank accession numbers of the species in the phylogenetic study. An asterisk (*) indicates obtained from NCBI. The generic assignment for species follows MolluscaBase (2021a–p; 2022a–c).

Taxa	GenBank accession numbers 16S/ITS2	Museum voucher	Voucher information
***Acusta* E. von Martens, 1860**			
Acusta sieboldiana (L. Pfeiffer, 1850)	ON261686/ON261774	HBUMM04882_2	Fukuoka, Japan; coll. Guo, J.-Y. [郭建英], 2004-X-12
	ON261687/ON261775	HBUMM04882_3	
Acusta rhodostoma (Möllendorff, 1884)	ON261688/ON261776	HBUMM05089c2	Haikou, Hainan; coll. Wu, M., 2005-VIII-15
	ON261689/ON261777	HBUMM05089c4	
***Aegista* Albers, 1850**			
Aegista chinensis (Philippi, 1845)	ON261690/ON261778	HBUMM06480	Zhenjiang, Jiangsu; coll. Wu, M., Xu, Q., 2011-VI-12
***Bradybaena* H. Beck, 1837**			
Bradybaena brevispira (H. Adams, 1870)	ON261691/ON261779	HBUMM05104_2	Zhongxian, Chongqing; coll. Wu, M., 2004-VII-16
	ON261692/ON261780	HBUMM05122_2	Fengjie, Chongqing; coll. Wu, M., 2004-VII-18
	ON261693/ON261781	HBUMM05122_3	
	ON261694/ON261782	HBUMM05112_2	Guangan [广安], Sichuan; coll. Wu, M.
Bradybaena controversa monotaeniata Pilsbry, 1934	ON261695/ON261783	HBUMM01031_2	Maoxian, Sichuan; coll. Wu, M., 2001-X-11
	ON261696/ON261784	HBUMM01031_3	
Bradybaena eris pachychila (Möllendorff, 1899)	ON261697/ON261785	HBUMM05493_3	Wenxian, Gansu; coll. Wu, M., 2006-IX-28
Bradybaena qixiaensis Wu & Asami, 2017	MW810081*/ON261787	HBUMM06900_1/ HBUMM06900_2	Qixiashan [栖霞山], Jiangsu; coll. Wu, M.
Bradybaena similaris (Rang, 1831)	HQ245444*/AY014138*	/	Koehler, unpublished data; Wade et al. 2001
Bradybaena strictotaenia (Möllendorff, 1899)	ON261701/ON261790	HBUMM05406_2	Wenxian, Gansu; coll. Wu, M., 2006-IX-27
	ON261702/ON261791	HBUMM05406_3	
	ON261699/ON261788	HBUMM05446_2	Wenxian, Gansu; coll. Wu, M., 2006-IX-27
	ON261700/ON261789	HBUMM05446_3	
Bradybaena sueshanensis Pilsbry, 1934	ON261703/ON261792	HBUMM06603	Jiuzhaigouxian, Sichuan; coll. Wu, M., 2011-VIII-11
Bradybaena twenhuaensis (Ping & Yen, 1932)	ON261704/ON261793	HBUMM08276a1	Changbaishan [长白山], Jilin; coll. Shen, X.-F., 2018-VIII-18
	ON261705/ON261794	HBUMM08276a2	
***Buliminidius* Heude, 1890**			
Buliminidius achatininus (Möllendorff, 1899)	ON261758/ON261848	HBUMM06678	Wenxian, Gansu; coll. Wu, M., 2011-VIII-9
Buliminidius hirsutus (Möllendorff, 1899)	ON261759/ON261849	HBUMM06676	Wenxian, Gansu; coll. Wu, M., 2011-VIII-9
***Camaenella* Pilsbry, 1893**			
Camaenella platyodon (L. Pfeiffer, 1846)	ON261706/ON261795	HBUMM05089a_2	Haikou [海口], Hainan; coll. Wu, M., 2005-VIII-15
	ON261707/ON261796	HBUMM05089a_3	
	ON261708/ON261797	HBUMM05089a_4	
***Cathaica* Möllendorff, 1884**			
Cathaica ottoi Pilsbry, 1934	ON261709/ON261798	HBUMM08358a1	Wenchuanxian, Sichuan; coll., Liu, Z.-P., 2019-VII-5
	ON261710/ON261799	HBUMM08358a3	
Cathaica fasciola (Draparnaud, 1801)	ON261711/ON261800	HBUMM05168_1	Haidian [海淀], Beijing; coll. Wu, M., 2006-VII
	ON261712/ON261801	HBUMM05368_3	Qingdao [青岛], Shandong; coll. Wu, M., 2006-X-17
Cathaica gansuica Möllendorff, 1899	ON261714/ON261803	HBUMM05602cb	Wudu, Gansu; coll. Liu, J.-M. and Zheng, W., 2006-IX-30
	ON261713/ON261802	HBUMM05655	Dangchang, Gansu; coll. Liu, J.-M. and Zheng, W., 2006-X-2
Cathaica ochthephiloides Möllendorff, 1899	ON261715/ON261804	HBUMM06560	Jiuzhaigouxian, Sichuan; coll. Wu, M., 2011-VIII-14
Cathaica pulveratricula (Martens, 1882)	ON261716/ON261805	HBUMM08208a	Dingxi, Gansu; coll. Shen, X.-F., 2017-VIII-4
***Karaftohelix* Pilsbry, 1927**			
Karaftohelix middendorffi (Gerstfeldt, 1859)	ON261698/ON261786	HBUMM05933	forest between Vladivostok and Artion cities, Russia; coll. Sayenko, E.M., 2005-VI-26

Taxa	GenBank accession numbers 16S/ITS2	Museum voucher	Voucher information
***Helix* Linnaeus, 1758**			
Helix pomatia Linnaeus, 1758	KR705016*/ KR705093*	/	Europe
***Laeocathaica* Möllendorff, 1899**			
Laeocathaica amdoana Möllendorff, 1899	ON261746/ON261835	HBUMM08432a1	See in the text
	ON261741/ON261830	HBUMM08432a2	
Laeocathaica carinifera (H. Adams, 1870)	ON261718/ON261807	HBUMM05103_2	See in the text
	ON261719/ON261808	HBUMM05103_3	
	ON261720/ON261809	HBUMM05131_2	See in the text
	ON261721/ON261810	HBUMM05131_3	
Laeocathaica cheni Wu, sp. nov.	ON261727/ON261816	HBUMM08368a	See in the text
	ON261728/ON261817	HBUMM08368a3	
	ON261729/ON261818	HBUMM08368a4	
	ON261751/ON261840	HBUMM08428a2	See in the text
	ON261737/ON261826	HBUMM08428a4	
Laeocathaica distinguenda Möllendorff, 1899	ON261717/ON261806	HBUMM05407_3	See in the text
Laeocathaica filippina (Heude, 1882)	ON261730/ON261819	HBUMM01256b_2	See in the text
	ON261731/ON261820	HBUMM01256b_3	
	ON261732/ON261821	HBUMM05097_2	See in the text
Laeocathaica odophora Möllendorff, 1899	ON261736/ON261825	HBUMM08430a1	See in the text
Laeocathaica phaeomphala Möllendorff, 1899	ON261742/ON261831	HBUMM08424a2	See in the text
Laeocathaica polytyla Möllendorff, 1899	ON261722/ON261811	HBUMM05411_4	See in the text
Laeocathaica potanini Möllendorff, 1899	ON261723/ON261812	HBUMM05409_2	See in the text
	ON261724/ON261813	HBUMM05409_3	
	ON261725/ON261814	HBUMM05409_4	
Laeocathaica prionotropis Möllendorff, 1899	ON261726/ON261815	HBUMM05440_3	See in the text
	ON261744/ON261833	HBUMM08421a1	See in the text
	ON261749/ON261838	HBUMM08421a3	
	ON261748/ON261837	HBUMM08421a4	
	ON261739/ON261828	HBUMM08423a1	See in the text
	ON261747/ON261836	HBUMM08423a2	
Laeocathaica qiminglii Wu, sp. nov.	ON261740/ON261829	HBUMM08422a1	See in the text
Laeocathaica stenochone Möllendorff, 1899	ON261743/ON261832	HBUMM08431a1	See in the text
	ON261738/ON261827	HBUMM08431a2	
	ON261750/ON261839	HBUMM08431a3	
Laeocathaica tropidorhaphe Möllendorff, 1899	ON261733/ON261822	HBUMM05688	See in the text
	ON261735/ON261824	HBUMM05617	See in the text
	ON261734/ON261823	HBUMM05716	See in the text
	ON261745/ON261834	HBUMM08425a1	See in the text
***Metodontia* Möllendorff, 1886**			
Metodontia houaiensis (Crosse, 1882)	ON261752/ON261841	HBUMM05164_2	Quyang [曲阳], Hebei; coll. Wu, M., Wu, Q., 2006-V-4
	ON261753/ON261842	HBUMM05164_3	
	ON261754/ON261843	HBUMM05164_4	
***Nesiohelix* Kuroda & Emura, 1943**			
Nesiohelix moreletiana (Heude, 1882)	MW810080*/ON261844	HBUMM06796	Hangzhou [杭州], Zhejiang; coll. Wu, M., Xu, Q., 2012-V-21
***Plectotropis* E. von Martens, 1860**			
Plectotropis sterilis (Heude, 1890)	ON261755/ON261845	HBUMM04909_2	Badong, Hubei; coll. Wu, M., Wu, Q., Qi, G., 2004-VII-31
	ON261756/ON261846	HBUMM04909_3	
***Pseudiberus* Ancey, 1887**			
Pseudiberus strophostoma (Möllendorff, 1899)	ON261757/ON261847	HBUMM06586b	Jiuzhaigouxian, Sichuan; coll. Wu, M., 2011-VIII-14
***Pseudobuliminus* Gredler, 1886**			
Pseudobuliminus piligerus (Möllendorff, 1899)	ON261760/ON261850	HBUMM05412_2	Wenxian, Gansu; coll. Wu, M., 2006-IX-27
Pseudobuliminus subcylindricus (Möllendorff, 1899)	ON261761/ON261851	HBUMM06720	Jiuzhaigouxian, Sichuan; coll. Wu, M., 2011-VIII-12

Taxa	GenBank accession numbers 16S/ITS2	Museum voucher	Voucher information
***Satsuma* A. Adams, 1868**			
Satsuma guandi Zhang, Zhu & Lyu, 2020	MW804648*/ON261852	HBUMM08239a_1	Shaoguan [韶关], Guangdong; coll. Yu, Di [余迪]
	MW804647*/ON261853	HBUMM08239a_2	
***Stilpnodiscus* Möllendorff, 1899**			
Stilpnodiscus entochilus Möllendorff, 1899	ON261762/ON261854	HBUMM05451	Wenxian, Gansu; coll. Wu, M., 2006-IX-27
Stilpnodiscus moellendorffi Wu, 2001	ON261763/ON261855	HBUMM05439_2	Wenxian, Gansu; coll. Wu, M., 2006-IX-27
Stilpnodiscus sp.	ON261764/ON261856	HBUMM05491c_2	Wenxian, Gansu; coll. Wu, M., 2006-IX-28
Stilpnodiscus vernicinus Möllendorff, 1899	ON261765/ON261857	HBUMM05528	Wenxian, Gansu; coll. Wu, M., 2006-IX-29
***Traumatophora* Ancey, 1887**			
Traumatophora triscalpta (E. von Martens, 1875)	ON261766/ON261858	HBUMM08302a	Wuhan, Hubei; coll. Chen, Zhe-Yu [陈哲宇], 2019-III-20
***Trichobradybaena* Wu & Guo, 2003**			
Trichobradybaena submissa (Deshayes, 1874)	ON261767/ON261859	HBUMM01221_3	Meitan, Guizhou; coll. Wu, M., 2003-VIII-2
	ON261768/ON261860	HBUMM04904_2	Badong, Hubei; coll. Wu, M., 2004-VIII
	ON261769/ON261861	HBUMM04904_3	
	ON261770/ON261862	HBUMM05095_2	Zigui, Hubei; coll. Wu, M., 2004-VIII-2
	ON261771/ON261863	HBUMM05095_3	
	ON261772/ON261864	HBUMM05123_2	Fengjie, Chongqing; coll. Wu, M., 2004-VII-18
	ON261773/ON261865	HBUMM05132_2	Wuxi, Chongqing; coll. Wu, M., 2004-VII-22

Laeocathaica nordsiecki Wu, sp. nov.

https://zoobank.org/BBBD09C3-661E-4E70-AA52-59A2B8E818A3
Figs 2A, B, 37D, 47E, F, 49C; Table 2
[诺氏射带蜗牛]

Type material. ***Holotype*** HBUMM08446-spec.1, fully mature shell with immature genital system, Guoyuanxiang [郭元乡], Jiuzhaigouxian, Sichuan Province; near point (33.125506°N, 104.329876°E); 2021-IX-24, coll. Chen, Z.-G. ***Paratypes*** HBUMM08446-spec.2–3, 2 fms; HBUMM08446-spec.4–5, 2 subadults; same data of holotype. HBUMM08447-spec.1–2, 2 fms and 3 living juvs (in rearing), Qinglongcun [青龙村], Guoyuanxiang, Jiuzhaigouxian, Sichuan Province; (33.085615°N, 104.348250°E); 2020-VII, coll. Chen, Z.-G.

Measurement of holotype. Shell height 3.7 mm, maximum diameter 10.8 mm, aperture height 3.0 mm, aperture breadth 3.3 mm, umbilicus diameter 5.0 mm, protoconch whorls $1^1/_2$, whorls $5^1/_8$.

Diagnosis. Protoconch with dense fine granules. Umbilicus very broad, ~ $^1/_2$ of maximum diameter. Body whorl shouldered above periphery. On shoulder with a white band. Peristome continuous. Shell strongly glossy as in *Stilpnodiscus*, almost transparent.

Description of shell. Sinistral, depressed, thin but somewhat solid. Shell with $5–5^1/_8$ convex whorls. Suture impressed. Protoconch $1^1/_2–1^5/_8$ whorls, densely with tiny granules (each ~ 10 μm long) which are obscured by erosion or weathering. Growth lines indistinct. Shell in pale brown, strongly glossy, almost transparent. Body whorl shouldered above periphery, with a white band on shoulder. Aperture oblique, round, abruptly descending in front. A white thickening within aperture and thickened callus

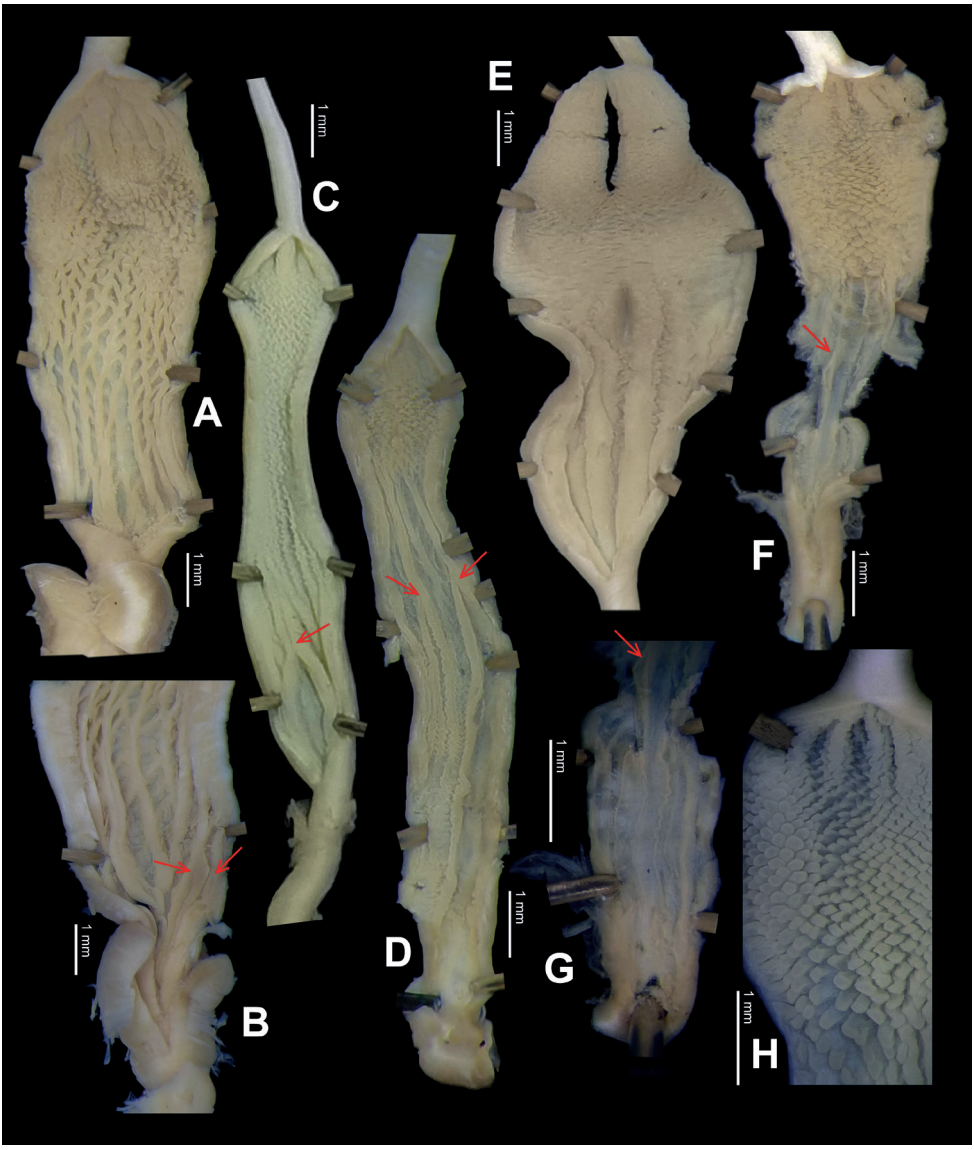

Figure 44. Internal view of penis **A, B** *Laeocathaica tropidorhaphe* Möllendorff, 1899 **A** general view, HBUMM05619-spec.1 **B** proximal penis, HBUMM05664-spec.1 **C** *L. qishilii* Wu, sp. nov., general view, HBUMM08298-spec.1, holotype **D** *L. zhengpingliui* Wu, sp. nov., general view, HBUMM05553-spec.1, holotype **E** *L. qingchuanensis* Wu, sp. nov., general view, HBUMM01179-spec.1, holotype **F–H** *L. cheni* Wu, sp. nov. **F, G** HBUMM05553b-spec.1, holotype **F** general view **G** proximal penis **H** HBUMM08428-spec.1, paratype, partial internal view of distal penis. Arrows indicate the position where two penial internal pilasters fuse into one distal pilaster.

forming a continuous peristome. Peristome expanded and slightly reflexed at lower part. Columella oblique. Umbilicus very broad, ~ $^{1}/_{2}$ of maximum diameter. Protoconch visible through umbilicus.

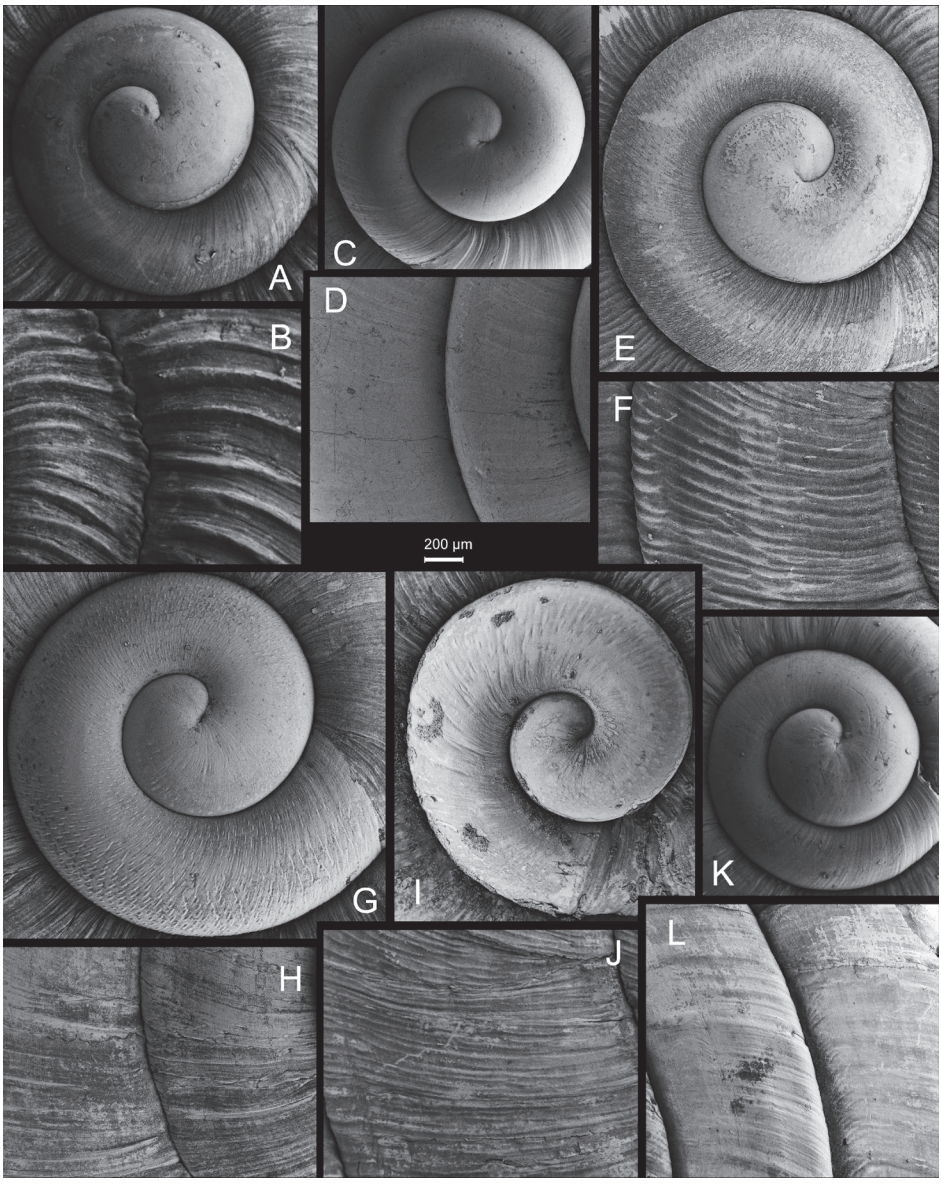

Figure 45. SEM micrographs **A, B** *Laeocathaica potanini* Möllendorff, 1899, HBUMM00633 **A** protoconch **B** teleoconch **C, D** *L. dityla* Möllendorff, 1899, HBUMM00698 **C** protoconch **D** teleoconch **E, F** *L. qingchuanensis* Wu, sp. nov., HBUMM01179a-spec.6, paratype **E** protoconch **F** teleoconch **G, H** *L. christinae* (H. Adams, 1870), HBUMM01251a **G** protoconch **H** teleoconch **I, J** *L. carinifera* (H. Adams, 1870), HBUMM04162 **I** protoconch **J** teleoconch **K, L** *L. polytyla* Möllendorff, 1899, HBUMM05437 **K** protoconch **L** teleoconch.

Etymology. This cute new species is named in memory of Hartmut Nordsieck, a German malacologist who showed strong interest in the snails of the South Gansu Plateau and was a good friend of the first author.

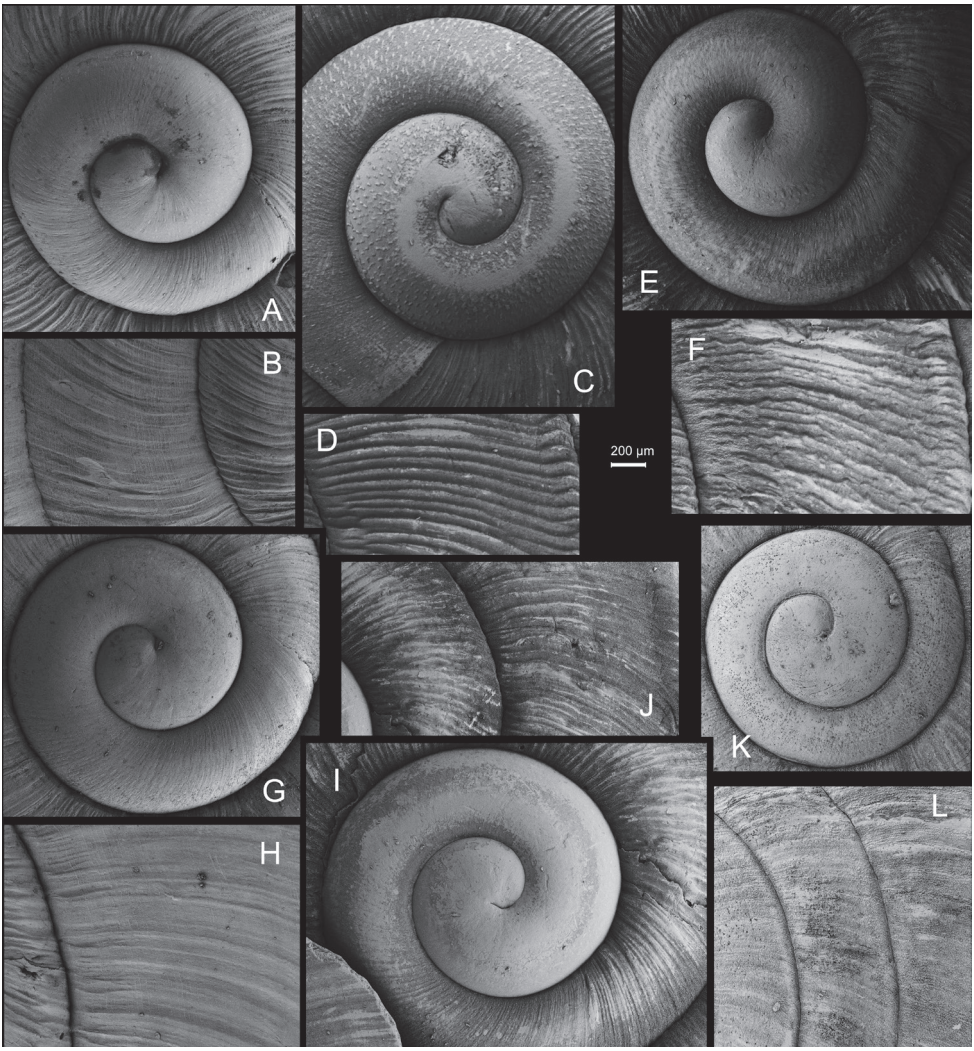

Figure 46. SEM micrographs **A, B** *Laeocathaica distinguenda* Möllendorff, 1899, HBUMM05479 **A** protoconch **B** teleoconch **C, D** *L. stenochone* Möllendorff, 1899, HBUMM05495 **C** protoconch **D** teleoconch **E, F** *L. prionotropis* Möllendorff, 1899, HBUMM05549 **E** protoconch **F** teleoconch **G, H** *L. amdoana* Möllendorff, 1899, HBUMM05640 **G** protoconch **H** teleoconch **I, J** *L. tropidorhaphe* Möllendorff, 1899, HBUMM05664 **I** protoconch **J** teleoconch **K, L** *L. cheni* Wu, sp. nov., HBUMM08368, paratype, juvenile **K** protoconch **L** teleoconch.

Ecology. This species was found on bare earth with a few broken rocks.

Distribution. Only known from two localities where the types were found.

Remarks. The new species is the smallest species in *Laeocathaica*, where it is provisionally placed due to its chirality, granules on the protoconch and the similarity of the shell to

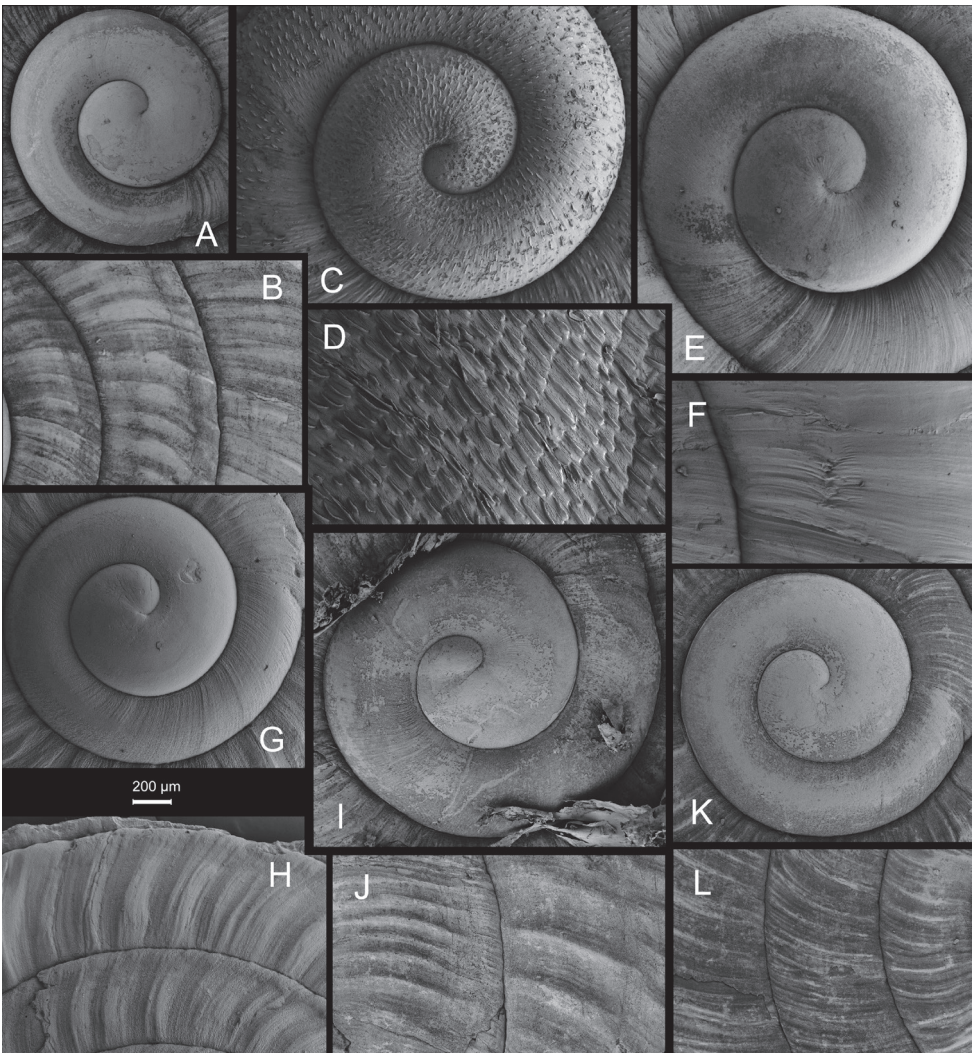

Figure 47. SEM micrographs **A, B** *Laeocathaica odophora* Möllendorff, 1899, HBUMM08430 **A** protoconch **B** teleoconch **C, D** *L. dolani* (Pilsbry, 1934), HBUMM08439 **C** protoconch **D** teleoconch **E, F** *L. nordsiecki* Wu, sp. nov., HBUMM08446, paratype, subadult **E** protoconch **F** teleoconch **G, H** *L. pewzowi* Möllendorff, 1899, HBUMM08452 **G** protoconch **H** teleoconch **I, J** *L. carinalis* Chen & Zhang, 2004, HBUMM08453 **I** protoconch **J** teleoconch **K, L** *L. zhengpingliui* Wu, sp. nov., HBUMM05553-spec.2, paratype, juvenile **K** protoconch **L** teleoconch.

that of *Laeocathaica dityla*. The very glossy shell also makes this species distinctive, reminiscent of the genus *Stilpnodiscus* Möllendorff, 1899, which appears in the phylogram (Fig. 51) as the sister group of all the *Laeocathaica* species. Undoubtedly, final generic assignment of this species will depend on further anatomical information and molecular studies.

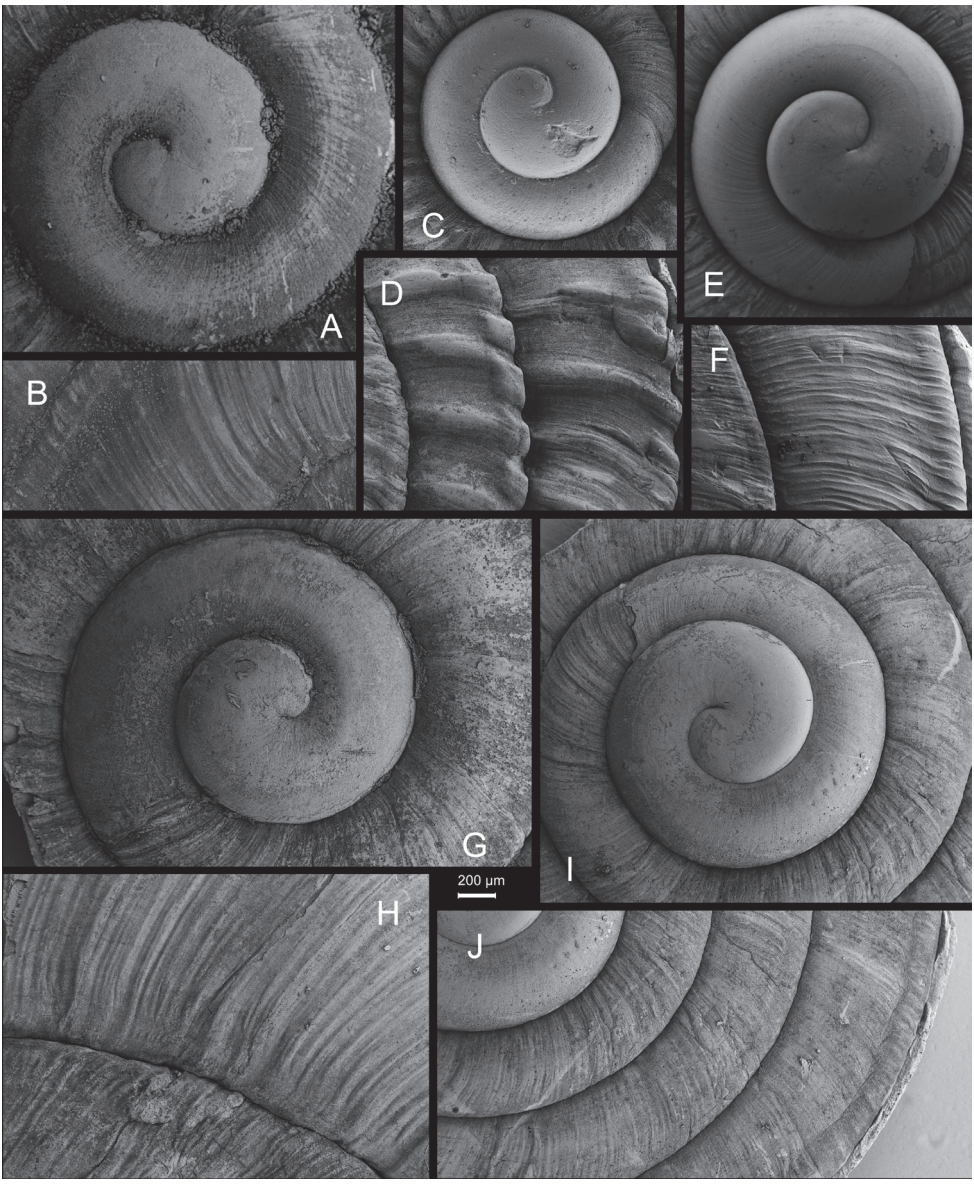

Figure 48. SEM micrographs **A, B** *Laeocathaica qishilii* Wu, sp. nov., HBUMM08298, paratype **A** protoconch **B** teleoconch **C, D** *L. qiminglii* Wu, sp. nov., HBUMM08448, paratype **C** protoconch **D** teleoconch **E, F** *L. phaeomphala* Möllendorff, 1899, CZG202008-w3, subadult **E** protoconch **F** teleoconch **G, H** *L. filippina* (Heude, 1882), HBUMM04166 **G** protoconch **H** teleoconch **I, J** *L. parapolytyla* Wu, sp. nov., HBUMM06640-spec.9, paratype **I** protoconch **J** teleoconch.

Phylogenetics

To investigate the systematic position of the putative *Laeocathaica* clade (because of the absence of type species of *Laeocathaica L. christinae*), 13 species of *Laeocathaica* and 33

Figure 49. Habitats (excluding **D**) **A, B** *Laeocathaica qishilii* Wu, sp. nov., border of Jiuzhaigou County and Wen County **C** *L. nordsiecki* Wu, sp. nov., Guoyuanxiang, Jiuzhaigou **D** *L. qiminglii* Wu, sp. nov., an indoor photograph **E** *L. qingchuanensis* Wu, sp. nov., Dagou Nature Reserve, Qingchuan County **F** *L. cheni* Wu, sp. nov., Hengdan, Wenxian.

species of another 16 camaenid genera, whether or not they bear a dart sac, are included in the analyses (Table 3). The final dataset contains sequences from 47 species including the outgroup *Helix pomatia*. Seventy-nine of the 94 original sequences have the unique combined sequence 16S + ITS2. The model "GTR+G+I" was selected as the best nucleotide substitution model for the combined dataset (lnL = –11126.1, BIC = 24124.9).

The phylograms produced by both Maximum Likelihood and Bayesian Inference based on partial 16S and partial ITS2 sequences are topologically identical in the major branches with the exception of different positions of two nodes (orange parts in Fig. 51). The phylogenetic trees are robust that their most nodes received strong support as showed by the high Bayesian posterior probability (BPP) and/or Maximum-likelihood bootstrap values (BP) (Fig. 51). The clades *Nesiohelix*, *Satsuma* and *Traumatophora* represent the most basal offshoot in the phylogenetic trees. In Fig. 51, those clades which include the type species of a genus are recognizable by lack of quotation marks around the generic name. So, the lineage separated under

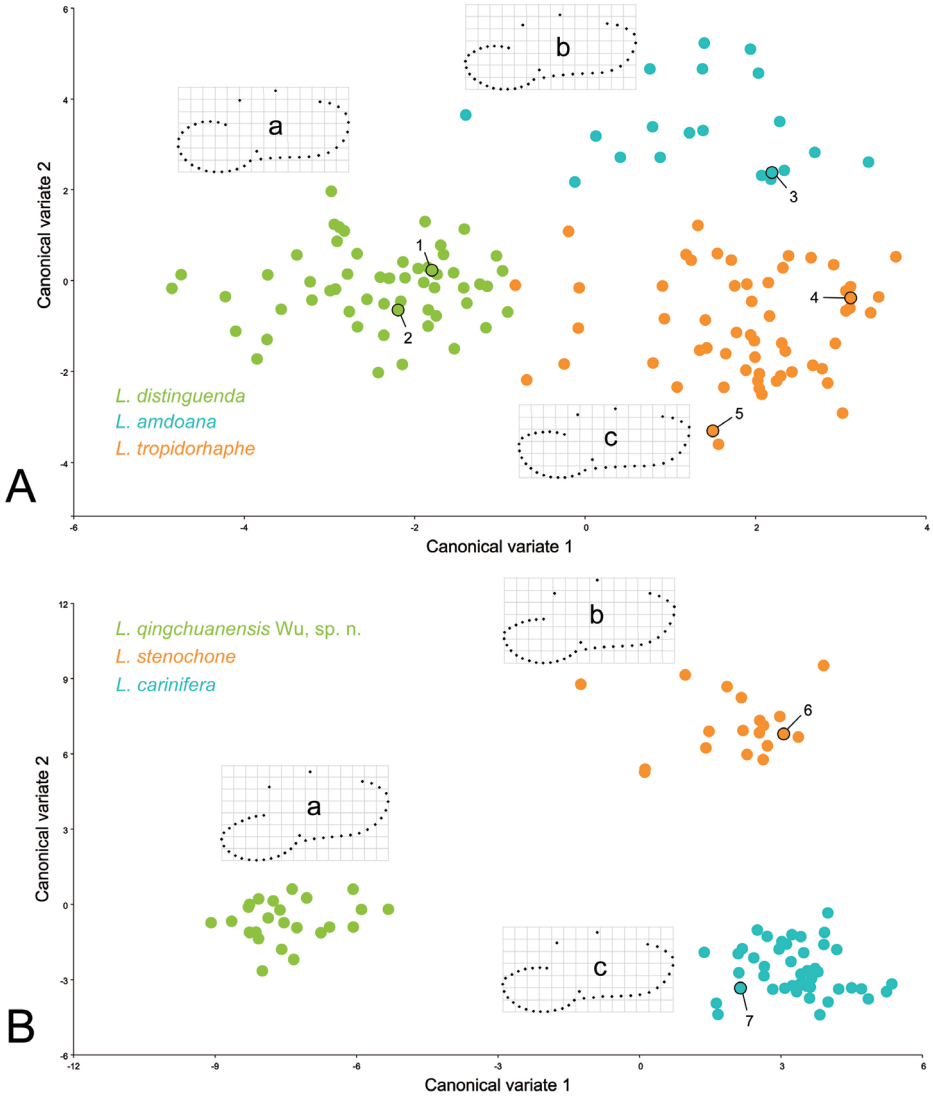

Figure 50. Scatter plots of canonical variate 1 against canonical variate 2 (Canonical Variate Analysis), showing the shell morphological relationships among **A** *Laeocathaica distinguenda* Möllendorff, 1899 (green dots; a, average shape), *L. amdoana* Möllendorff, 1899 (blue dots; b, average shape) and *L. tropidorhaphe* Möllendorff, 1899 (orange dots; c, average shape) **B** *L. qingchuanensis* Wu, sp. nov. (green dots; a, average shape), *L. stenochone* Möllendorff, 1899 (orange dots; b, average shape) and *L. carinifera* (H. Adams, 1870) (blue dots; c, average shape). Encircled dots: 1, SMF 8959, lectotype; 2, HBUMM05436-spec.1; 3, SMF 8952, lectotype; 4, SMF 9074, lectotype; 5, paratype of *L. dangchangensis* Chen & Zhang, 2004; 6, SMF 9071, lectotype; 7, syntype, NHMUK 1870.7.16.7. Data for 5 from fig. 7D, 6 and 7 from fig. 12 in Páll-Gergely et al. 2022.

Clade D for example contains a clade that includes *Helix similaris*, the type species of *Bradybaena*. Subsequently, species which cluster here, in fact constitute members of that genus, while those clustering elsewhere and are commonly affiliated to

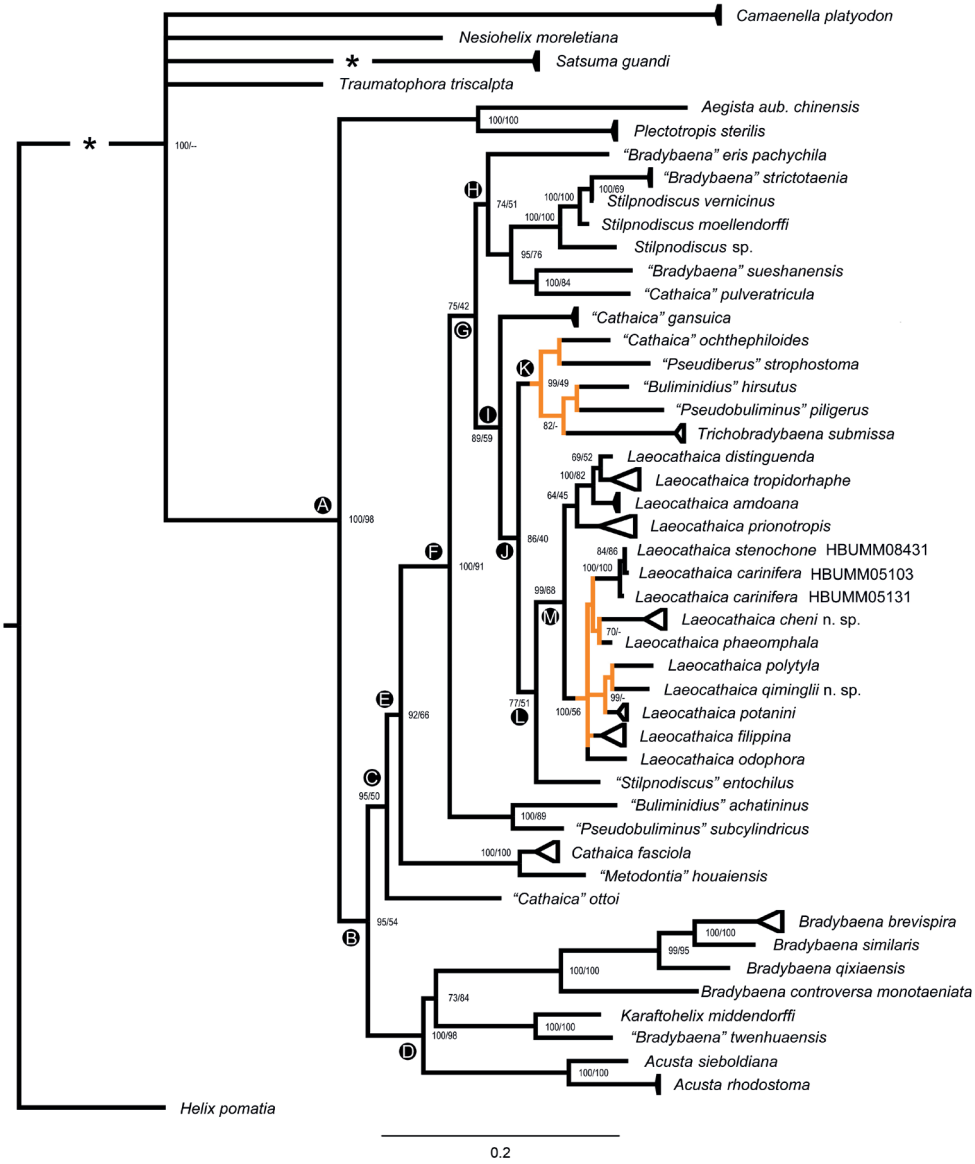

Figure 51. Bayesian phylogram of camaenid species (for detail see in Table 1) based on the concatenated partial mitochondrial 16S and partial ITS2 sequences. The tree is rooted with *Helix pomatia*. Numbers near nodes indicating Bayesian posterior probabilities and Maximum-likelihood bootstrap values are given as BPP/BP. Black or orange part shows the topology where the result yielded by using Bayesian-Inference method agrees with that by using Maximum-likelihood method or not, respectively. An asterisk indicates the branch is exactly one third shortened in length. Scale bar is for substitutions per site.

Bradybaena, have to be included in other genera by future studies. Although we did not sequence *Helix christinae*, the type species of *Laeocathaica*, our result shows a single clade supported by BPP/bootstrap value 99/68 that includes all species

considered belonging to this group. Thus, we hypothesize for the time being that this is the correct *Laeocathaica* clade.

The indigenous dart-sac-bearing camaenids aggregated in Central China, which are grouped into the genera "*Pseudobuliminus*", "*Buliminidius*", "*Bradybaena*", "*Cathaica*", "*Stilpnodiscus*", "*Pseudiberus*", and *Laeocathaica*, could form a strongly supported monophyletic Clade F (Fig. 51), in which the members of each of the first five genera cannot be grouped together and the branch "*Pseudiberus*" is not represented by the type species. The present phylogeny (Fig. 51) shows the following five points:

1. *Stilpnodiscus* is a polyphyletic group divided into two separated parts. The first is a monophyletic clade including "*Bradybaena*" *strictotaenia*, which is sister to the type species of *Stilpnodiscus*. The second is "*Stilpnodiscus*" *entochilus* Möllendorff, 1899 which is the sister group of all the *Laeocathaica* species examined here.
2. the monophyly of *Cathaica* Möllendorff, 1884 is rejected because "*Cathaica*" *pulveratricula* (Martens, 1882), "*Cathaica*" *ottoi* Pilsbry, 1934, *Cathaica fasciola* (Draparnaud, 1801) and "*Cathaica*" *gansuica* (Möllendorff, 1899) occur on different branches on the tree (Fig. 51) and these species can constitute independent evolutionary units.
3. *Bradybaena controversa monotaeniata* Pilsbry, 1934 is confirmed as genuine *Bradybaena*, as it appears as the sister group of *B. brevispira* (H. Adams, 1870) + *B. qixiaensis* Wu & Asami, 2017 + *B. similaris* (Rang, 1831) (type of *Bradybaena*; Nordsieck 2002) on Clade D (Fig. 51), which extends the occupancy of *Bradybaena* far to the west region. The remaining "*Bradybaena*" species occurred on Clade H and were mixed with *Stipnodiscus* and "*Cathaica*" species.
4. Both "*Pseudobuliminus*" and "*Buliminidius*" are not monophyletic as indicated by the phylogram.
5. "*Bradybaena*" *twenhuaensis* is a species of *Karaftohelix* which is a sister group of *Bradybaena*. Here, the species under the genera inside quotation marks refer to those having problematic generic assignments as indicated by this work.

Discussion

More than 200 species belonging to 28 genera were recorded as bradybaenine or believed to be dart-sac-bearing camaenids in Chinese Mainland (Wu and Guo 2003; Schileyko 2004; Wu 2004; Chen and Zhang 2004; Wu 2019; Zhang et al. 2019; Wu et al. 2019a; Wu et al. 2019b). This work confirms that the distribution range of the least known genus *Laeocathaica* is limited to W Hubei, Chongqing, Sichuan, S Gansu, and W Shaanxi and does not extend to other adjacent regions, as shown in Fig. 2A. In this area, *Laeocathaica carinifera*, mainly active in artificial environments, occupies the largest habitat (~ 76,500 km^2, Fig. 2C) and seems to be the most successful species there. A previous work suggested that the parallel mountains situated at

eastern Sichuan provided a series of relatively stable intermountainous environments in which populations of *Laeocathaica carinifera* (= *L. subsimilis* in Wu and Chen 1998) exhibited divergent shell morphology, reflecting microevolution in relatively isolated environments (Wu and Chen 1998). In contrast, most other congeners of *Laeocathaica carinifera* show a pattern of much narrower distribution. The South Gansu Plateau, a narrow region in northern Sichuan and the southern corner of Gansu, has nineteen *Laeocathaica* species that largely geographically overlap. Each species usually occupies only one or a few small areas, for extreme examples ~ 10 km^2 for *Laeocathaica phaeomphala* and ~ 100 km^2 for *L. potanini* (Fig. 3), which are much more endemic in the limited local environment than for some other camaenids (e.g., *Exiligada*, Criscione et al. 2012). The variously conditioned rugged terrain of mountains and intermountainous valleys with multiple species make this region a hotspot for land snails, where the malacodiversity in this region is approximately 30 times richer than that in the rest territory of China (Wu and Xu 2013; Wu 2018).

The work of Páll-Gergely et al. (2022), in which all species in the genus *Laeocathaica* were revised, has served as an essential basis for the present study. *Laeocathaica stenochone*, treated by Páll-Gergely et al. (2022) as a synonym of *L. carinifera* based on conchological characteristics, has a much denser granulation on the embryonic shell, a higher relative shell height, and differently structured genital organ compared to the latter. The phylogram based on partial 16S and partial ITS2 data could indicate that the branch ((*Laeocathaica stenochone* HBUMM08431 + *L. carinifera* HBUMM05103) + *L. carinifera* HBUMM05131) represents a single species or two species if the problem identified by Will et al. is taken into account (Will et al. 2005: fig. 1) for species identification using the barcode protocol. The sequence data of HBUMM08431, HBUMM05103, and HBUMM05131 share the same ITS2 sequence and only differ in three sites on the 16S gene. Therefore, the present phylogenetic analyses on these three samples are identical to those obtained by a traditional barcoding method for identifying species. In the present work we therefore prefer to treat *Laeocathaica stenochone* and *L. carinifera* as two species, since they are morphologically distinguishable. Nevertheless, the present phylogram suggests that *Laeocathaica carinifera* has a deep phylogenetic affinity to *L. stenochone*.

Until now, the systematic position of *Laeocathaica* remained an open question. Before this work, one of the two studies on the systematic position of *Laeocathaica* was based on a morphological character-based phylogram, in which *Laeocathaica carinifera* (= *L. subsimilis*, *L. filippina* in Wu 2004) is deeply embedded and receives very weak non-homoplasious support based on that dataset (Wu 2004). Based on partial mitochondrial 16S and CO1 sequences, another work involving *Laeocathaica polytyla* and *L. distinguenda* provided phylograms which both indicate that *Laeocathaica* shares the same robustly supported branch with *Acusta* Martens, 1860 and *Pseudobuliminus* Gredler, 1886 (Chen et al. 2021). In this second work, the monophyly of *Laeocathaica* was questioned because *Laeocathaica polytyla* is close to *Acusta* and *Pseudobuliminus* instead of close to *L. distinguenda*, which does not agree with our work, where the *Laeocathaica*

is possibly monophyletic, when more congeners (i.e., 13 *Laeocathaica* species) join the analyses based on the combined ITS2 and 16S dataset (Fig. 51).

The present phylogenetic inference is consistent with the phylogram of Wade et al. (2007), since *Satsuma* A. Adams, 1868 and *Nesiohelix* Kuroda & Emura, 1943 are basal on the phylogram, reflecting the evolutionary relationships of eastern Asian camaenids. The camaenine ingroup genus *Satsuma*, which agrees regarding its basal location on phylogram with some authors (Chiba 1999; Wade et al. 2007; Chen et al. 2021), shows a minute difference between *Nesiohelix* and *Traumatophora* Ancey, 1887 in the sequences of 16S rDNA and ITS2. The presence of a flagellum only on basal clades, represented by *Nesiohelix*, *Satsuma*, *Camaenella*, *Traumatophora*, *Aegista* Albers, 1860, and *Plectotropis* Martens, 1860, which are representatives of SE Chinese Mainland, Taiwan, Hainan, and Japan (Pfeiffer 1865; Azuma 1982; Zhou et al. 2011; Wu and Asami 2017; Wu 2019) and clearly diverge from those genera distributed in Central China (Möllendorff 1899; Chen and Zhang 2004; Wu and Prozorova 2006), agrees with that the presence or absence of the flagellum can be used as a character state coding for higher-level classification (Hirano et al. 2014; Jirapatrasilp et al. 2022). The positions of *Nesiohelix*, *Aegista*, *Acusta*, and *Bradybaena* Beck, 1837 (represented by *Bradybaena* spp. on Clade D, Fig. 51), from the basal part to the upper part, correspond topologically to the phylogenies of Wade et al. (2007). Comparing the basal part, the taxa on Clade F (Fig. 51) could present a highly evolved and diverse group among the East Asian camaenids. However, the present phylogenetic analyses suggest that *Pseudobuliminus*, *Buliminidius*, *Bradybaena*, *Cathaica*, and *Stilpnodiscus* are polyphyletic and an intensive revision is required.

Clade F (Fig. 51), which roughly corresponds to the clade containing *Acusta*, *Laeocathaica*, *Pseudobuliminus*,and *Bradybaena* in the phylogram proposed by Chen et al. (2021), is characterized by the presence of a penial sheath and a dart sac, and the absence of an epiphallic papilla, a penial caecum, or a flagellum. On Clade F, the proximal accessory sac is widely present in different subclades including *Stilpnodiscus moellendorffi* (Wu 2001: fig. 4A, E; Wu 2004: fig. 16A, C), "*Cathaica*" *pulveratricula* (Fig. 52B), *Laeocathaica* spp. (text figures listed below most species in this study; Fig. 52C, E, F), and "*Stilpnodiscus*" *entochilus* (Wu 2004: fig. 16D, E). On Clade C, the proximal accessory sac is also present in *Cathaica fasciola*. However, the structures of the terminal genitalia including the proximal accessory sac of the taxa on Clade C are divergent. In *C. fasciola* there are two small proximal accessory sacs attaching at both lateral-ventral sides of the dart sac (Fig. 52A) while in "*Cathaica*" *pulveratricula* there is a single proximal accessory sac on the left side of dart sac (Fig. 52B). However, in both *Cathaica* species the accessory sac is absent and the mucous glands open into dart sac chamber (Fig. 52A, B) in contrast to all examined *Laeocathaica* species, where the accessory sac is present and the mucous glands open into the dart chamber via an accessory sac (Fig. 52C, E, F). The frequent occurrence of a proximal accessory sac in the subclades of Clade C indicates this structure might be one of the most valuable characters and deserving of detailed examination in respect of taxonomy and evolution in the dart-sac-bearing camaenids.

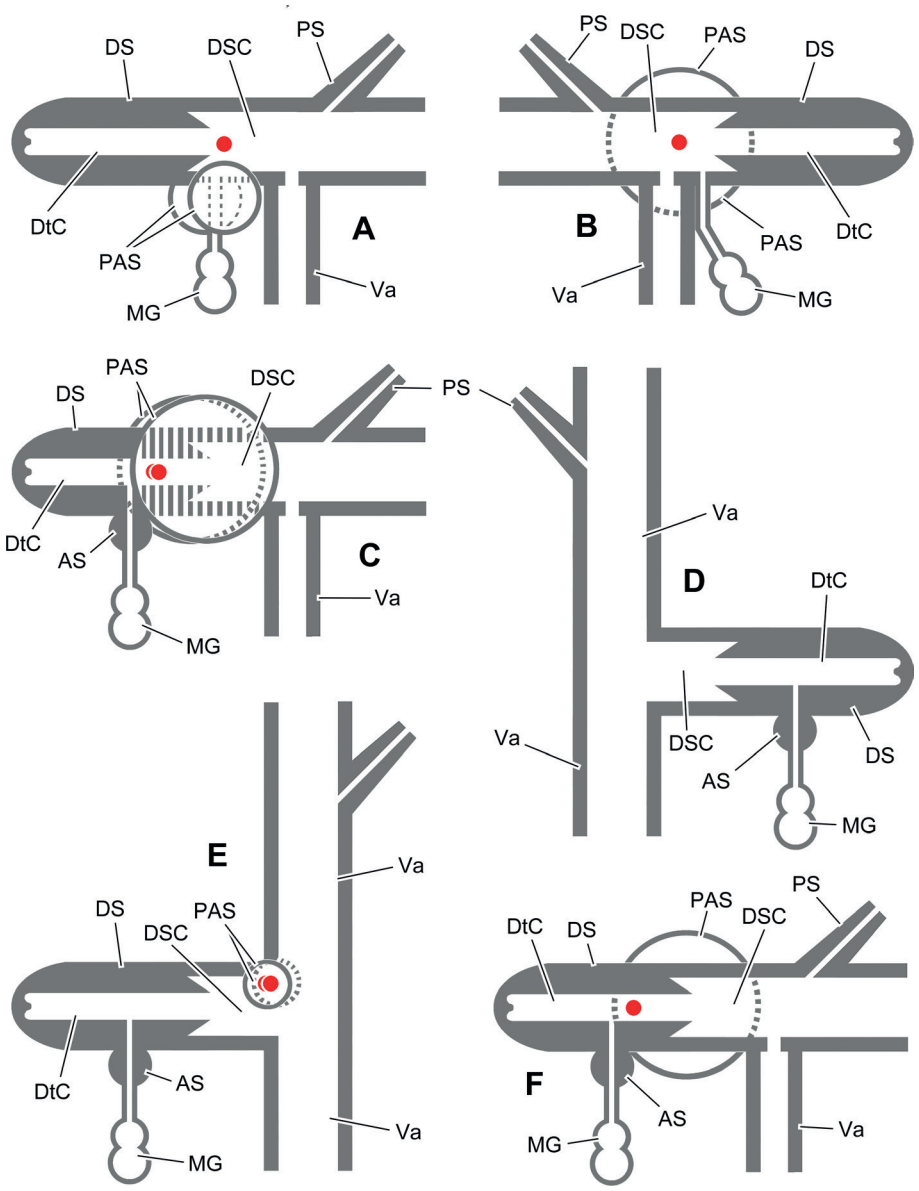

Figure 52. Schematics of terminal genitalia of some dart-sac-bearing camaenids **A** *Cathaica fasciola* (Draparnaud, 1801) (stylized pattern from HBUMM8142-spec.1–15, 9 fma; Qingyang, Gansu, 35.738°N, 107.701°E, 1353 m a.s.l.; coll. Sheng, X.-F., 2017-VII) **B** *"Cathaica" pulveratricula* (Martens, 1882) (stylized pattern from HBUMM08208), one proximal accessory sac is present at the left side of dart sac **C** *Laeocathaica* spp. with two proximal accessory sacs at both sides of dart sac **D** *L. phaeomphala* Möllendorff, 1899, without proximal accessory sac and with elongated vagina above dart sac **E** *L. amdoana* Möllendorff, 1899, with two tiny proximal accessory sacs and with elongated vagina above dart sac **F** *L. dolani* (Pilsbry, 1934), with a proximal accessory sac at the right side of dart sac. Notes: any fleshy septum inside dart sac chamber is not shown; red dots indicate openings of proximal accessory sac. Abbreviations: AS – accessory sac; DS – dart sac; DSC – dart sac chamber; DtC – a chamber containing love dart; MG – mucous glands; PAS – proximal accessory sac; PR – penial retractor muscle; PS – penial sheath; Va – vagina.

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RESEARCH ARTICLE

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A study of *Anthaxia* subgen. *Thailandia* Bílý, 1990 from China (Coleoptera, Buprestidae, Buprestinae)

Zhihao Qi[1,2], Hongmu Ai[2], Xueyou He[1], Rongxiang Su[1], Shouping Cai[1], Haitian Song[1]

1 *Fujian Academy of Forestry, Fuzhou, Fujian, 350012, China* **2** *College of Plant Protection, Fujian Agriculture and Forestry University, Fuzhou, Fujian, 350002, China*

Corresponding authors: Shouping Cai (caishouping@163.com); Haitian Song (haitiansong@126.com)

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Abstract

In this paper, the subgenus *Thailandia* Bílý, 1990 of the genus *Anthaxia* Eschscholtz, 1829 from China is reported, including two species: *A.* (*T.*) *svatoplukbilyi* Qi & Song, **sp. nov.** from Guangxi and *A.* (*T.*) *rondoni* Baudon, 1962 from Yunnan. The description and illustrations of the new species are provided, the illustrations and information of *A.* (*T.*) *rondoni* from Yunnan are given for the first time, and the diagnostic characters are provided to distinguish the new species from other related species.

Keywords

Guangxi, jewel beetle, new species, taxonomy, Yunnan

Introduction

Thailandia Bílý, 1990 is a small subgenus of the genus *Anthaxia* Eschscholtz, 1829 (Buprestinae, Anthaxiini). Bílý (1990) first established *Thailandia* as a monotypic genus of the tribe Anthaxiini Gory & Laporte, 1839 on account of the enlarged head, unusually short antennae, margined prosternal process, transverse elliptical scutellum, and particular shape of other structures, such as pronotum, anal sternite in females and elytral epipleura. In 2004, Bílý studied numerous related specimens from Southeast Asia and found that the characters mentioned in Bílý (1990) were insufficient for separating *Thailandia* as an independent genus. Then he downgraded *Thailandia* to the

subgeneric rank in the genus *Anthaxia* (Bílý 2004). In a more recent study, *Thailandia* was well-defined due to the conspicuously wide head, convex frons, extremely wide vertex, and typical colouration (Bílý 2019).

Until now, only six species of the subgenus *Thailandia* have been described, and these are mainly distributed in Southeast Asia (Bílý 2005, 2019; Bellamy 2008). Recently, Bílý (2022) reported the occurrence of *Anthaxia* (*Thailandia*) *rondoni* Baudon, 1962 in Yunnan, China, for the first time but without more information. In this paper, we describe a new species, *A.* (*T.*) *svatoplukbilyi* Qi & Song, sp. nov., from Guangxi and give diagnostic notes. Additionally, we provide the first illustrations and further information on *A.* (*T.*) *rondoni* Baudon, 1962 from Yunnan.

Materials and methods

Measurement criteria are used as follows

Body length	length between anterior margin of head and apex of elytra;
Body width	the widest point across elytra;
Aedeagus length	length between base and apex of parameres;
Aedeagus width	the widest part of parameres.

Abbreviations for collections in this study are

FAF Fujian Academy of Forestry, Fuzhou, China;
KIZ Kunming Institute of Zoology, Chinese Academy of Sciences, Kunming, China.

Photographs (Figs 1, 2) of habitus and detail features were taken using a Keyence VHX-5000 digital microscope with a Keyence VH-Z20R zoom lens (20–200×). Photographs of Fig. 3 were taken using a Nikon D610 digital camera with a Nikon SMZ18 lens by Dr Kai-Qin Li (KIZ). The images were processed and combined into figures using Adobe Photoshop CC 2019.

Taxonomy

Family Buprestidae, Leach, 1815
Subfamily Buprestinae, Leach, 1815
Tribe Anthaxiini Gory & Laporte, 1839
Genus *Anthaxia* Eschscholtz, 1829

Subgenus *Thailandia* Bílý, 1990

Type species. *Anthaxia* (*Thailandia*) *paradoxa* (Bílý, 1990).

***Anthaxia* (*Thailandia*) *svatoplukbilyi* Qi & Song, sp. nov.**
https://zoobank.org/FE47A429-B906-4BB6-8691-9BDA9D1A3516
Figs 1, 2

Type locality. China, Guangxi Zhuang Autonomous Region, Baise City, Leye County, Yachang Township, Ergou Mountain.

Type specimen. ***Holotype*** ♂ (FAF): China, Guangxi Zhuang Autonomous Region, Baise City [百色市], Leye County [乐业县], Yachang Township [雅长乡], Ergou Mountain [二沟], alt. 1200 m, 18.VII.2020, Ming-Biao Li leg.

Description of holotype. Well preserved ♂ specimen. Length 5.41 mm, width 1.60 mm, length/width ratio: 3.4; aedeagus length: 1.55 mm, width: 0.31 mm, length/width ratio: 5.1.

Body (Fig. 1A, B) small, elongate, spindle-shaped, whole body densely punctate; dorsal surface bicolour: light part metallic yellow to golden green and dark part metallic dark violet to black; most of ventral surface golden green, end of abdomen nearly black.

Head (Fig. 2A–D) large, transverse, wider than anterior pronotal margin; most part golden green, posterior part nearly black. Frons (Fig. 2C) slightly convex, vertex 1.6× as wide as width of eye, with distinct white pubescence. Eyes large, ocular distance wide, lateral margins distinct convex, inner margins strongly concave at base. Sculpture of head homogeneous, consisting of small, dense, oval to polygonal cells. Antennae (Fig. 2B) compact and setose with 11 antennomeres, the length of antenna shorter than the total length of head and pronotum; 1st antennomere longest, pear-shaped, 3.0× as long as wide, 2nd antennomere subcylindrical, 1.7× as long as wide, 3rd antennomere weakly triangular, 1.8× as long as wide, antennomeres 4–10 rhomboid, 1.1–1.5× as long as wide (not in the order of the antennomeres), terminal antennomere slightly ovoid, 1.9× as long as wide; antennomeres 1–6 in dorsal view golden green, antennomeres 7–11 in dorsal view black. Mentum (Fig. 2D) small, nearly trapezoidal, golden green. Maxillae yellowish brown, maxillar palpi golden green.

Pronotum (Fig. 2A) short, 1.5× as wide as long, sculpture consisting of elongate, transverse, irregular cells in middle and rounded cells on both sides, cells without central grains; anterior margin curved, gently convex in the middle; posterior margin widely arcuate with a row of small, dense teeth; lateral margins slightly curved, weakly convergent near base; laterobasal pronotal depressions absent; pronotum golden green with two longitudinal, broad, distinct, black stripes nearly reaching both anterior and posterior pronotal margins, with an indistinct boundary between the two stripes (midline).

Scutellum (Fig. 2A) small, subpentagonal, with several wrinkles and more finely microsculptured; the whole dark and slightly golden green.

Elytra (Fig. 1A) elongate, spindle-shaped, 2.4× as long as wide, elytral sculpture almost homogeneous, consisting of fine, dense, simple punctures; lateral margins gradually narrowed from apical third and finely serrate, apex rounded. Anterior half of elytron mainly light (metallic yellow to golden green), with two large, basal, black spots; apical half of elytron mainly dark (dark violet to black), with wide, golden-green stripes along the lateral margins.

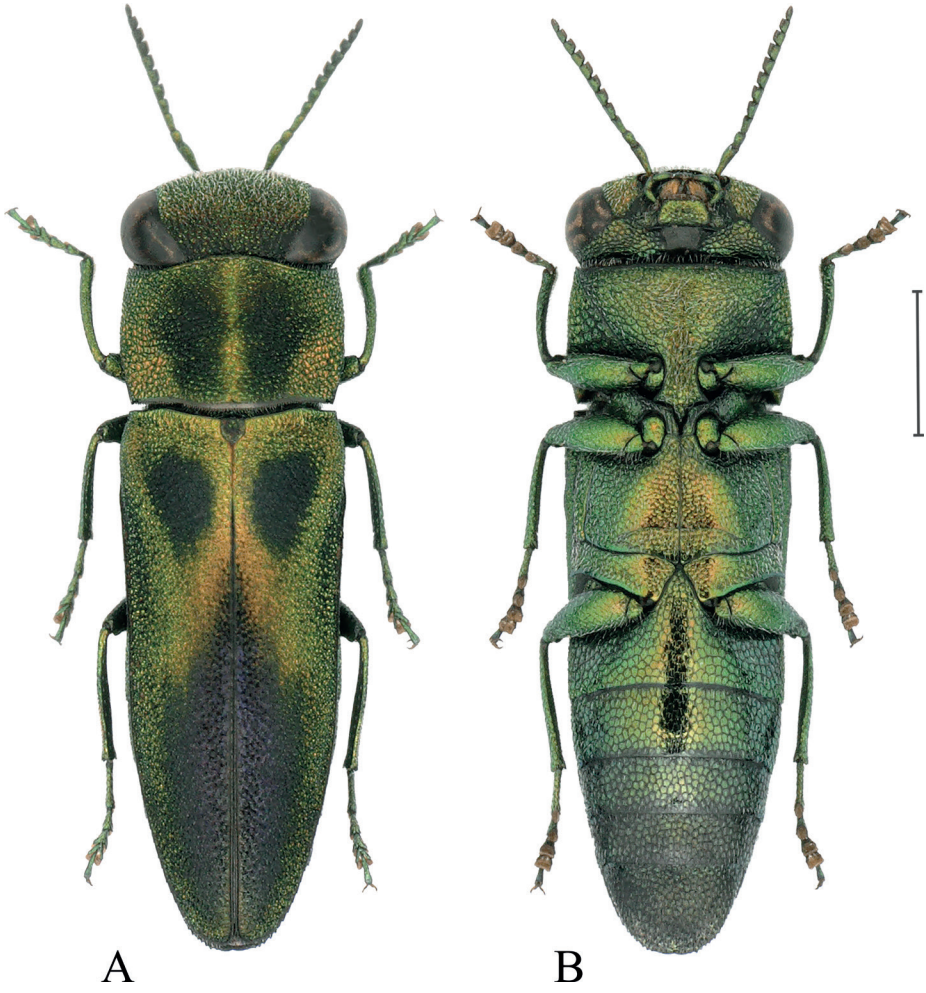

Figure 1. Habitus of *Anthaxia* (*Thailandia*) *svatoplukbilyi* Qi & Song, sp. nov. (holotype) **A** dorsal view **B** ventral view. Scale bar: 1 mm.

Legs lustrous, with dense, short setae. Protibiae slightly curved inward; metatibiae (Fig. 2F) not modified, without teeth along inner margin.

Ventral side (Fig. 1B) lustrous with dense, white setae; sternal part with ocellate sculpture; cells without central grains, each one with a white pubescence; prosternal process (Fig. 2E) widely expanded behind procoxae and sharply pointed apically (apical denticle), with two lateral dents at base of apex dent; lateral dents more obtuse than apical one. Abdominal ventrites with ocellate sculpture gradually smaller and darker apically; anal ventrite (Fig. 2G) lateral margins serrate, not notched at tip.

Aedeagus (Fig. 2H) subparallel, apexes of parameres sharp and translucent, apical portion of each paramere lateral expand with one sharp outer tooth, base of the extension part translucent and completely surrounded by black chitinous parts (red arrows in Fig. 2H); medial lobe roughly serrate laterally, moderately acuminate apically.

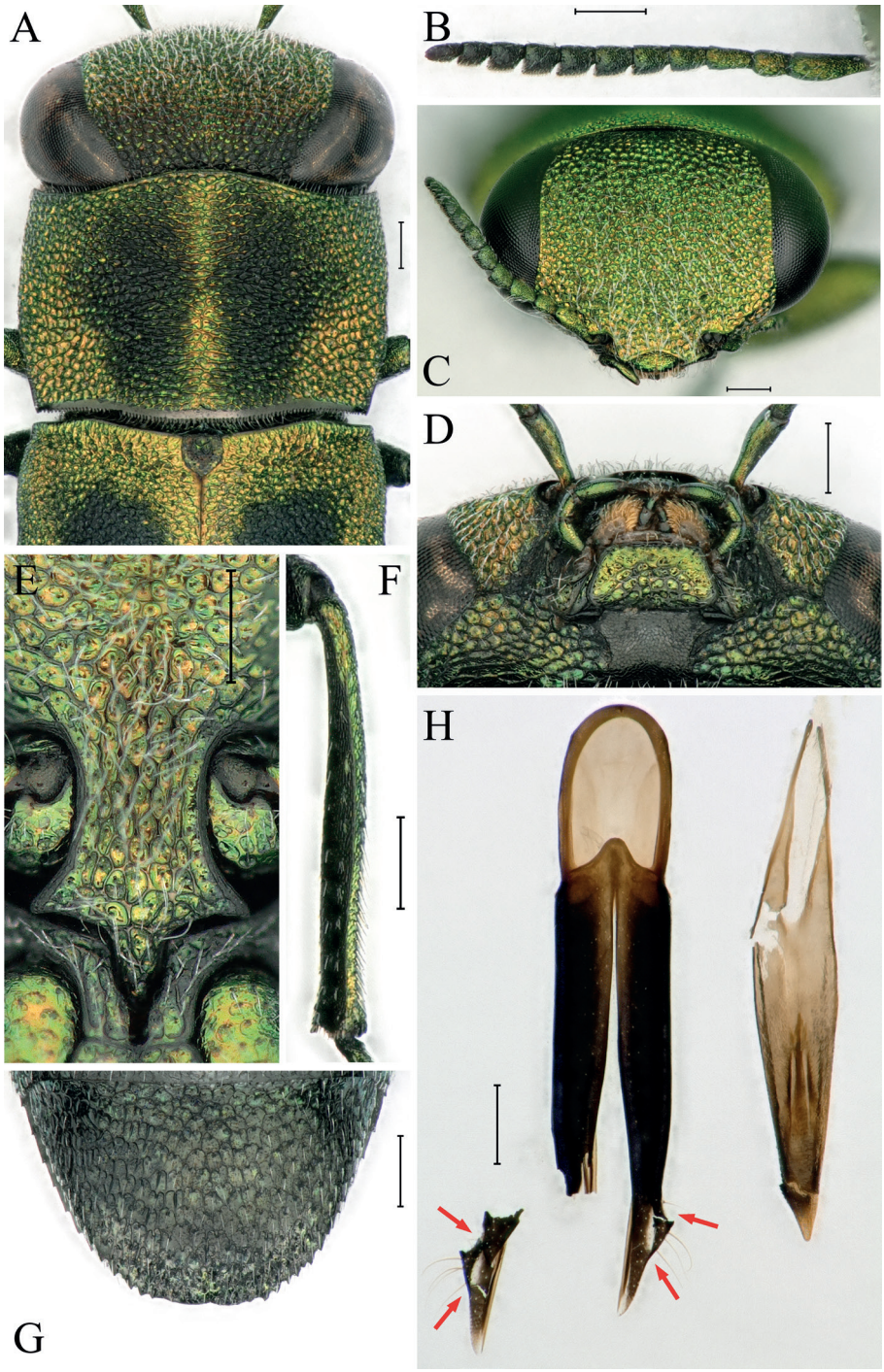

Figure 2. Detail features of *Anthaxia* (*Thailandia*) *svatoplukbilyi* Qi & Song, sp. nov. (holotype) **A** dorsal view of head, pronotum and scutellum **B** dorsal view of right antennae **C** frontal view of head **D** mentum **E** prosternal process **F** dorsal view of right metatibia **G** anal ventrite **H** dorsal view of aedeagus (left: parameres, right: medial lobe). Scale bars: 0.2 mm.

Etymology. This species is named in memory of the eminent Czech coleopterist, the late Dr Svatopluk Bílý, an excellent taxonomist in buprestid beetles. He helped us greatly and encouraged us in our work.

Distribution. China (Guangxi).

Diagnosis. In addition to the new species, the subgenus *Thailandia* contains six other species: *A.* (*T.*) *capitata* Kerremans, 1892, *A.* (*T.*) *paradoxa* (Bílý, 1990), *A.* (*T.*) *phyllanthi* Obenberger, 1956, *A.* (*T.*) *rondoni* Baudon, 1962, *A.* (*T.*) *siamensis* Bílý, 2005 and *A.* (*T.*) *svobodai* Bílý, 2005. Of these, *A.* (*T.*) *rondoni* is the one most similar to *A.* (*T.*) *svatoplukbilyi* Qi & Song, sp. nov. The following set of characters will help to recognize this new species more precisely from *A.* (*T.*) *rondoni*: 1) elytra 2.4× as long as wide, rather than 2.1–2.3×; 2) pronotum with two weakly limited black stripes nearly reaching both anterior and posterior pronotal margins (Fig. 2A), rather than with two small, black, slightly elongate, well-limited spots not reaching both anterior and posterior pronotal margins (Fig. 3A); 3) scutellum almost dark rather than metallic green or metallic blue; 4) base of apical extension part of each paramere with a small longitudinal translucent stripe completely surrounded by the black chitinous part (red arrow in Fig. 2H), rather than partly surrounded by the black chitinous part with an obvious gap near lateral tooth (see Bílý 2019: fig. 75). It is easier to separate the new species from the other related species: 1) bicoloured, rather than unicoloured as in *A.* (*T.*) *paradoxa*; 2) elytra with two large, nearly oval, basal, black spots, rather than without two large, basal, black spots as in *A.* (*T.*) *capitata*, *A.* (*T.*) *paradoxa*, *A.* (*T.*) *phyllanthi*, *A.* (*T.*) *siamensis* and *A.* (*T.*) *svobodai*; 3) metatibiae without teeth on inner margin, rather than with some teeth on inner margin as in *A.* (*T.*) *capitata*, *A.* (*T.*) *phyllanthi* and *A.* (*T.*) *svobodai*. Moreover, the combination of characters of the male genitalia of the new species differs from all other known species.

Remarks. This new species is difficult to collect, and females, variation, and the host plant are all unknown.

Anthaxia (*Thailandia*) *rondoni* Baudon, 1962

Fig. 3

Anthaxia rondoni Baudon, 1962: 28.
Anthaxia (*Haplanthaxia*) *rondoni*: Bílý 1997: 109.
Anthaxia (*Thailandia*) *rondoni*: Bílý 2004: 2.

Type localiy. Central Laos, Tha Ngon.

Material examined. 1♀ (KIZ): China, Yunnan Province, Nujiang of the Lisu Autonomous Prefecture, Lushui City [泸水市], Liuku [六库], 11.VI.1983, Yong-Han Long leg.

Distribution. China (Yunnan); Thailand; Laos; Vietnam; India (verification needed).

Remarks. The colour and pattern of this species are variable. Body usually metallic blue or metallic green; elytra usually with two large, basal, black spots (see Baudon

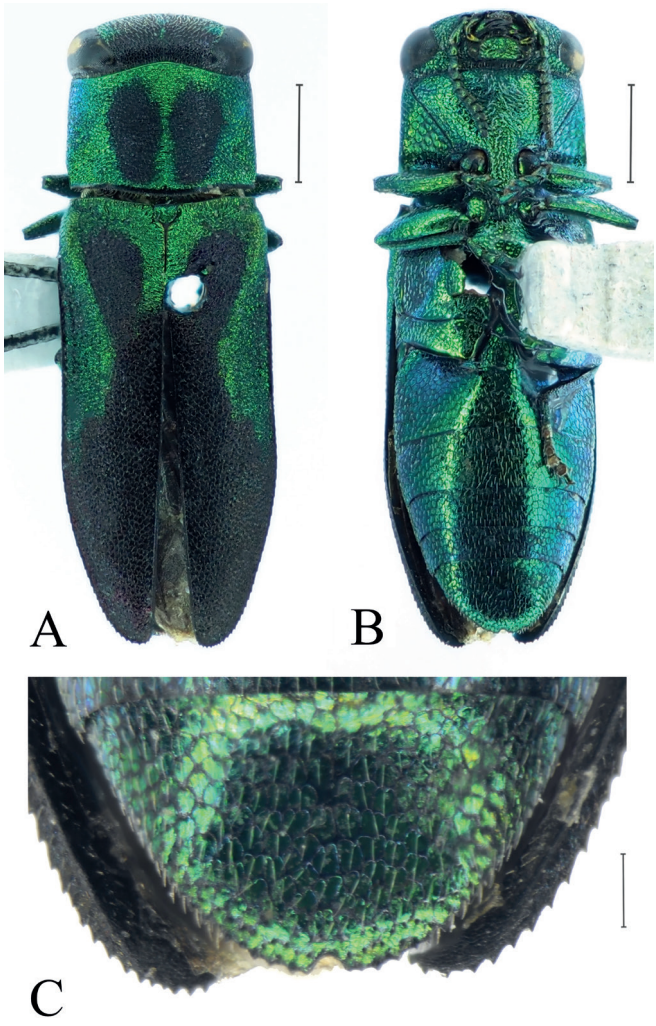

Figure 3. Female habitus of *Anthaxia* (*Thailandia*) *rondoni* Baudon, 1962 (Yunnan) **A** dorsal view **B** ventral view **C** anal ventrite. Scale bars: 1 mm (**A, B**), 0.2 mm (**C**).

1966: pl. 4 fig. b; Bílý 2005: fig. 3) or black part not separated by light part, forming a black Y-shape in the middle (Fig. 3A; Bílý 2019: fig. 18).

Bílý (2022) first reported the occurrence of *A.* (*T.*) *rondoni* from Yunnan, China. This is also the first record of the subgenus *Thailandia* in China. Unfortunately, neither figures nor collecting data of this species from China were given, while a specimen from "India" was provided in the colour figures. India was also a new record of this species but not mentioned in the catalogue's distribution information. Thus, the distribution of *A.* (*T.*) *rondoni* in Yunnan and India is uncertain. Moreover, the distribution of the species in Vietnam (Bílý 2005) seems to be missing from the newest catalogue (Bílý 2022). In our study, the habitus (Fig. 3A, B) and anal ventrite (Fig. 3C) of a fe-

male *A.* (*T.*) *rondoni* from Yunnan are figured for the first time, and the collecting data confirms the occurrence of the species in Yunnan.

According to Bílý's (2005) description, adults of this species have been repeatedly collected in northern and central Thailand and in southern Vietnam on the flowers of *Castanopsis* sp.

Discussion

Our research proves again that the distribution of *Thailandia* is not limited in Southeast Asia, but that the subgenus also occurs in Yunnan, southwestern China. Moreover, we extend the distribution of this subgenus to Guangxi. As plants and climate are similar, we believe that *Thailandia* may also be present on Hainan Island and in southern Guangdong Province. In future research, we expect to have more specimens and discoveries from China and be able to better understand sexual individual differences, distribution, host plants, and life history of these interesting species.

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RESEARCH ARTICLE

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Revision of *Aplosonyx* Chevrolat, 1836 (Coleoptera, Chrysomelidae, Galerucinae) from China, with descriptions of three new species

Chuan Feng[1,2], Xing-Ke Yang[1,3], Yang Liu[2], Zhi-Qiang Li[1]

1 *Guangdong Public Laboratory of Wild Animal Conservation and Utilization, Guangdong Key Laboratory of Animal Conservation and Resource Utilization, Institute of Zoology, Guangdong Academy of Sciences, Guangzhou, Guangdong 510260, China* **2** *Key Laboratory of Resource Biology and Biotechnology in Western China (Northwest University), Shaanxi Key Laboratory for Animal Conservation, College of Life Science, Northwest University, Taibai North Road 229, Xi'an 710069, China* **3** *Key Laboratory of Zoological Systematics and Evolution, Institute of Zoology, Chinese Academy of Sciences, Beijing 100101, China*

Corresponding authors: Zhi-Qiang Li (lizq@giz.gd.cn); Yang Liu (liuyangent@nwu.edu.cn)

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Abstract

In this study, 21 species of the leaf-beetle genus *Aplosonyx* in China are described, including three new species, *Aplosonyx ancorella* **sp. nov.**, *Aplosonyx nigricornis* **sp. nov.** and *Aplosonyx wudangensis* **sp. nov.**, and 1 new record, *Aplosonyx duvivieri* Jacoby, 1900. Additionally, *Aplosonyx ancora fulvescens* Chen, 1964 is elevated to species. A key to the Chinese species of *Aplosonyx* is provided.

Keywords

Aplosonyx, leaf beetles, new record, new species, taxonomy, China

Introduction

The genus *Aplosonyx* was established by Chevrolat (1836). *Galleruca albicornis* (Wiedemann, 1821) was designated as type species by Duponchel and Chevrolat (1842). Although Gistel (1848) emended it to *Haplosonyx*, *Aplosonyx* is regarded as the valid name (Maulik 1936; Gressitt and Kimoto 1963; Kimoto 1989; Yang 1995). *Aplosonyx*

is the senior synonym of the genus *Berecyntha* Baly, 1865 synonymized by Chapuis (1875), *Caritheca* Baly, 1877 synonymized by Kimoto (1989) and *Haplonyx* Jacobson, 1895 synonymized by Weise (1924). The genus is distributed in the Oriental Region and southern Palearctic and comprises 60 species worldwide; 21 of them occur in China. The main generic characters for *Aplosonyx* were described by Maulik (1936) and were supplemented by Yang (1995). The species of this genus can be distinguished by the following characters: Head small, frontal tubercles distinct, antennae slender, extend to middle of each elytron, generally three basal antennomeres shining, antennomere 2 the shortest, antennomere 3 longer than antennomere 2, antennomere 4 longest and longer than antennomeres 2 and 3 combined. Pronotum wider than head, nearly 2 × as broad as it is long, basal border not margined, apical border and lateral borders margined; anterior angle thickened, and posterior angle angulated, each corner with large seta-bearing pore; disc of pronotum with transverse depression across the middle. Scutellum triangular, smooth, normally impunctate, in some species, finely covered with punctures. Base of elytra wider than pronotum, humeri are strongly convex, disc is raised, covered with large and deep punctures. Elytral epipleuron broad at the base, gradually narrows from its center, extending to apex of the elytron. Procoxal cavity is closed behind, procoxa is globose. Claws are appendiculate. Male with apex of last visible sternite three lobed; female with the last visible sternite complete.

Materials and methods

The morphological characters were examined with an Olympus SZ61 microscope. The genitalia of males from each species were dissected using the following procedure: for dried or ethanol preserved specimens, the abdomen was removed from each specimen, bathed in boiling water for 5–10 minutes, then transferred to a vial containing 10% KOH solution. The abdomen with the aedeagus was washed in distilled water 3 or 4 times, transferred onto a cavity slide using fine forceps and the aedeagus was separated from the abdomen using a hooked, fine dissecting needle.

Habitus images were taken using a Canon 5DSR/Nikon SMZ25 digital camera. Aedeagus images were taken using a Nikon D610 digital camera, attached to a Zeiss V/A1 microscope (with 5× objective lens). A cable shutter release was used to prevent the camera from shaking. To obtain the full depth of focus, all images were stacked using HELICON FOCUS 7 and the resulting output was edited with Adobe Photoshop CC.

Abbreviations and depositories used in the paper

TL type locality;
IZGAS Institute of Zoology, Guangdong Academy of Sciences, Guangzhou, China;
IZAS Institute of Zoology, Chinese Academy of Sciences, Beijing, China;
SYSU Entomological Collection of Sun Yat-sen University, Guangzhou, China;
NHMUK The Natural History Museum, London, UK.

Results

Aplosonyx is similar to several genera, and a short key to the more closely related genera of *Aplosonyx* in the Hylaspini is provided below.

Key to the similar genera of Hylaspini

1 Anterior metasternal process not extending beyond the front edge of the meso-coxal cavities, basal border of pronotum not margined **2**

– Anterior metasternal process extending beyond the front edge of the meso-coxal cavities, pronotum borders margined, disc with or without a pair of transverse depressions ..... ***Gallerucida*** **Motschulsky, 1860**

2 Anterior and lateral border of pronotum margined, posterior corner of pronotum acute, disc with deep transverse depressions ..... ***Aplosonyx*** **Chevrolat, 1836**

– Lateral border of pronotum margined, posterior corner of pronotum rounded, disc without deep transverse depressions ..... ***Sphenoraia*** **Clark, 1865**

Aplosonyx **Chevrolat, 1836**

Aplosonyx Chevrolat, 1836: 375. Type species: *Galleruca albicornis* Wiedemann, 1821, designated by Duponchel and Chevrolat (1842).

Haplosonyx Gistel, 1848: 14 (emend. for *Aplosonyx* Chevrolat).

Berecyntha Baly, 1865: 98. Type species: *Berecyntha tibialis* Baly, 1865, original designation. Synonymized by Chapuis (1875: 226).

Caritheca Baly, 1877: 226. Type species: *Caritheca quadripustulata* Baly, 1877, by monotypy. Synonymized by Kimoto (1989: 169).

Haplonyx Jacobson, 1895: 555 (unjustified emendation). Synonymized by Weise (1924: 147).

Distribution. Oriental Region.

Key to Chinese species of *Aplosonyx*

1 Elytral punctures stronger, interstices of punctures equal to or narrower than diameter of single puncture..... **2**

– Elytral punctures relatively not strong, interstices of punctures wider than diameter of single puncture..... **5**

2 Elytron reddish brown with a broad purplish band anterior to middle, which extends forward along suture and expands again on base; in some specimens' dorsal surface entirely reddish brown **3**

– Elytron black with all margins yellow, including the suture..... ..... ***A. cinctus*** **Chen, 1964**

3 Elytral punctures close, interstices of punctures narrower than diameter of single puncture; punctures in pronotum close and more in number.....**4**
– Elytral punctures sparse, interstices of punctures equal to diameter of single puncture; punctures in pronotum sparse and fewer in number ....***A. fulvescens*** **Chen, 1964**
4 Abdomen without black spots, elytral surface without wrinkles ....***A. ancora*** **Laboissière, 1934**
– Abdomen with five pair of black spots, elytral surface somewhat wrinkled.... .....***A. ancorella*** **sp. nov.**
5 Elytron entirely yellow or yellowish brown.....**6**
– Elytron partly or largely pitchy or metallic.....**10**
6 Pronotum black.....**7**
– Pronotum yellowish brown.....**8**
7 Elytron reddish brown; elytron with punctures arranged in approximately 10 longitudinal striae.....***A. rufipennis*** **Duvivier, 1892**
– Elytron pale yellow; elytron with very close punctures, which arranged in approximately 20 irregular longitudinal striae.....***A. flavipennis*** **Chen, 1964**
8 Legs black with femur yellowish brown; abdomen yellowish brown; antennae pitchy black with first antennomere brown.....***A. orientalis*** **Jacoby, 1892**
– Legs entirely black.....**9**
9 Abdomen pitchy black; antennae yellowish brown with apical two or three antennomeres blackish.....***A. robinsoni*** **Jacoby, 1905**
– Abdomen yellowish brown; antennae black .....***A. duvivieri*** **Jacoby, 1900**
10 Elytron entirely or mostly metallic.....**11**
– Elytron brownish with pitchy markings.....**13**
11 Pronotum black, elytron dark bluish green with apex cupreous..... .....***A. emeishanicus*** **(Lopatin, 2005)**
– Pronotum brownish, elytron entirely bluish or violaceous.....**12**
12 Pronotum with four raised areas in front of transverse furrow; elytron blue or purplish-blue .....***A. chalybaeus*** **(Hope, 1831)**
– Pronotum without any distinctly raised areas in front of transverse furrow; elytron violaceous or greenish .....***A. sublaevicollis*** **Jacoby, 1889**
13 Pronotum black.....**14**
– Pronotum yellowish brown with black spots.....**17**
14 Elytron with blackish band.....**15**
– Elytron with black spots, without blackish band.....**16**
15 Elytron with a broad black band at middle, which extends along suture and expands again on base.....***A. ornatus*** **Jacoby, 1892**
– Elytron with a broad black band at side, which extends along lateral margin of elytron.....***A. gansuicus*** **(Chen, 1942)**
16 Elytron each with 5 black spots.....***A. nigriceps*** **Yang, 1995**
– Elytron each with 6 black spots.....***A. nigricornis*** **sp. nov.**

17 Pronotum with 3 black spots, elytron with 5 spots.....**18**
– Pronotum with only 1 black spot.....**19**
18 Black spots on both sides are large on pronotum.....
.....***A. yunlongensis* Jiang, 1992**
– Black spots on both sides are small on pronotum and almost invisible.....
.....***A. wudangensis* sp. nov.**
19 Elytron with 5 spots.....***A. omeiensis* Chen, 1942**
– Elytron with 2 longitudinal strips, 1 or 2 black spots apically **20**
20 Apex of elytron with 1 spot.....***A. pictus* Chen, 1942**
– Apex of elytron with 2 spots .....***A. tianpingshanensis* Yang, 1995**

***Aplosonyx ancora* Laboissière, 1934**
Figs 1A–F, 2A

Aplosonyx ancora Laboissière, 1934: 110.
Aplosonyx ancora ancora: Chen 1964: 204.

Specimens examined. 3♂♂2♀♀, China, **Guangdong Province**, Nanling, Chengjia; 720 m a. s. l.; 26 May 2022; Chuang Feng leg.; IZGAS. 1♂2♀♀, China, **Guangdong Province**, same data as for preceding; 31 May 2022; Chuang Feng leg.; IZGAS. 3♂♂4♀♀, China, **Guangdong Province**, Foshan, Lutian; 1 Sept 2021; Zulong Liang leg.; IZGAS. ♀, China, **Guangxi Province**, Jinxiu, Luoxiang; 400 m a. s. l.; 15 May 1999; Decheng Yuan leg.; IZAS; IOZ(E)1566707. ♀, same data as for preceding; 400 m a. s. l.; 15 May 1999; Yanzhou Zhang leg.; IZAS; IOZ(E)1566708. ♀, China, **Guangxi Province**, Napo; 440 m a. s. l.; 7 Apr. 1998; Wenzhu Li leg.; IZAS; IOZ(E)1566709. ♀, China, **Guangxi Province**, Longrui; 20 May 1984; Shimei Song leg.; IZAS; IOZ(E)1566744. ♀, same data as for preceding, IZAS; IOZ(E)1566735. ♂, China, **Guangxi Province**, Longzhou; 200 m a. s. l.; 26 Mar. 1998; Chaodong Zhu leg.; IZAS; IOZ(E)1566713. ♀, China, **Guangxi Province**, Napo, Beidou; 550 m a. s. l.; 12 Apr. 1998 Chunsheng Wu leg.; IZAS; IOZ(E)1566714. ♂, China, **Guangxi Province**, Napo, Beidou; 550 m a. s. l.; 12 Apr. 1998 Chunsheng Wu leg.; IZAS; IOZ(E)1566719. ♂, China, **Guangxi Province**, Napo, Baihe; 440 m a. s. l.; 7 Apr. 1998; Chunsheng Wu leg.; IZAS; IOZ(E)1566715. ♀, China, **Guangxi Province**, Napo, Beidou; 550 m a. s. l.; 12 Apr. 1998 Chunsheng Wu leg.; IZAS; IOZ(E)1566718. ♀, China, **Guangxi Province**, Jinxiu, Luoxiang; 400 m a. s. l.; 14 Apr. 1994; Wenzhu Li leg.; IZAS; IOZ(E)1566717. ♀, same data as for preceding; 15 May 1999; Fusheng Huang leg.; IZAS; IOZ(E)1566720. ♀, same data as for preceding; 15 May 1999; Decheng Yuan leg.; IZAS; IOZ(E)1566721. ♀, China, **Yunnan Province**, Xishuangbanna, Yunjinghong; 710 m a. s. l.; 29 Apr. 1958; Yiran Zhang leg.; IZAS; IOZ(E)1566749. ♀, same data as for preceding; 800 m a. s. l.; 29 Apr. 1958; Leyi Zheng leg.; IZAS;

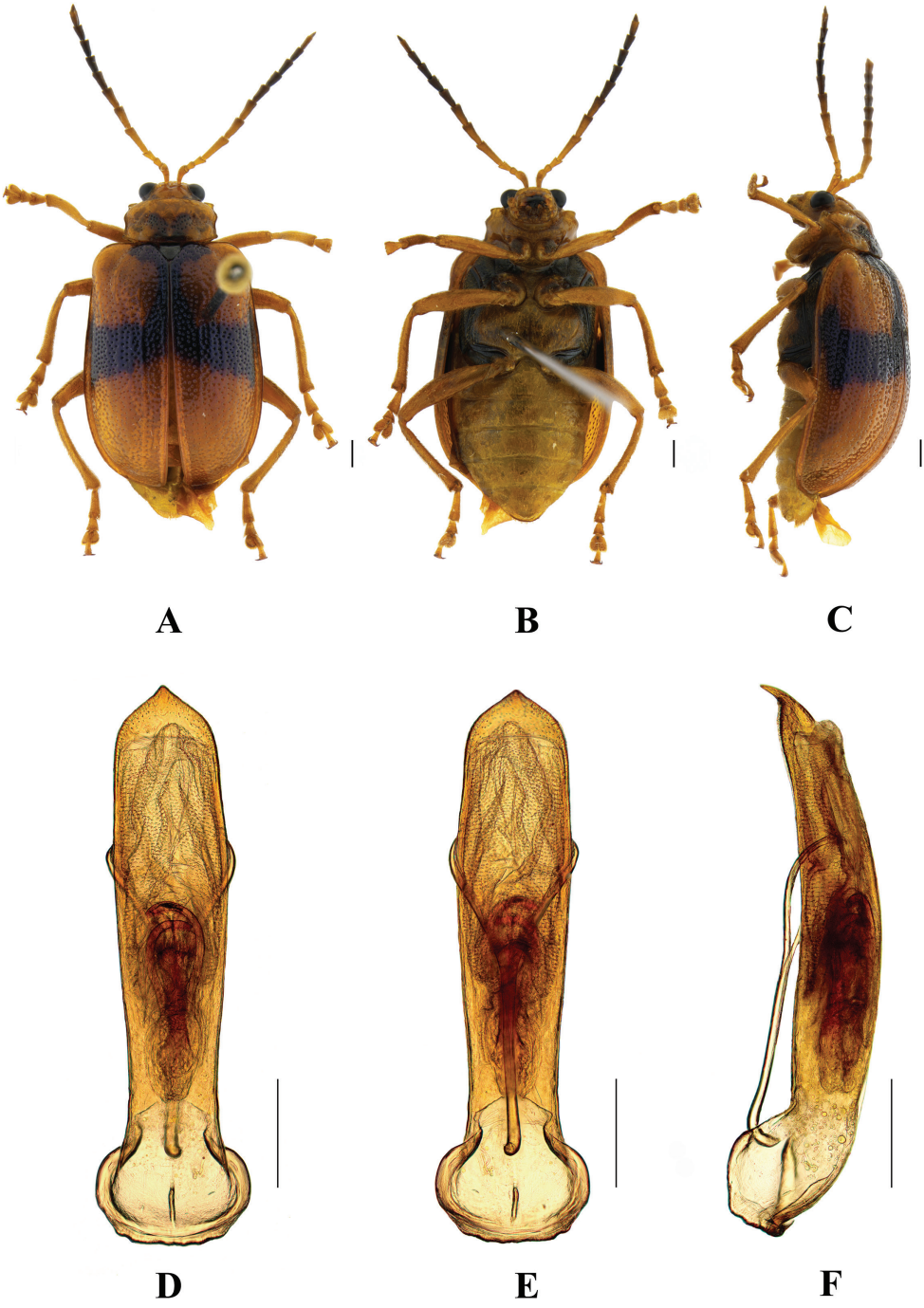

Figure 1. *Aplosonyx ancora* **A–C** habitus **D–F** aedeagus **A, D** dorsal views **B, E** ventral views **C, F** lateral views. Scale bars 0.5 mm (**D–F**); 1 mm (**A–C**).

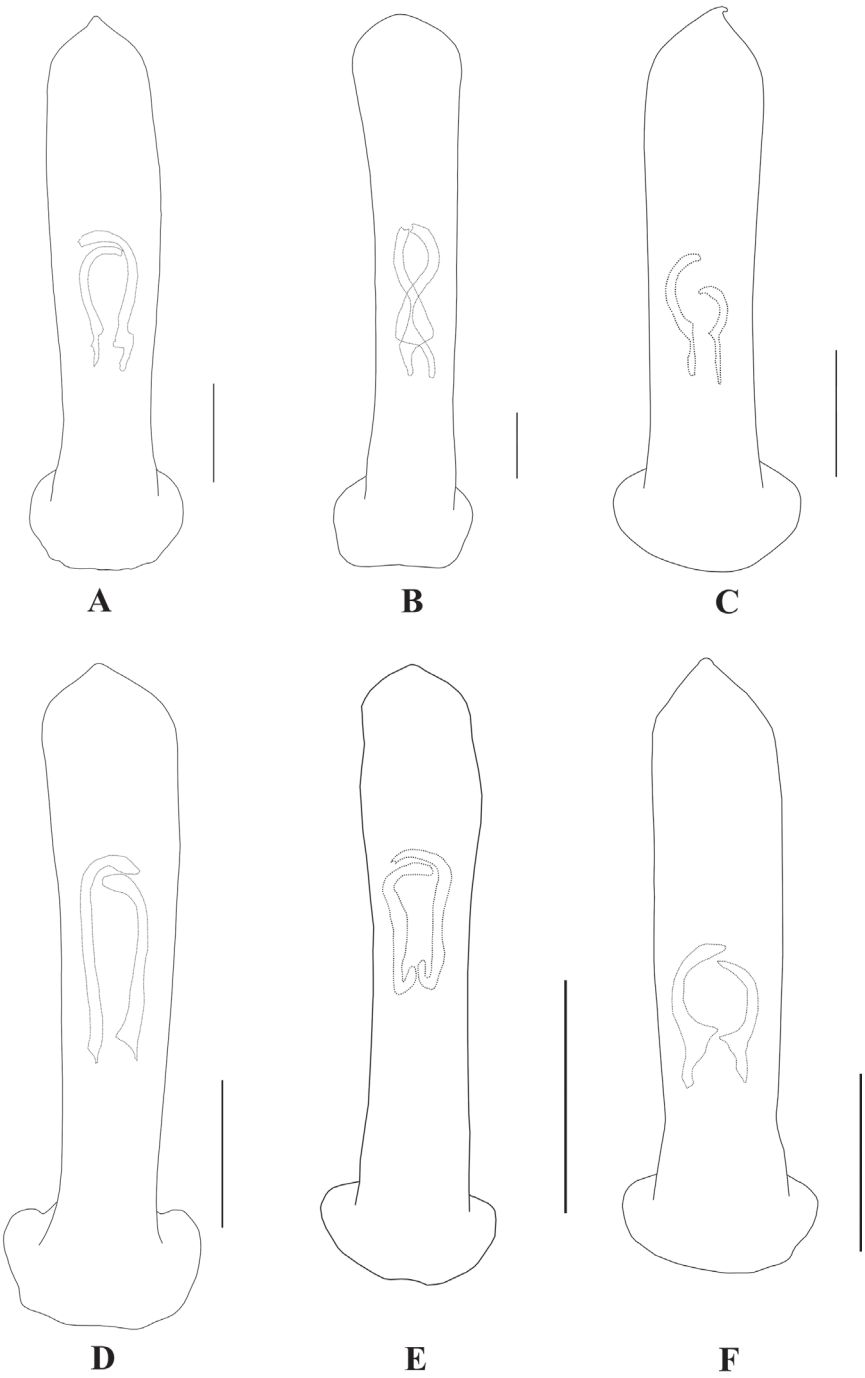

Figure 2. Aedeagus in dorsal view **A** *A. ancora* **B** *A. chalybeus* **C** *A. cinctus* **D** *A. duvivieri* **F** *A. emeishanicus* **E** *A. flavipennis*. Scale bars: 0.5 mm (**A–E**).

IOZ(E)1566745. ♂, China, **Yunnan Province**, Xishuangbanna, Menga; 18 Apr. 1982; Subai Liao leg.; IOZ(E)1566748.

Diagnosis. This species differs from *A. fulvescens* Chen in the antennae with antennomeres 1–6 yellow and antennomeres 7–11 brown, pronotum and elytron densely covered with large punctures, and the aedeagus apex is distinctly pointed. However, the pronotum and elytron of *A. fulvescens* are sparsely covered with punctures, the antennae are brown with antennomeres 1–3 yellow, and the aedeagus is narrowed in the middle with its apex slightly pointed; in lateral view the apex is strongly bent. This species differs from *A. ancorella* sp. nov. in the abdomen having no black spots, and the interstices of punctures in the elytron not being wrinkled.

Redescription. Male. Length 9.8–12.6 mm, width 5.8–6.6 mm.

Head, pronotum, abdomen, and leg orange, elytra orange or reddish brown, antennae with antennomeres 1–6 yellow and antennomeres 7–11 brown, scutellum black, ventral surface of the thorax black with yellow middle, pronotum with single purple or black spot at base, elytron with a broad purplish band from anterior to middle, extending forward along suture and expanding again on base.

Vertex finely and sparsely covered with punctures. Interocular space 2 × as wide as transverse diameter of eye. Interantennal space 1.3 × as wide as transverse diameter of antennal socket. Frontal tubercles transverse, distinctly raised, each separated by a deep furrow; antennae slender, extended to the middle of the elytra, 0.75 × as long as body; antennomeres 1–3 shiny; antennomeres 4–11 covered with pubescence, antennomere 2 shortest, antennomere 3 longer than antennomere 2, approximately 1.8 × as long as second; antennomere 4 longest, approximately 1.5 × as long as antennomeres 2 and 3 combined; antennomeres 5–10 gradually shortened, shorter than antennomere 4; antennomere 11 slightly longer than antennomere 10, pointed.

Pronotum approximately 2 × as wide as long, lateral border margined, widest at anterior 1/3; disc with transverse furrow, densely covered with large punctures, the interstices of punctures slightly narrower than diameter of punctures, with sparse small punctures in base and apex area of pronotum.

Scutellum triangular, finely covered with punctures.

Elytra wider than pronotum, 0.8 × as long as body, 1.6 × as long as wide, epipleura basally widened, dorsal surface slightly convex, irregularly covered with large and deep punctures, the interstices of punctures narrower than diameter of punctures and lightly covered with small punctures in interstices.

Metasternum 2 × as long as mesosternum. Ventral surface of abdomen with five ventrites, ventrite 1 longest, ventrites 2–4 gradually shortened, apical ventrite slightly longer than ventrite 3, with two subtriangular incisions.

Aedeagus slender, parallel-sided, basally widened, apex pointed, in lateral view slightly bent.

Female. Length 9.6–13.2 mm, width 5.6–6.7 mm.

Antennae slightly thinner than in male, antennomere 2 shortest, antennomere 3 approximately 2.5 × as long as second; antennomere 4 longest, 1.2 × as long as antennomeres 2 and 3 combined; apical sternite without incisions.

Distribution. China: Fujian, Guangdong, Guangxi, Yunnan; Vietnam.

***Aplosonyx chalybeus* (Hope, 1831)**
Figs 2B, 3A–C, 4A–F

Galleruca chalybea Hope, 1831: 28.
Haplosonyx chalybeus: Duvivier 1892: 440.
Aplosonyx chalibea: Laboissière 1932: 170.
Aplosonyx chalybeus var. *Jeanvoinei* Laboissière, 1935: 109. Synonymized by Wilcox 1971: 193.

Type specimen examined. ♀ ***Syntype*** of *Galleruca chalybea*: *chalybea*. Hope. 4137; Hardwicke Bequest; Nepal. NHMUK014596221.

Additional specimens examined. ♀, China, **Yunnan province**, Lushui; 2150 m a. s. l.; 11 Jun. 1981; Subai Liao leg.; IZAS; IOZ(E)1566252. ♂, same data as for preceding; IZAS; IOZ(E)1566219. ♂, same data as for preceding; IZAS; IOZ(E)1566258. ♂, China, **Yunnan province**, Lushui; 1900 m a. s. l.; 8 Jun. 1981; Xuezhong Zhang leg.; IZAS; IOZ(E)1566256. ♂, same data as for preceding; Shuyong Wang leg.; IZAS; IOZ(E)1566257. ♀, China, **Yunnan province**, Ruili; 1100 m a. s. l.; 11 Jun. 1956; Tianrong Huang leg.; IZAS; IOZ(E)1566234. ♀, China, **Yunnan province**, Jinping, Hetouzhai; 1700 m a. s. l.; 12 May 1956; Keren Huang leg.; IOZ(E)1566235. ♀, same data as for preceding; 1600 m a. s. l.; 12 May 1956; Keren Huang leg.; IOZ(E)1566239. ♂, China, **Tibet**, Motuo; 850 m a. s. l.; 14 May 1983; Yinheng Han leg.; IZAS; IOZ(E)1566224. ♂, same data as for preceding; IOZ(E)1566210. ♀, same data as for preceding; IOZ(E)1566211. ♂, same data as for preceding; IOZ(E)1566212. ♂, China, **Tibet**, Motuo, Beibeng; 850 m a. s. l.; 17 May 1983; Yinheng Han leg.; IZAS; IOZ(E)1566213. ♂, same data as for preceding; IOZ(E)1566214. ♀, same data as for preceding; IOZ(E)1566215. ♀, China, **Tibet**, Motuo, Beibeng; 850 m a. s. l.; 24 May 1983; Yinheng Han leg.; IZAS; IOZ(E)1566216. ♂, same data as for preceding; IOZ(E)1566217. ♂, China, **Tibet**, Motuo, 1150 m a. s. l.; 17 Jun. 1983; Yinheng Han leg.; IZAS; IOZ(E)1566209. ♂, China, **Tibet**, Motuo, Xirang; 700 m a. s. l.; 24 Apr. 1983; Yinheng Han leg.; IZAS; IOZ(E)1566218.

Diagnosis. This species can be distinguished from other Chinese species by the yellow antennae with black antennomeres 5–8, the apex of the pronotum with four raised areas, and blue or purplish blue elytra. This species differs from *A. sublaevicollis* in pronotum being widest at anterior 1/3.

Redescription. Male. Length 12.2–14.0 mm, width 6.8–7.4 mm.

Head, pronotum, scutellum, and ventral surface of body yellow, antennae yellow with antennomeres 5–8 black, legs black with femur yellow, elytra blue or purplish blue.

Vertex covered with several large punctures; Interocular space 2.6 × as wide as transverse diameter of eye. Interantennal space 1.9 × as wide as transverse diameter of antennal socket. Frontal tubercles transverse, distinctly raised, each separated by a deep furrow; antennae slender, extended to the middle of the elytra, 0.65 × as long as body; antennomeres 1–3 shiny; antennomeres 4–11 covered with pubescence, antennomere 2 shortest, antennomere 3 twice as long as second; antennomere 4 longest, slightly longer than antennomeres 2 and 3 combined; antennomeres 5–10 gradually shortened, shorter than antennomere 4; antennomere 11 slightly longer than antennomere 10, pointed.

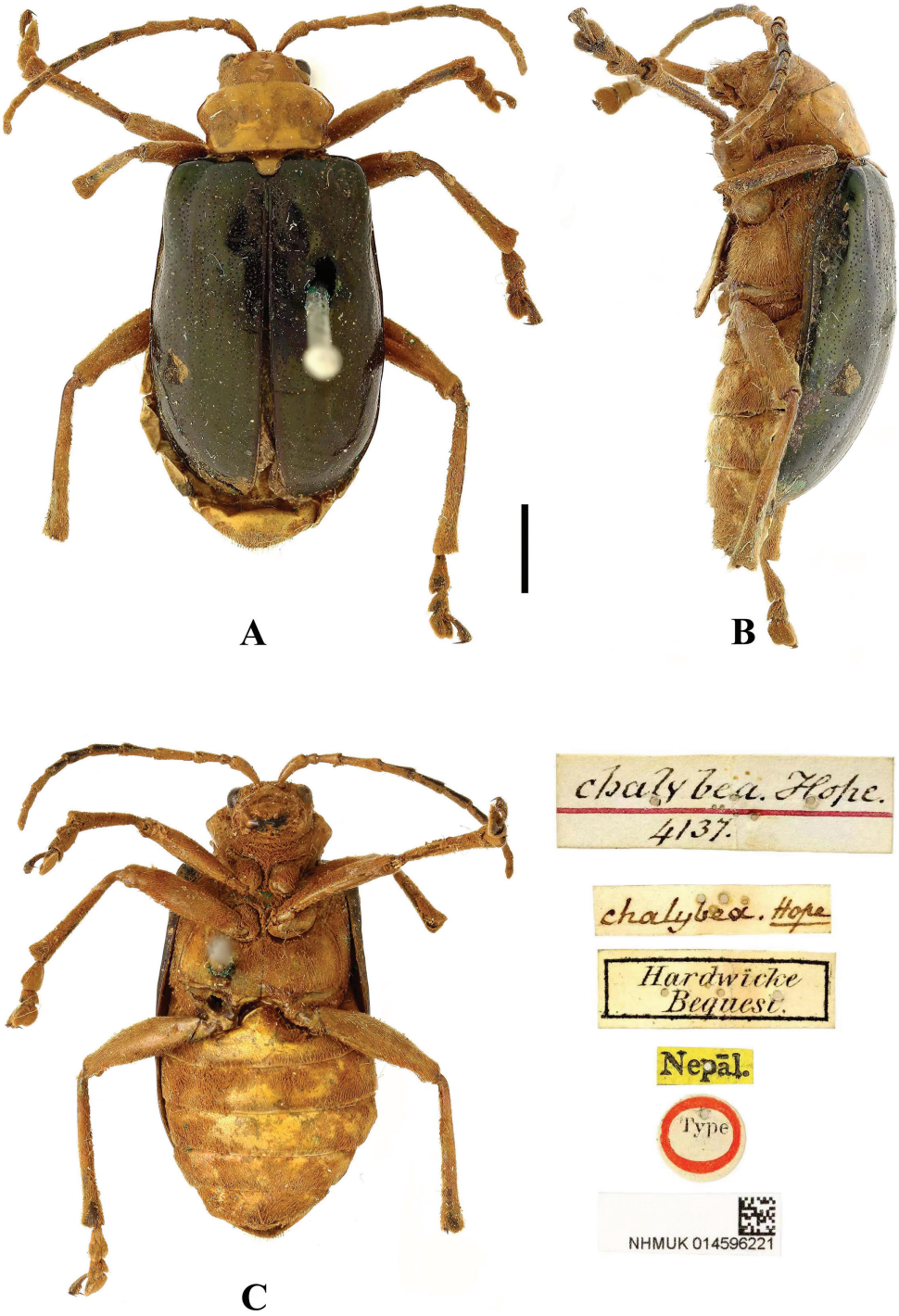

Figure 3. *Aplosonyx chalybeus* **A–C** habitus of syntype, NHMUK **A** dorsal view **B** ventral view **C** lateral view. Scale bar: 2 mm (**A–C**).

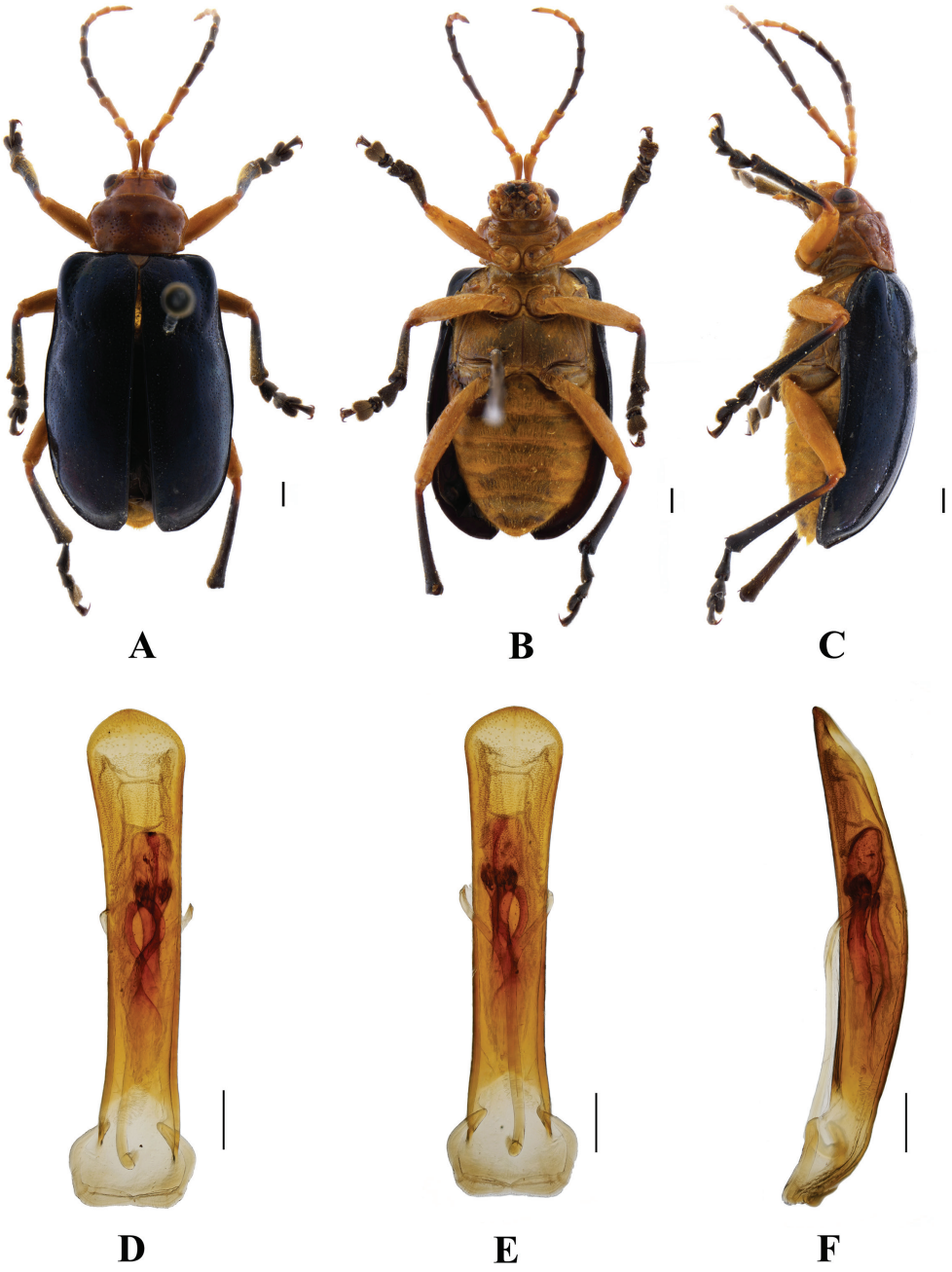

Figure 4. *Aplosonyx chalybeus* **A–C** habitus **D–F** aedeagus **A, D** dorsal views **B, E** ventral views **C, F** lateral views. Scale bars 0.5 mm (**D–F**); 1 mm (**A–C**).

Pronotum approximately 1.6 × as wide as long, lateral border margined, widest at anterior 1/3, apex of disc with four raised areas, middle of disc with deep transverse furrow; closely covered with large punctures in furrow and with sparsely small punctures in other parts of pronotum.

Scutellum triangular, finely covered with punctures.

Elytra wider than pronotum, 0.75 × as long as body, 1.9 × as long as wide, with lateral margins straight and subparallel, epipleura basally widened, posteriorly gradually narrowing towards apex, dorsal surface slightly convex, irregularly covered with large punctures, the interstices of punctures wider than diameter of individual punctures, approximately 2 × as wide as diameter of punctures and lightly covered with small punctures in interstices.

Metasternum 2 × as long as mesosternum. Ventral surface of abdomen with five ventrites, ventrite 1 longest, ventrites 2–4 gradually shortened, apical ventrite slightly longer than ventrite 3, with two subtriangular incisions.

Aedeagus slender, parallel-sided, basally widened, apex slightly pointed, in lateral view base and apex slightly bent.

Female. Length 12.0–14.2 mm, width 6.6–7.8 mm.

Antennae slightly thinner than in male, antennomere 2 shortest, antennomere 3 approximately 1.5 × as long as second; antennomere 4 longest, 1.4 × as long as antennomeres 2 and 3 combined; apical sternite without incisions.

Distribution. China: Yunnan, Xizang; Vietnam; Myanmar; India; Nepal; Sikkim.

Aplosonyx cinctus Chen, 1964

Figs 2C, 5A–F

Aplosonyx cinctus Chen 1964: 203.

Type specimens examined. ***Holotype***: ♀, China, **Yunnan province**, Jinping, Changpotou; 1200 m a. s. l.; 23 May 1956; Keren Huang leg.; IZAS; IOZ(E)215623.

Paratype: ♀, same data as for holotype; IOZ(E)215624.

Additional specimens examined. ♂, China, **Yunnan province**, Xishuangbanna, Damenglong; 650 m a. s. l.; 4 May 1958; Chunpei Hong leg.; IZAS; IOZ(E)1566412. ♂, same data as for preceding; 6 May 1958; Fuji Pu leg.; IZAS; IOZ(E)1566413. ♂, same data as for preceding; 6 May 1958; Fuji Pu leg.; IZAS; IOZ(E)1566414. ♂, same data as for preceding; 6 May 1958; Shuyong Wang leg.; IZAS; IOZ(E)1566418. ♂, same data as for preceding; 6 Oct. 1958; Zhizi Chen leg.; IZAS; IOZ(E)1566419. ♂, same data as for preceding; 4 May 1958; Chunpei Hong leg.; IZAS; IOZ(E)1566420. ♀, China, **Yunnan province**, Xishuangbanna, Mengzhe; 870 m a. s. l.; 5 Sep. 1958; Fuji Pu leg.; IZAS; IOZ(E)1566421. ♂, China, **Yunnan province**, Xishuangbanna, Damenglong; 650 m a. s. l.; 6 May 1958; Fuji Pu leg.; IZAS; IOZ(E)1566422. ♂, same data as for preceding; Chunpei Hong leg.; IZAS; IOZ(E)1566423. ♂, China, **Yunnan province**, Xishuangbanna, Damenglong; 650 m a. s. l.; 6 May 1958; Leyi Zheng leg.; IZAS; IOZ(E)1566424. ♀, China, **Yunnan province**, Xishuangbanna, Mengzhe; 870 m a. s. l.; 8 Jul. 1958; Shuyong Wang leg.; IZAS; IOZ(E)1566425. ♀, China, **Yunnan**

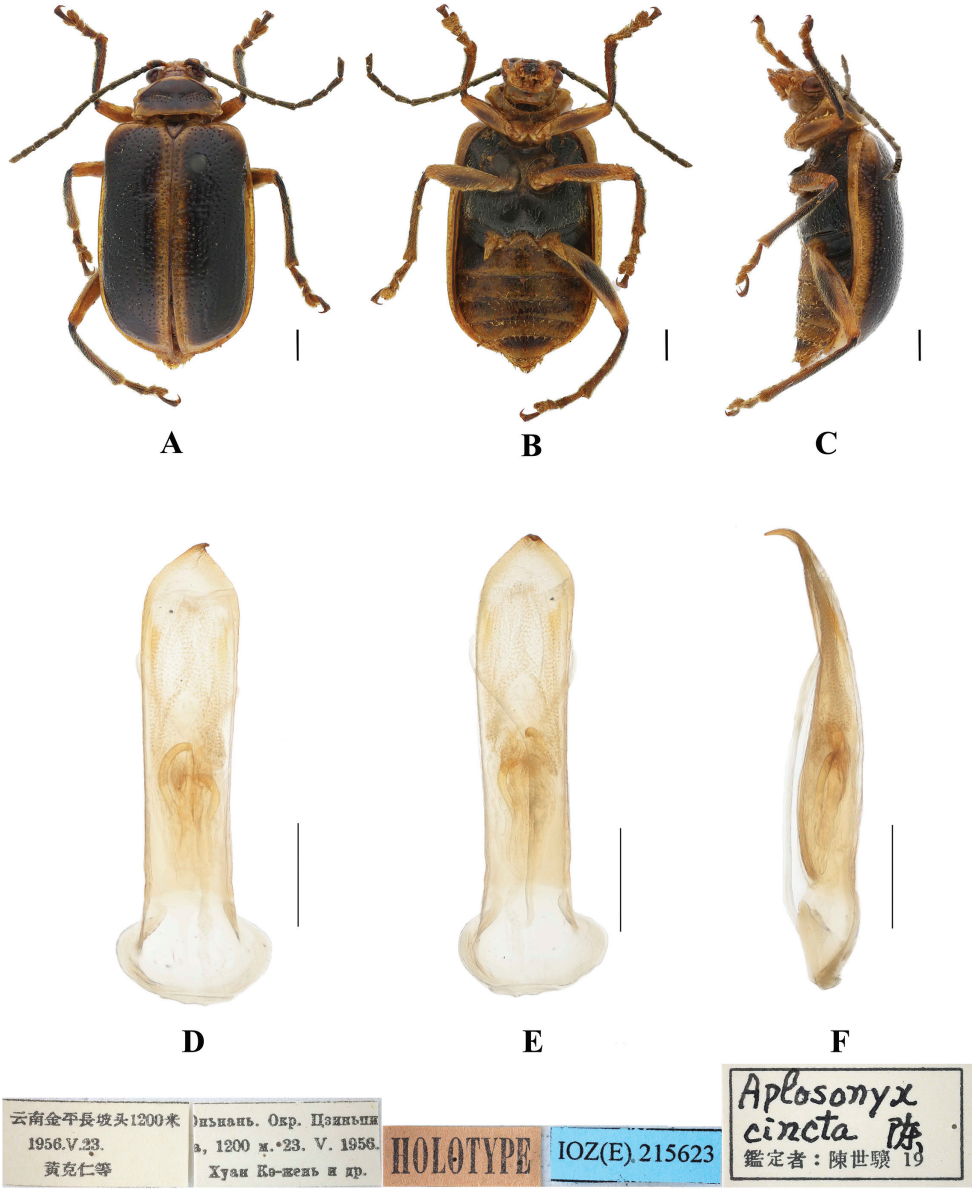

Figure 5. *Aplosonyx cinctus* **A–C** habitus of holotype, IZAS **D–F** aedeagus **A, D** dorsal view **B, E** ventral view **C, F** lateral view. Scale bars 0.5 mm (**D–F**); 1 mm (**A–C**).

province, Xishuangbanna, Damenglong; 650 m a. s. l.; 6 May 1958; Shuyong Wang leg.; IZAS; IOZ(E)1566393. ♀, same data as for preceding; 4 Oct. 1958; Zhizi Chen leg.; IZAS; IOZ(E)1566395. ♀, same data as for preceding; 4 Oct. 1958; Zhizi Chen leg.; IZAS; IOZ(E)1566396. ♀, China, **Yunnan province**, Xishuangbanna, Mengzhe; 870 m a. s. l.; 10 Jul. 1958; Shuyong Wang leg.; IZAS; IOZ(E)1566397. ♀, same data as for preceding; IOZ(E)1566398. ♀, same data as for preceding; IOZ(E)1566399.

Diagnosis. This species can be distinguished from other congeners by the black pronotum and elytra, all margins of pronotum and elytra yellow, including the yellow suture. This species differs from *A. orientalis* in the color of the body, the slender aedeagus, and in lateral view the apex is strongly bent.

Redescription. Male. Length 9.0–10.2 mm, width 5.0–6.0 mm.

Head and abdomen yellow, antennae and ventral surface of thorax black, elytra black with all margins yellow, including the suture of elytra; scutellum black with apex yellow; femur and tibia outside black inside yellow, tarsus and claws brown.

Vertex finely covered with punctures. Interocular space 2.2 × as wide as transverse diameter of eye. Interantennal space 1.7 × as wide as transverse diameter of antennal socket. Frontal tubercles distinctly raised, hook-like, each separated by a deep furrow; antennae slender, 0.7 × as long as body; antennomeres 1–3 shiny; antennomeres 4–11 covered with pubescence, antennomere 2 shortest, antennomere 3 approximately 1.2 × as long as second; antennomere 4 longest, approximately 1.8 × as long as antennomeres 2 and 3 combined; antennomeres 5–10 gradually shortened, shorter than antennomere 4; antennomere 11 slightly longer than antennomere 10, pointed.

Pronotum 2 × as wide as long, lateral border margined, widest at posterior corners, disc with deep transverse furrow, less distinct in middle; closely covered with large punctures in furrow and with sparsely small punctures in other parts of pronotum.

Scutellum triangular, finely covered with punctures.

Elytra wider than pronotum, 0.75 × as long as body, 1.6 × as long as wide, epipleura wide at anterior 1/4, posteriorly gradually narrowing towards apex, dorsal surface slightly convex, irregularly covered with punctures, the interstices of punctures lightly wider than diameter of individual punctures and covered with small punctures in the interstices.

Metasternum 2 × as long as mesosternum. Ventral surface of abdomen with five ventrites, ventrite 1 longest, ventrites 2–4 gradually shortened, apical ventrite slightly longer than ventrite 3, with two subtriangular incisions.

Aedeagus slender, parallel-sided, slightly narrowed in middle, strongly narrowing in apical tenth, ending in pointed apex, in lateral view apex strongly bent.

Female. Length 9.6–10.4 mm, width 5.0–5.8 mm.

Antennae slightly thinner than in male, antennomere 2 shortest, antennomere 3 twice as long as second; antennomere 4 longest, 1.7 × as long as antennomeres 2 and 3 combined; apical sternite without incisions.

Distribution. China: Yunnan.

Aplosonyx duvivieri Jacoby, 1900 (new record)

Figs 2D, 6, 7

Haplosonyx duvivieri Jacoby, 1900, 7: 130.
Aplosonyx duvivieri: Maulik 1936: 618.

Type specimen examined. ♀, syntype of *Haplosonyx duvivieri* Jacoby; Andrewes Bequest; B.M.1922-221; NHMUK 014596218.

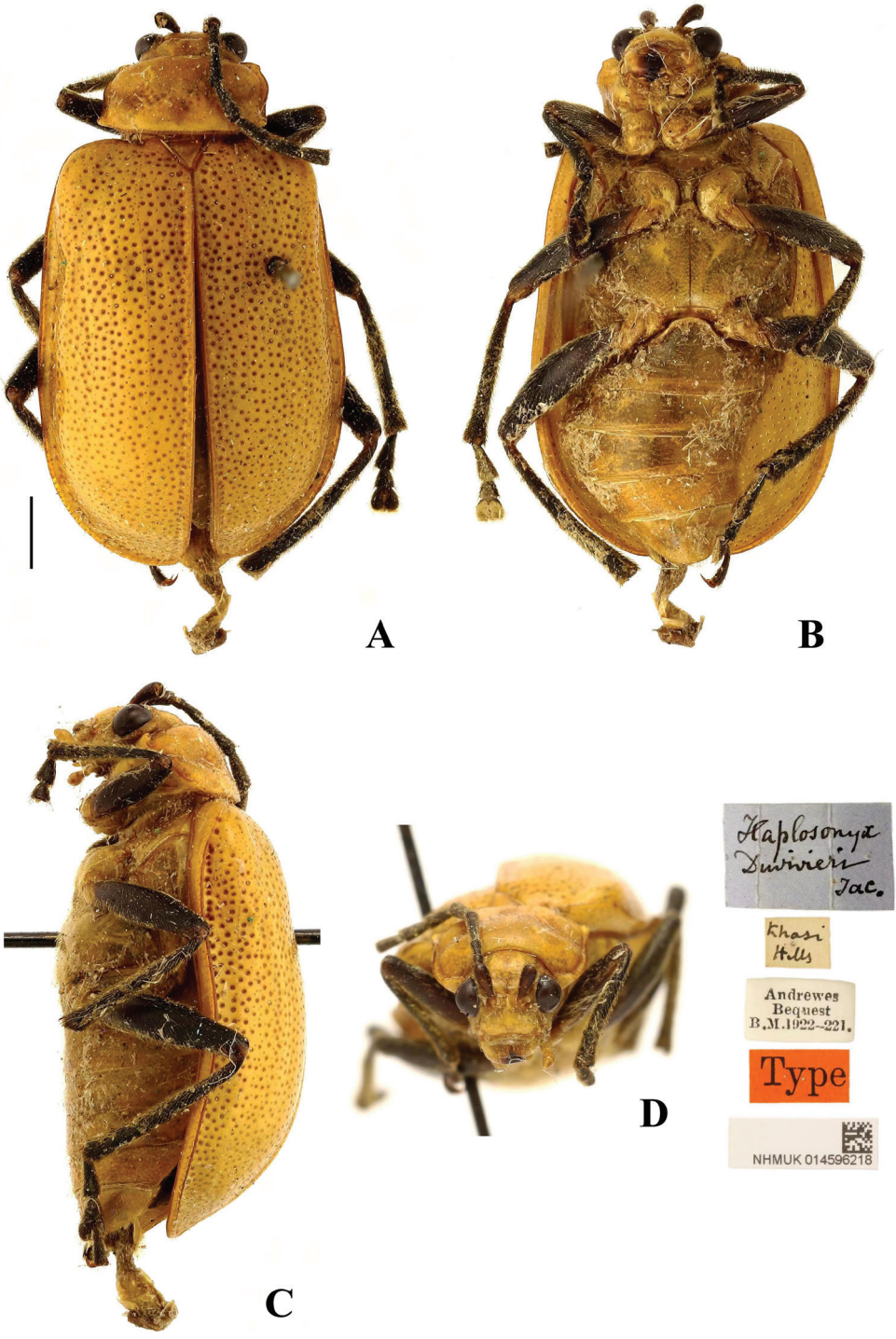

Figure 6. *Aplosonyx duvivieri* **A–D** habitus of syntype, NHMUK014596218 **A** dorsal view **B** ventral view **C** lateral view **D** head view. Scale bar: 1 mm (**A–D**).

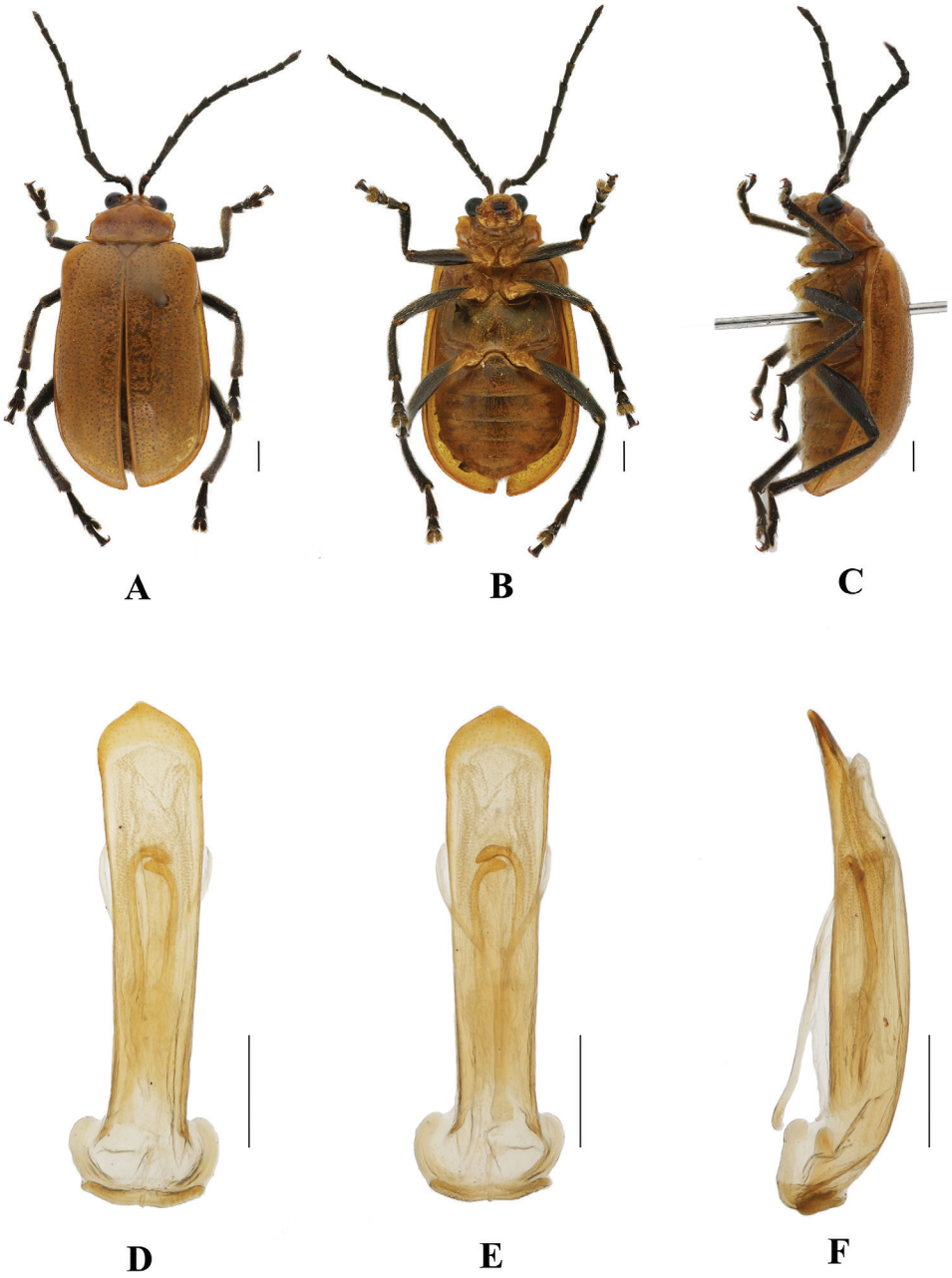

Figure 7. *Aplosonyx duvivieri* **A–C** habitus **D–F** aedeagus **A, D** dorsal views **B, E** ventral views **C, F** lateral views. Scale bars 0.5 mm (**D–F**); 1 mm (**A–C**).

Additional specimen examined. ♂, China, **Yunnan Province**, Xishuangbanna, Menga; 29 May. 1958; Shuyong Wang leg.; IOZ(E)1566284.

Diagnosis. This species can be distinguished from other Chinese species by yellow body, antennae, legs, labrum, and mandible black, and dense punctures on the elytra.

This species differs from *A. flavipennis* in the head, pronotum, scutellum, and ventral surface of the thorax all being yellow.

Redescription. Male. Length 8.9 mm, width 4.4 mm.

Body yellow; antennae, legs, labrum, and mandibles black.

Vertex covered with punctures. Interocular space 2.5 × as wide as transverse diameter of eye. Interantennal space 1.5 × as wide as transverse diameter of antennal socket. Frontal tubercles transverse, each separated by a deep furrow; antennae slender, extended to the middle of the elytra, 0.7 × as long as body; antennomeres 1–3 shiny; antennomeres 4–11 covered with pubescence, antennomere 2 shortest, antennomere 3 approximately 1.8 × as long as second; antennomere 4 longest, approximately 1.5 × as long as antennomeres 2 and 3 combined; antennomeres 5–10 gradually shortened, shorter than antennomere 4; antennomere 11 slightly longer than antennomere 10, pointed.

Pronotum approximately 2 × as wide as long, lateral border margined, widest at posterior corners; disc with deep transverse furrow, covered with large punctures in furrow and with sparsely small punctures in other parts of pronotum.

Scutellum triangular, covered with fine punctures.

Elytra wider than pronotum, 0.7 × as long as body, 1.65 × as long as wide, with lateral margins straight and almost parallel, epipleura wide at anterior 1/4, posteriorly gradually narrowing towards apex, dorsal surface slightly convex, regularly covered with large deep punctures, the interstices of punctures narrower than diameter of punctures, and covered with small punctures in interstices.

Metasternum 2 × as long as mesosternum. Ventral surface of abdomen with five ventrites, ventrite 1 longest, ventrites 2–4 gradually shortened, apical ventrite slightly longer than ventrite 3, two subtriangular incisions.

Aedeagus slender, parallel-sided, basally widened, narrowed in middle, apex pointed, in lateral view moderately bent.

Female. Length 9.4 mm, width 4.7 mm.

Antennae slightly thinner than in male, antennomere 2 shortest, antennomere 3 twice as long as second; antennomere 4 longest, 1.7 × as long as antennomeres 2 and 3 combined; apical sternite without incisions.

Distribution. China: Yunnan; India.

Aplosonyx emeishanicus (Lopatin, 2005)

Figs 2E, 8A–F

Gallerucida emeishanica Lopatin, 2005: 877.

Aplosonyx metallicus Chen in Zhang et al. 2008: 65. Synonymized by Bezděk 2012: 383.

Aplosonyx emeishanica: Bezděk 2012: 383.

Additional specimens examined. ♂, China, **Sichuan Province**, Mount Emei; 18 Jun. 1955; Keren Huang leg.; IZAS; IOZ(E)1566815. ♀, same data as for preceding; IOZ(E)1566561. ♀, same data as for preceding; IOZ(E)1566576. ♀, same data

as for preceding; IOZ(E)1566816. ♂, same data as for preceding; IOZ(E)1566568. ♂, same data as for preceding; IOZ(E)1566571. ♂, same data as for preceding; IOZ(E)1566578. ♂, same data as for preceding; IOZ(E)1566565. ♂, same data as for preceding; IOZ(E)1566566. ♂, same data as for preceding; IOZ(E)1566584. ♂, same data as for preceding; IOZ(E)1566585. ♂, same data as for preceding; IOZ(E)1566586. ♂, China, **Sichuan Province**, Mount Emei; 24 Jun. 1955; Le Wu leg.; IZAS; IOZ(E)1566574. ♂, same data as for preceding; IOZ(E)1566576. ♂, China, **Sichuan Province**, Mount Emei; 1600 m–2100 m a. s. l.; 24 Jun. 1955; Bingrong Ou leg.; IZAS; IOZ(E)1566574. ♀, China, **Sichuan Province**, Mount Emei, Jiulaodong; 1900 m a. s. l.; 22 Jul. 1957; Keren Huang leg.; IZAS; IOZ(E)1566793. ♀, China, **Sichuan Province**, Mount Emei, Jiulaodong; 1800 m a. s. l.; 22 Jul. 1957; Keren Huang leg.; IZAS; IOZ(E)1566794. ♂, China, **Sichuan Province**, Mount Emei, Jiulaodong; 9 Jul. 1957; Zongyuan Wang leg.; IZAS; IOZ(E)1566811. ♀, same data as for preceding; IOZ(E)1566812.

Diagnosis. This species can be distinguished from other Chinese species by the dark bluish green color of the head, pronotum, and elytra.

Redescription. Male. Length 4.4–4.8 mm, width 2.6–3.0 mm.

Head, pronotum, scutellum, and ventral surface of body green, antennae and legs brown, elytra dark bluish green with apex cupreous.

Vertex covered with several large punctures. Interocular space 2.3 × as wide as transverse diameter of eye. Interantennal space 1.4 × as wide as transverse diameter of antennal socket. Frontal tubercles transverse, each separated by a deep furrow; antennae slender, 0.85 × as long as body; antennomeres 1–3 shiny; antennomeres 4–11 covered with pubescence, antennomere 2 shortest, antennomere 3 approximately 1.6 × as long as second; antennomere 4 longest, approximately 1.2 × as long as antennomeres 2 and 3 combined; antennomeres 5–10 gradually shortened, shorter than antennomere 4; antennomere 11 slightly longer than antennomere 10, pointed.

Pronotum approximately 1.6 × as wide as long, lateral border margined, widest at anterior 1/3, disc with transverse furrow, finely covered with punctures, only with several large punctures in furrow.

Scutellum triangular, smooth, impunctate.

Elytra wider than pronotum, 0.8 × as long as body, 1.65 × as long as wide, epipleura wide at anterior 1/3, posteriorly gradually narrowing towards apex, dorsal surface slightly convex, regularly covered with punctures, partially arranged in ten rows in each elytron, interstices between punctures approximately 3.5 × as wide as diameter of individual punctures and lightly covered with small punctures.

Metasternum 2 × as long as mesosternum. Ventral surface of abdomen with five ventrites, ventrite 1 longest, ventrites 2–4 gradually shortened, apical ventrite slightly longer than ventrite 3, with two subtriangular incisions.

Aedeagus slender, parallel-sided, basally widened, middle narrowed, apex pointed, in lateral view base and apex slightly bent.

Female. Length 4.4–5.0 mm, width 2.5–3.0 mm.

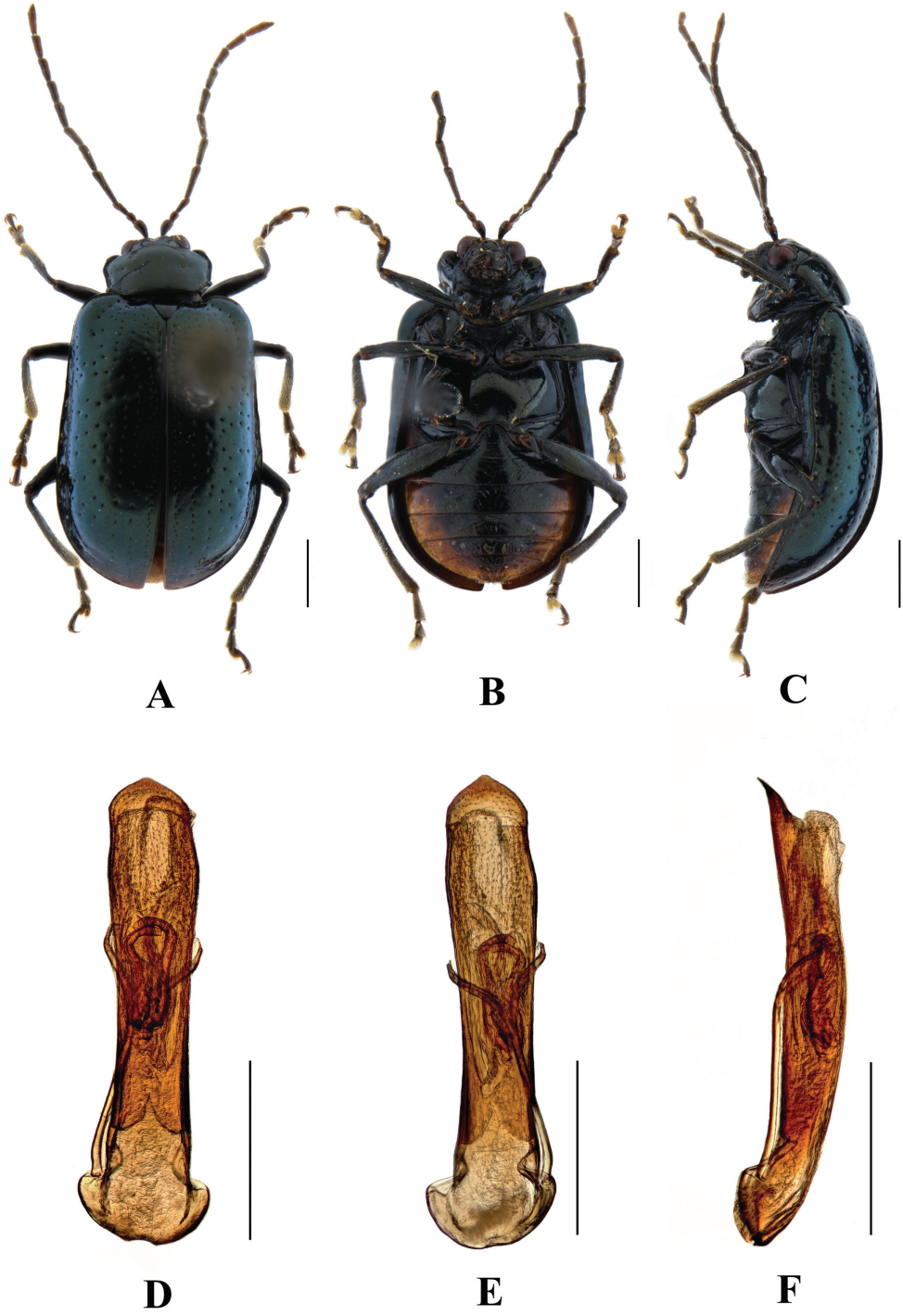

Figure 8. *Aplosonyx emeishanica* **A–C** habitus **D–F** aedeagus **A, D** dorsal views **B, E** ventral views **C, F** lateral views. Scale bars 0.5 mm (**D–F**); 1 mm (**A–C**).

Antennae slightly thinner than in male, antennomere 2 shortest, antennomere 3 approximately 1.2 × as long as second; antennomere 4 longest, 1.5 × as long as antennomeres 2 and 3 combined; apical sternite without incisions.

Distribution. China: Sichuan.

Aplosonyx flavipennis Chen, 1964

Figs 2F, 9A–F

Aplosonyx flavipennis Chen, 1964: 203.

Type specimens examined. ***Holotype*:** ♂, China, **Yunnan Province**, Xishuangbanna, Menghun; 750 m a. s. l.; 3 Jun. 1958; IZAS; IOZ(E)215625.

***Paratype*:** ♂, China, **Yunnan Province**, Xishuangbanna, Menga; 1050 m a. s. l.; 7 Jun. 1958; Shuyong Wang leg.; IZAS; IOZ(E)215627. ♀, China, **Yunnan Province**, Xishuangbanna, Menga; 1050 m a. s. l.; 7 Jun. 1958; Shuyong Wang leg.; IZAS; IOZ(E)215628. ♀, China, **Yunnan Province**, Xishuangbanna, Menga; 1050 m a. s. l.; 7 Jun. 1958; Shuyong Wang leg.; IZAS; IOZ(E)215629.

***Allotype*:** ♀, China, **Yunnan Province**, Xishuangbanna, Mengzhe; 870 m a. s. l.; 7 Jul. 1958; Shuyong Wang leg.; IZAS; IOZ(E)215626.

Additional specimens examined. ♀, China, **Yunnan Province**, Xishuangbanna, Menga; 1050 m a. s. l.; 7 Jun. 1958; Shuyong Wang leg.; IZAS; IOZ(E)1566487. ♀, China, **Yunnan Province**, Xishuangbanna, Menga; 1050 m a. s. l.; 7 Jun. 1958; Shuyong Wang leg.; IZAS; IOZ(E)1566488. ♀, China, **Yunnan Province**, Xishuangbanna, Menga; 1080 m a. s. l.; 7 Jun. 1958; Shuyong Wang leg.; IZAS; IOZ(E)1566489. ♂, China, **Yunnan Province**, Xishuangbanna, Menga; 1080 m a. s. l.; 11 May 1958; Fuji Pu leg.; IZAS; IOZ(E)1566490. ♂, China, **Yunnan Province**, Xishuangbanna, Menga; 1050 m a. s. l.; 7 May 1958; Chunpei Hong leg.; IZAS; IOZ(E)1566491. ♀, China, **Yunnan Province**, Xishuangbanna, Menga; 1050 m a. s. l.; 7 Jun. 1958; Shuyong Wang leg.; IZAS; IOZ(E)1566492. ♀, China, **Yunnan Province**, Xishuangbanna, Mengzhe; 1200 m a. s. l.; 15 Jun. 1958; Fuji Pu leg.; IZAS; IOZ(E)1566493. ♀, China, **Yunnan Province**, Xishuangbanna, Mengzhe; 1200 m a. s. l.; 15 Jun. 1958; Fuji Pu leg.; IZAS; IOZ(E)1566494. ♀, China, **Yunnan Province**, Xishuangbanna, Menga; 1050 m a. s. l.; 19 Jun. 1958; Fuji Pu leg.; IZAS; IOZ(E)1566496. ♀, China, **Yunnan Province**, Xishuangbanna, Menga; 1000 m a. s. l.; 19 Jun. 1958; Fuji Pu leg.; IZAS; IOZ(E)1566497. ♀, China, **Yunnan Province**, Xishuangbanna, Menga; 1050 m a. s. l.; 7 Jun. 1958; Shuyong Wang leg.; IZAS; IOZ(E)1566498. ♀, China, **Yunnan Province**, Xishuangbanna, Mengzhe; 870 m a. s. l.; 30 Jul. 1958; Shuyong Wang leg.; IZAS; IOZ(E)1566499. ♀, China, **Yunnan Province**, Xishuangbanna, Menga; 1050 m a. s. l.; 17 Oct. 1958; Zhizi Chen leg.; IZAS; IOZ(E)1566500. ♀, China, **Yunnan Province**, Xishuangbanna, Menghun; 750 m a. s. l.; 3 Jun. 1958; Zhizi Chen leg.; IZAS; IOZ(E)1566502. ♀, China, **Yunnan Province**, Xishuangbanna, Menghun; 750 m–950 m a. s. l.; 7 May 1958; Chunpei Hong leg.; IZAS; IOZ(E)1566482. ♂, China, **Yunnan Province**, Xishuangbanna, Menghun; 750 m a. s. l.; 7 May 1958; Chunpei Hong leg.; IZAS; IOZ(E)1566483.

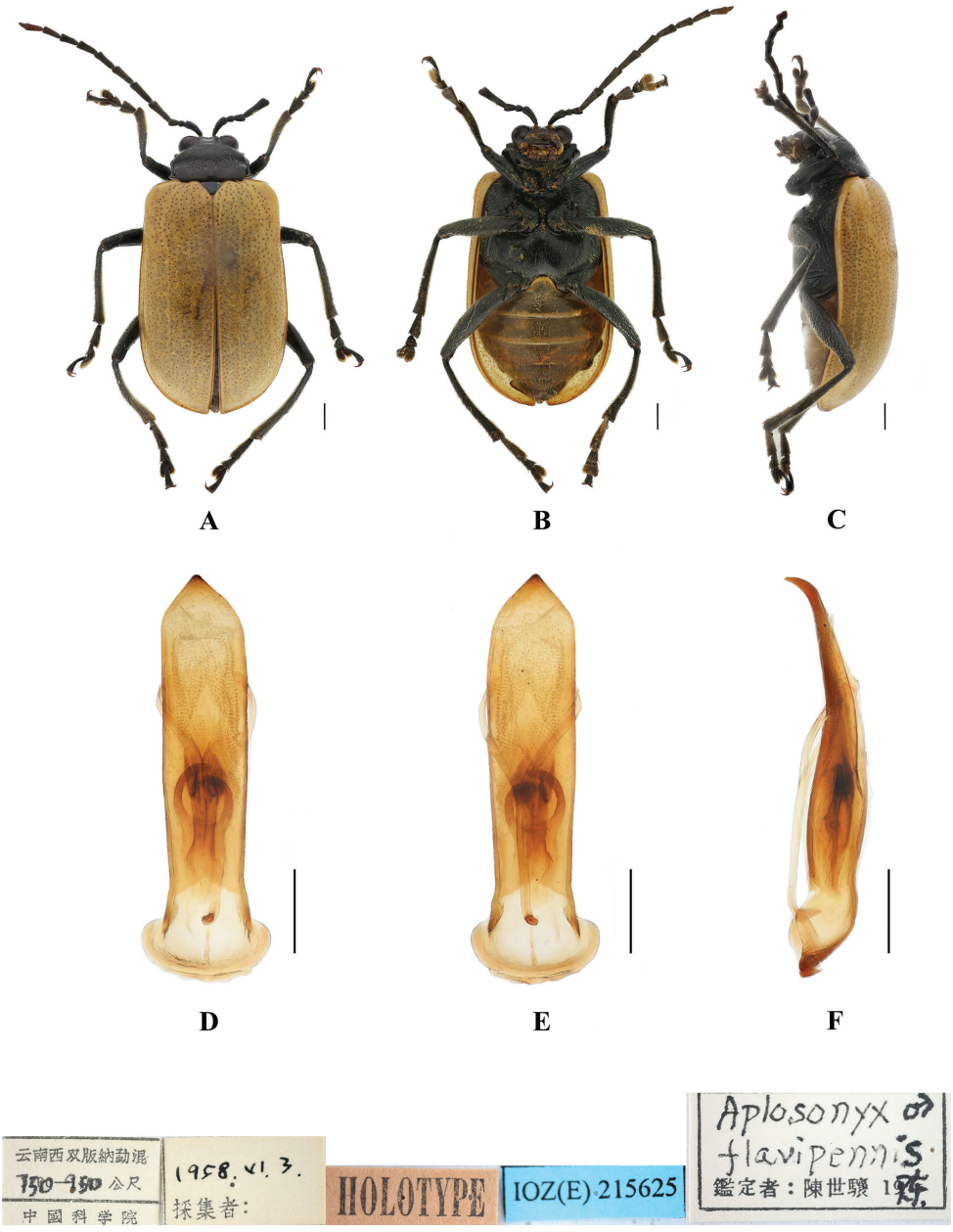

Figure 9. *Aplosonyx flavipennis* **A–C** habitus of holotype, IZAS IOZ(E)215625 **D–F** aedeagus **A, D** dorsal views **B, E** ventral views **C, F** lateral views. Scale bars 0.5 mm (**D–F**); 1 mm (**A–C**).

Diagnosis. This species can be distinguished from other Chinese species by its black head and pronotum, and the elytra without any spots. This species differs from *A. duvivieri* in the color of the head, pronotum, scutellum, and ventral surface of thorax being black.

Redescription. Male. Length 8.8–10.8 mm, width 4.8–6.0 mm.

Head, antennae, pronotum, scutellum, leg, and ventral surface of thorax black, elytra and abdomen yellow.

Vertex finely covered with punctures. Interocular space 2 × as wide as transverse diameter of eye. Interantennal space 1.5 × as wide as transverse diameter of antennal socket. Frontal tubercles transverse, distinctly raised, each separated by a deep furrow; antennae slender, 0.75 × as long as body; antennomeres 1–3 shiny; antennomeres 4–11 covered with pubescence, antennomere 2 shortest, antennomere 3 approximately 1.4 × as long as second; antennomere 4 longest, approximately 1.8 × as long as antennomeres 2 and 3 combined; antennomeres 5–10 gradually shortened, shorter than antennomere 4; antennomere 11 slightly longer than antennomere 10, pointed.

Pronotum approximately 1.8 × as wide as long, lateral border margined, widest at posterior corners; disc with deep transverse furrow, closely covered with large punctures in furrow and sparsely with small punctures in other parts of pronotum, the interstices of punctures equal to diameter of individual punctures in furrow, and smooth, impunctate in middle of furrow.

Scutellum triangular, finely covered with punctures.

Elytra: wider than pronotum, 0.8 × as long as body, 1.7 × as long as wide, epipleura moderately wide at anterior 1/4, posteriorly gradually narrowing towards apex, dorsal surface slightly convex, regularly covered with large and deep punctures, partially arranged in twenty rows in each elytron, the interstices between punctures wider than the diameter of individual punctures, approximately 2 × as wide as diameter of punctures and lightly covered with small punctures in the interstices.

Metasternum 2 × as long as mesosternum. Ventral surface of abdomen with five ventrites, ventrite 1 longest, ventrites 2–4 gradually shortened, apical ventrite slightly longer than ventrite 4, with two subtriangular incisions.

Aedeagus slender, parallel-sided, basally widened, narrowed in middle, apex distinctly pointed, in lateral view base and apex distinctly bent.

Female. Length 9.0–10.2 mm, width 4.8–5.5 mm.

Antennae slightly thinner than in male, antennomere 2 shortest, antennomere 3 1.6 × as long as second; antennomere 4 longest, 2 × as long as antennomeres 2 and 3 combined; apical sternite without incisions.

Distribution. China: Yunnan.

***Aplosonyx fulvescens* Chen, 1964, stat. nov.**
Figs 10A–F, 11A

Aplosonyx ancora fulvescens Chen, 1964: 204.

Type specimens examined. ***Holotype*:** ♂, China, **Hainan Province**; 25 Mar. 1934; IZAS; IOZ(E)215620.

***Paratype*:** ♂, same data as for preceding; IOZ(E)215622. ♀, China, **Fujian Province**, Fuzhou; IZAS; IOZ(E)215621.

Additional specimens examined. ♀, China, **Hainan Province**, Bawangling; 9 Apr. 1984; IZAS; IOZ(E)1566741. ♀, same data as for preceding; 28 Sep. 1981; IZAS; IOZ(E)1566743. 1♂1♀, China, **Hainan Province**, Jianfengling, Wufeng; 9 May 1981; Shaoying Liang leg.; SYSU. ♀, same data as for preceding, Sanfeng; 26 Aug. 1981; Shaoying Liang leg.; SYSU.

Diagnosis. Chen (1964) described the subspecies *Aplosonyx ancora fulvescens* from three specimens collected in Hainan and Fujian. Examination of the type specimen and the additional seven specimens revealed that this subspecies differs from *Aplosonyx ancora* in antennae with antennomeres 1–3 yellow and antennomeres 4–11 brown, the pronotum and elytra sparsely covered with small punctures, the apex of the aedeagus slightly pointed,

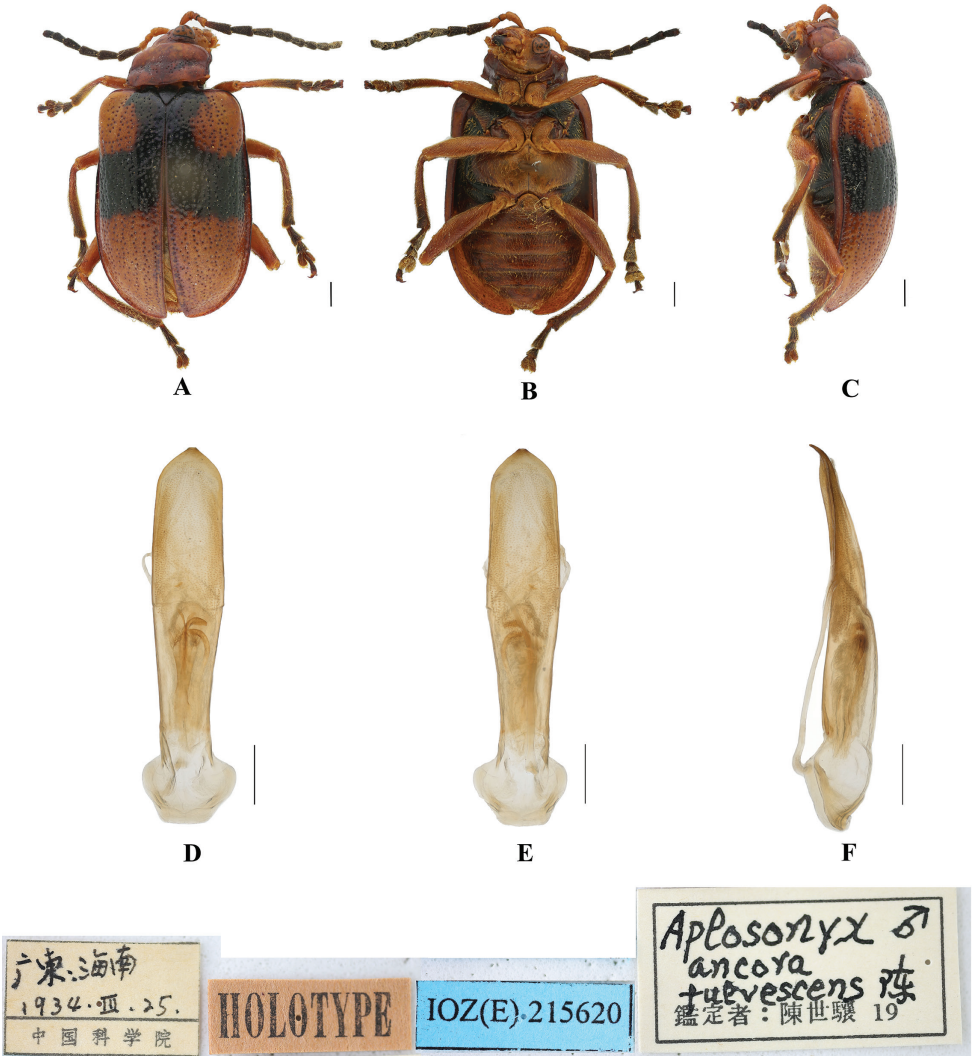

Figure 10. *Aplosonyx fulvescens* **A–C** habitus of holotype, IZAS IOZ(E)215620 **D–F** aedeagus **A, D** dorsal views **B, E** ventral views **C, F** lateral views. Scale bars 0.5 mm (**D–F**); 1 mm (**A–C**).

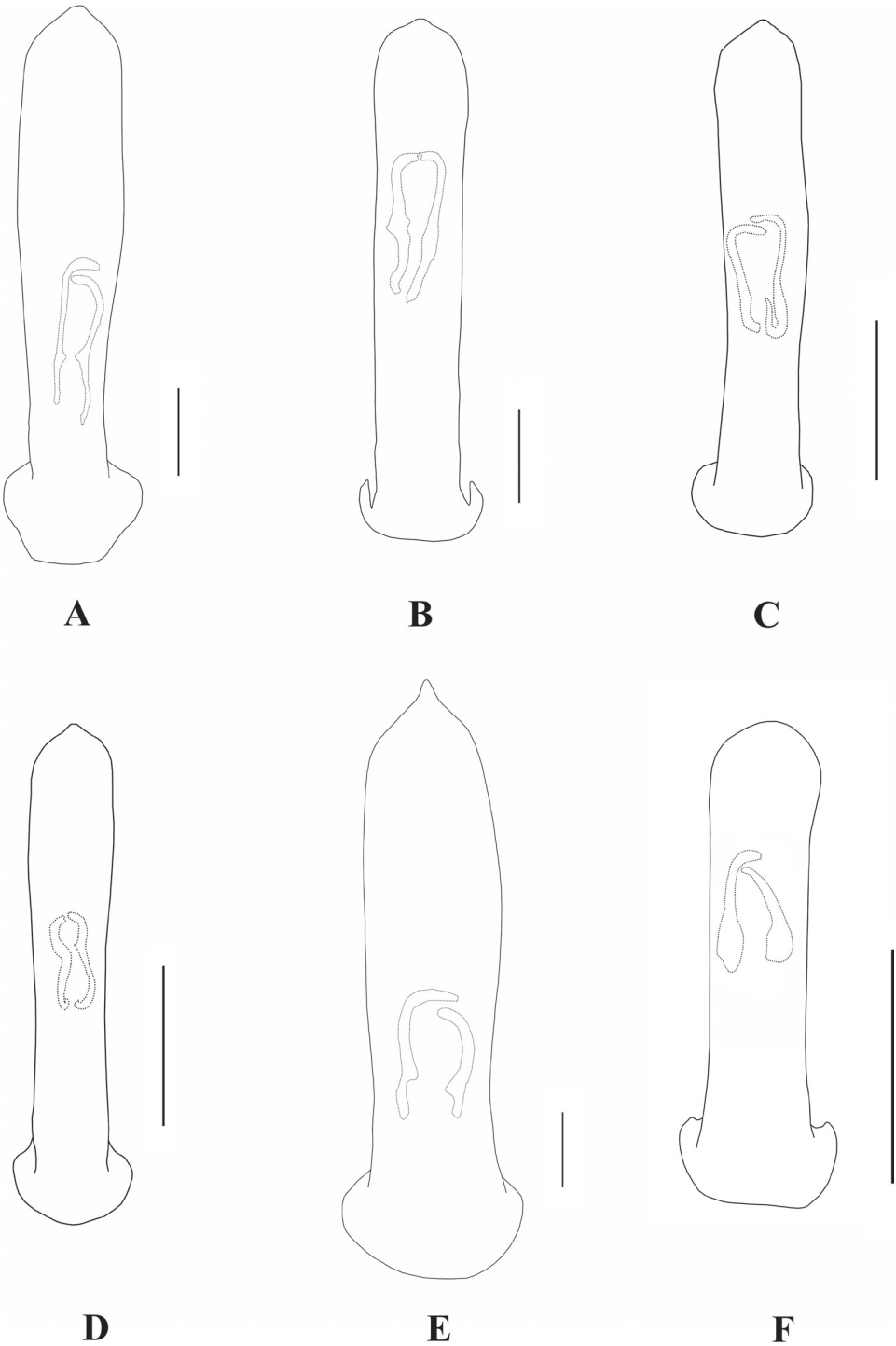

Figure 11. Aedeagus in dorsal view **A** *A. fulvescens* **B** *A. gancuicus* **C** *A. nigriceps* **D** *A. omeiensis* **E** *A. orientalis* **F** *A. ornatus*. Scale bars: 0.5 mm (**A–E**).

in lateral view apex is bent, the base is wide, and it gradually narrows to the apex. The pronotum and elytra of *Aplosonyx ancora* are densely covered with punctures, the antennomeres 1–6 yellow, the aedeagus apex is distinctly pointed. Because these differences are constant among the specimens examined, we elevate the subspecies *fulvescens* to species level. This species is also similar to *Aplosonyx ancorella* sp. nov., which differs in the antennae with antennomeres 1–7 yellow and antennomeres 8–11 brown, the abdomen with five pairs of black spots, and the pronotum and elytra densely covered with large punctures.

Redescription. Male. Length 10.6–12.6 mm, width 5.8–6.8 mm.

Head, pronotum, abdomen and leg yellow, elytra reddish brown, antennae brown with antennomeres 1–3 yellow, scutellum black, ventral surface of thorax black with yellow middle, pronotum with 1 small black spot in base, elytra with a broad purplish band from anterior to middle, which extends forward along suture and expends again on base.

Vertex finely covered with punctures. Interocular space 2.2 × as wide as transverse diameter of eye. Interantennal space 1.4 × as wide as transverse diameter of antennal socket. Frontal tubercles transverse, distinctly raised, each separated by a deep furrow; antennae slender, 0.65 × as long as body; antennomeres 1–3 shiny; antennomeres 4–11 covered with pubescence, antennomere 2 shortest, antennomere 3 approximately 1.5 × as long as second; antennomere 4 longest, approximately 1.5 × as long as antennomeres 2 and 3 combined; antennomeres 5–10 gradually shortened, shorter than antennomere 4; antennomere 11 slightly longer than antennomere 10, pointed.

Pronotum approximately 2 × as wide as long, lateral border margined, widest at posterior corners, disc with transverse furrow, sparsely covered with several large punctures, the interstices of punctures equal to diameter of individual punctures.

Scutellum triangular, finely covered with punctures.

Elytra wider than pronotum, 0.78 × as long as body, 1.65 × as long as wide, epipleura wide at anterior 1/4, posteriorly gradually narrowing towards apex, dorsal surface slightly convex, irregularly covered with punctures, the interstices of punctures equal to diameter of individual punctures and lightly covered with small punctures in the interstices.

Metasternum 2 × as long as mesosternum. Ventral surface of abdomen with five ventrites, ventrite 1 longest, ventrites 2–4 gradually shortened, apical ventrite slightly longer than ventrite 3, two subtriangular incisions.

Aedeagus slender, basally widened, apex slightly pointed, in lateral view apex bent.

Female. Length 10.8–12.4 mm, width 6.0–6.8 mm.

Antennae slightly thinner than in male, antennomere 2 shortest, antennomere 3 longer than antennomere 2, approximately 1.8 × as long as second; antennomere 4 longest, 1.6 × as long as antennomeres 2 and 3 combined; apical sternite without incisions.

Distribution. China: Fujian, Hainan.

Aplosonyx gancuicus (Chen, 1942)

Figs 11B, 12A–F

Galerucida [sic!] *gancuica* Chen, 1942: 38.

Gallerucida gancuica: Gressitt and Kimoto 1963: 724.
Aplosonyx gancuica: Xu, Nie and Yang 2022: 52.

Type specimen examined. *Holotype*: ♂, China, **Gansu Province**; 8 May 1919; IZAS. IOZ(E)215680.

Diagnosis. This species can be distinguished from other species by the elytra with a broad black band at the side, which extends along the lateral margin of each elytron, and three black spots on each side of the suture.

Redescription. Male. Length 6.1 mm, width 3.6 mm.

Head, antennae, pronotum, scutellum, legs, and ventral surface of body black, elytra yellow, each elytron with a broad black band and three black spots.

Vertex sparsely covered with punctures. Interocular space 2 × as wide as transverse diameter of eye. Interantennal space 1.8 × as wide as transverse diameter of antennal socket. Frontal tubercles transverse and raised, each separated by a deep furrow; antennae slender, antennomeres 1–3 shiny; antennomeres 4–8 covered with pubescence, antennomere 2 shortest, antennomere 3 approximately 1.5 × as long as second; antennomere 4 longest, approximately 1.5 × as long as antennomeres 2 and 3 combined; antennomeres 5–8 gradually shortened, shorter than antennomere 4.

Pronotum 1.8 × as wide as long, lateral border margined, widest at posterior corners, disc with sparse punctures.

Scutellum triangular, finely covered with punctures.

Elytra: wider than pronotum, 0.7 × as long as body, 1.6 × as long as wide, epipleura moderately wide at anterior 1/3, posteriorly gradually narrowing towards apex, dorsal surface slightly convex, covered with large deep punctures, partially arranged in ten rows in each elytron, the interstices between punctures wider than diameter of individual punctures, approximately 2 × as wide as the diameter of individual punctures and lightly covered with small punctures in interstices.

Metasternum 2 × as long as mesosternum. Ventral surface of abdomen with five ventrites, ventrite 1 longest, ventrites 2–4 gradually shortened, apical ventrite slightly longer than ventrite 3, with two subtriangular incisions.

Aedeagus slender, parallel-sided, apically pointed, in lateral view moderately wavy in apex.

Distribution. China: Gansu.

Aplosonyx nigriceps Yang, 1995

Figs 11C, 13A–F

Aplosonyx nigriceps Yang, 1995: 91.

Type specimens examined. *Holotype*: ♂, China, **Hubei Province**, Lichuan; 1300 m a. s. l.; 23 Jul. 1989; Shuyong Wang leg.; IZAS.

***Allotype*:** ♀, China, **Hubei Province**, Lichuan, Xingdou Mt; 810 m a. s. l.; 22 Jul. 1989; Shuyong Wang leg.; IZAS.

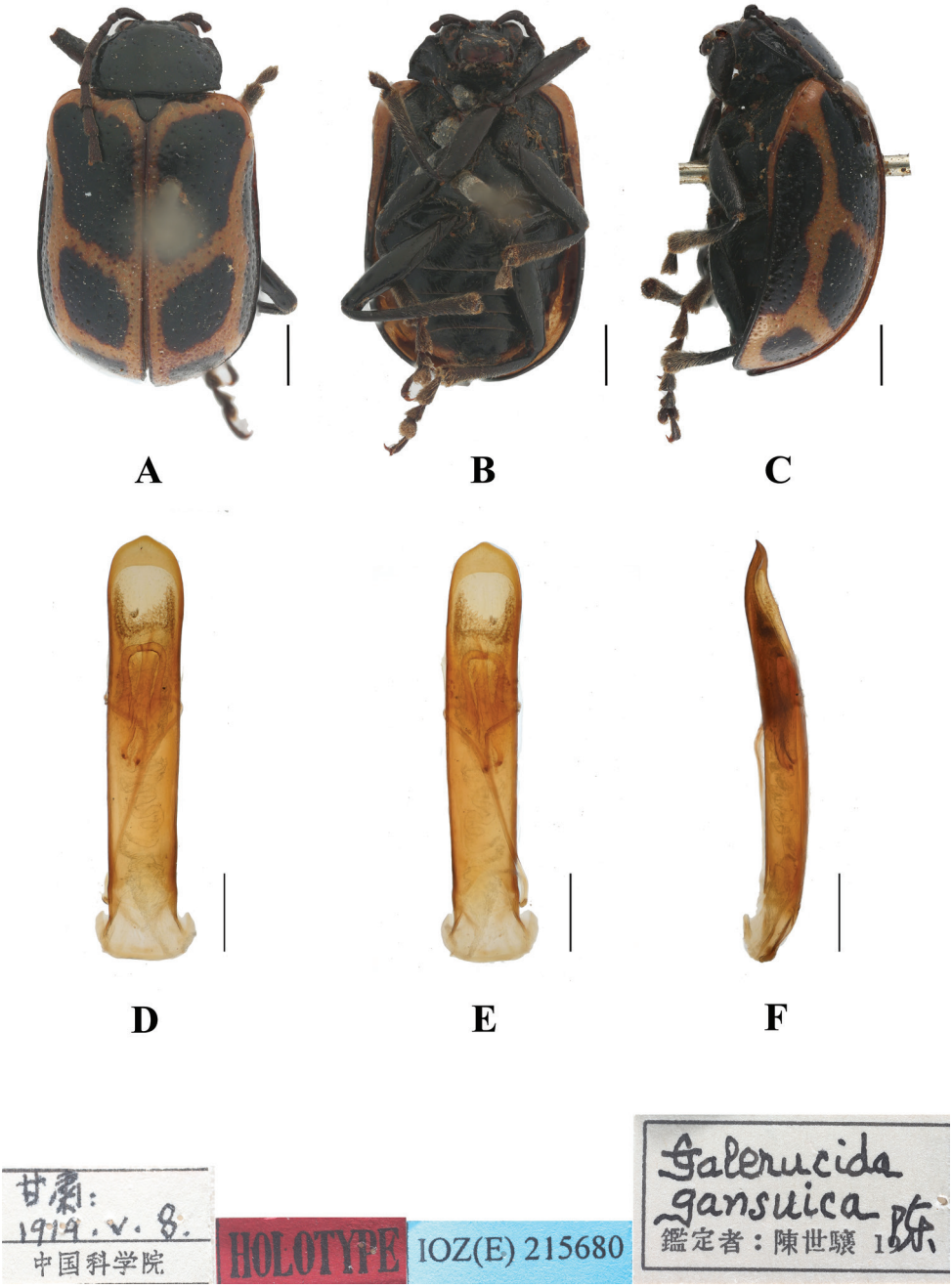

Figure 12. *Aplosonyx gansuica* **A–C** habitus of holotype, IZAS IOZ(E)215680 **D–F** aedeagus **A, D** dorsal views **B, E** ventral views **C, F** lateral views. Scale bars 0.5 mm (**D–F**); 1 mm (**A–C**).

***Paratype*:** 1♂1♀, China, **Hubei Province**, Lichuan; 1300 m a. s. l.; 23 Jul. 1989; Shuyong Wang leg.; IZAS. ♂, China, **Hubei Province**, Lichuan, Xingdou Mt; 1100 m a. s. l.; 22 Jul. 1989; Shuyong Wang leg.; IZAS. 2♀♀, China, **Hubei**

Province, Lichuan, Xingdou Mt; 1100 m a. s. l.; 22 Jul. 1989; Shuyong Wang leg.; IZAS. ♂, China, **Hubei Province**, Hefeng, shayuan; 1300 m a. s. l.; 1 Aug. 1989; Shuyong Wang leg.; IZAS. ♀, China, **Hubei Province**, Badong; 1700 m a. s. l.; 21 May 1989; Wenzhen Ma leg.; IZAS.

Diagnosis. This species can be distinguished from other species by its black pronotum, and each elytron with five black spots: one at the base near the scutellum, a pair in the middle, and apically two spots which are connected. This species differs from *A. omeiensis* in having a black head and pronotum, the abdomen yellowish brown, and the shape of the spots on the elytra.

Redescription. Male. Length 4.5–5.0 mm, width 2.7–3.2 mm.

Head, pronotum and scutellum black, antennae, ventral surface of the thorax and legs brown, abdomen yellowish brown, elytra yellow, each elytron with five black spots, one at base near scutellum, a pair in the middle, and a pair of apical spots which are connected.

Vertex finely and sparsely covered with punctures. Interocular space 2.1 × as wide as transverse diameter of eye. Interantennal space 1.5 × as wide as transverse diameter of antennal socket. Frontal tubercles transverse, each separated by a deep furrow; antennae slender, 0.75 × as long as body; antennomeres 1–3 shiny; antennomeres 4–11 covered with pubescence, antennomeres 2 and 3 shortest, antennomere 3 nearly equal in length and shape to antennomere 2, antennomere 4 longest, approximately 1.5 × as long as antennomeres 2 and 3 combined; antennomeres 5–10 gradually shortened, shorter than antennomere 4; antennomere 11 slightly longer than 10, pointed.

Pronotum 1.9 × as wide as long, lateral border margined, widest at anterior 1/3; disc with deep transverse furrow, less distinct in middle; closely covered with large punctures in furrow and with sparsely small punctures in other parts of pronotum.

Scutellum triangular, finely covered with punctures.

Elytra: wider than pronotum, 0.7 × as long as body, 1.5 × as long as wide, epipleura wide at anterior 1/3, posteriorly gradually narrowing towards apex, dorsal surface slightly convex, regularly covered with large and deep punctures, partially arranged in ten rows in each elytron, the interstices between punctures wider than diameter of individual punctures, approximately 2.5 × as wide as the diameter of individual punctures and lightly covered with small punctures in interstices.

Metasternum 2 × as long as mesosternum. Ventral surface of abdomen with five ventrites, ventrite 1 longest, ventrites 2–4 gradually shortened, apical ventrite slightly longer than ventrite 3, with two subtriangular incisions.

Aedeagus slender, parallel-sided, basally widened, apically pointed, in lateral view moderately bent.

Female. Length 4.6–5.0 mm, width 2.8–3.2 mm.

Antennae slightly thinner than in male, without short hairs, antennomere 4 longest, approximately 1.2 × as long as antennomeres 2 and 3 combined; apical sternite without incisions.

Distribution. China: Hubei, Sichuan.

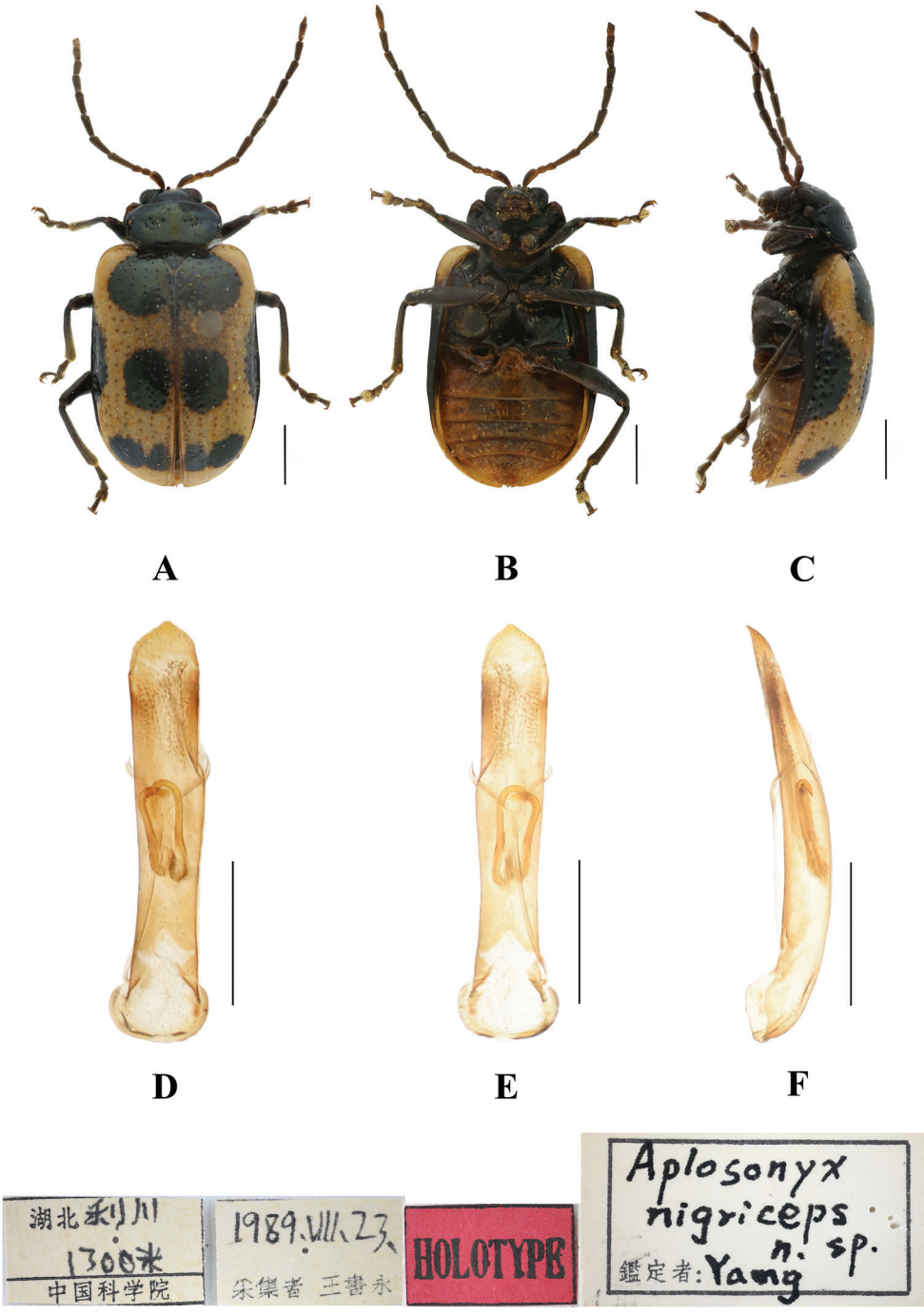

Figure 13. *Aplosonyx nigriceps* **A–C** habitus of holotype, IZAS **D–F** aedeagus **A, D** dorsal views **B, E** ventral views **C, F** lateral views. Scale bars 0.5 mm (**D–F**); 1 mm (**A–C**).

***Aplosonyx omeiensis* Chen, 1942**
Figs 11D, 14A–F

Aplosonyx pictus omeiensis Chen, 1942: 40.
Aplosonyx omeiensis: Zhang et al. 2008: 65. Raised from *Aplosonyx pictus omeiensis* Chen.

Type specimens examined. ***Paratypes*:** 2♂♂3♀♀, China, **Sichuan Province**, Mount Emei, Sep. 1912; IZAS.

Additional specimens examined. ♂, China, **Sichuan Province**, Mount Emei, Jiulaodong; 1800 m a. s. l.; 7 Jul. 1957; Fuxing Zhu leg.; IZAS. ♂, China, **Sichuan Province**, Mount Emei, Jiulaodong; 1800 m a. s. l.; 16 Jun. 1957; Youcai Yu leg.; IZAS. ♂, China, **Sichuan Province**, Mount Emei, Jiulaodong; 1800 m a. s. l.; 7 Jul. 1957; Zongyuan Wang leg.; IZAS; IOZ(E)1566650. ♂, China, **Sichuan Province**, Mount Emei, 17 Jun. 1955; Keren Huang leg.; IZAS; IOZ(E)1566630. ♀, China, **Sichuan Province**, Mount Emei, 17 Jun. 1955; Keren Huang leg.; IZAS; IOZ(E)1566632. ♀, China, **Sichuan Province**, Mount Emei, 17 Jun. 1955; Keren Huang leg.; IZAS; IOZ(E)1566639. ♂, China, **Sichuan Province**, Mount Emei, 17 Jun. 1955; Keren Huang leg.; IZAS; IOZ(E)1566647. ♂, China, **Sichuan Province**, Mount Emei, 1800 m a. s. l.; 24 Jun. 1955; Bingrong Ou leg.; IZAS; IOZ(E)1566634. ♂, China, **Sichuan Province**, Mount Emei, 1800 m a. s. l.; 23 Jun. 1955; Bingrong Ou leg.; IZAS; IOZ(E)1566635. ♂, China, **Sichuan Province**, Mount Emei, 2100 m a. s. l.; 24 Jun. 1955; Bingrong Ou leg.; IZAS; IOZ(E)1566636.

Diagnosis. This species can be distinguished from other species by the pronotum with a black spot, each elytron with five black spots, the middle and apex with one pair of spots, and one spot at the base. This species differs from *A. nigriceps* in having a black abdomen with pale margins.

Redescription. Male. Length 4.6–4.8 mm, width 2.6–2.8 mm.

Head, antennae, pronotum, elytra and leg yellow, vertex, scutellum and ventral surface of the body black, abdomen with pale margins, pronotum with a black spot in middle, each elytron with five black spots, middle and apex with one pair of spots, and base with one spot.

Vertex finely and sparsely covered with punctures. Interocular space 2 × as wide as transverse diameter of eye. Interantennal space 1.5 × as wide as transverse diameter of antennal socket. Frontal tubercles transverse, each separated by a deep furrow; antennae slender, 0.7 × as long as body; antennomeres 1–3 shiny; antennomeres 4–11 covered with pubescence, antennomere 2 shortest, antennomere 3 twice as long as second; antennomere 4 longest, approximately 1.2 × as long as antennomeres 2 and 3 combined; antennomeres 5–10 gradually shortened, shorter than antennomere 4; antennomere 11 slightly longer than antennomere 10, pointed.

Pronotum 1.8 × as wide as long, lateral border margined, widest at anterior 1/3; disc with deep transverse furrow, covered with several punctures in furrow and with sparsely small punctures in other parts of pronotum.

Scutellum triangular, finely covered with punctures.

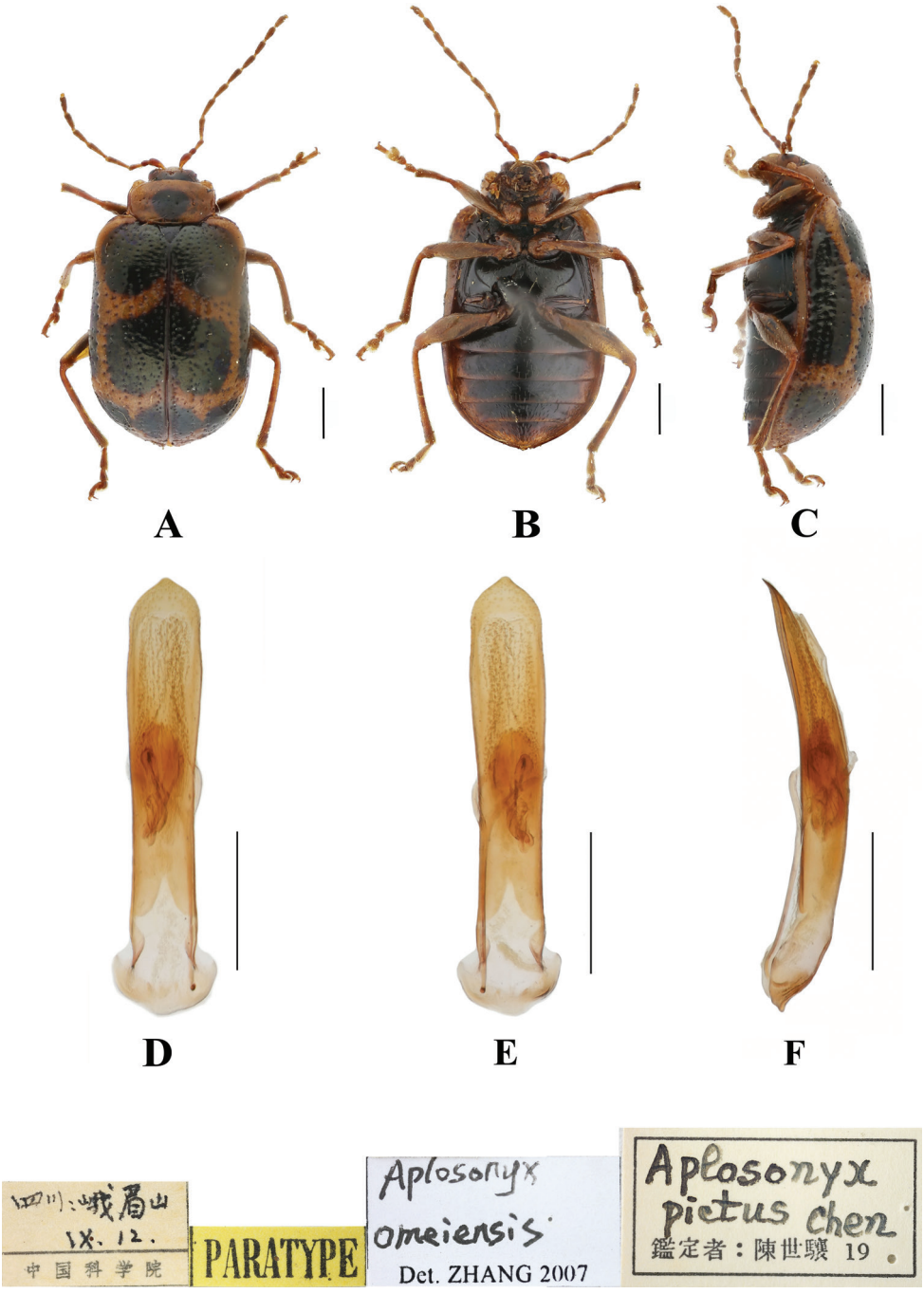

Figure 14. *Aplosonyx omeiensis* **A–C** habitus of paratype, IZAS **D–F** aedeagus **A, D** dorsal views **B, E** ventral views **C, F** lateral views. Scale bars 0.5 mm (**D–F**); 1 mm (**A–C**).

Elytra wider than pronotum, 0.7 × as long as body, 1.6 × as long as wide, epipleura wide at anterior 1/3, posteriorly gradually narrowing towards apex; dorsal surface slightly convex, covered with punctures in irregular rows, the interstices 2 × as wide as diameter of punctures and slightly covered with fine punctuation.

Metasternum 2 × as long as mesosternum. Ventral surface of abdomen with five ventrites, ventrite 1 longest, ventrites 2–4 gradually shortened, apical ventrite slightly longer than ventrite 3, with two subtriangular incisions.

Aedeagus slender, parallel-sided, slightly narrowed in middle, basally widened, apex pointed, in lateral view slightly bent.

Female. Length 4.4–4.8 mm, width 2.6–3.0 mm.

Antennae slightly thinner than in male, antennomere 2 shortest, antennomere 3 approximately 1.5 × as long as second; antennomere 4 longest, 1.5 × as long as antennomeres 2 and 3 combined; apical sternite without incisions.

Distribution. China: Sichuan.

Aplosonyx orientalis Jacoby, 1892

Figs 11E, 15A–D, 16A–F

Haplosonyx orientalis Jacoby, 1892: 962.
Haplosonyx varipes Jacoby, 1892: 964. Synonymized by Kimoto 1989: 171.
Sphenoraia tonkinensis Laboissière, 1922: 102. Synonymized by Kimoto 1989: 172.
Aplosonyx orientalis: Maulik 1936: 619.

Type specimen examined. ♀ ***Syntype*** of *Haplosonyx varipes*: *Haplosonyx varipes* Jac.; Malewoon (Tenasserim)L. Fea. VII. VIII. 87; Jacoby Coll. 1909-28a.; Type H. T.; NHMUK 014596215.

Additional specimens examined. 8♂♂7♀♀, China, **Guangdong Province**, Enping Qixingkeng; 22 Jun. 2022; Chuan Feng leg.; IZGAS. 4♂♂6♀♀, China, **Guangxi Province**, Maoershan; 25 Aug. 2020; IZGAS. ♂, China, **Yunnan Province**, Xishuangbanna, Menghun; 1200 m a. s. l.; 24 May 1958; Xuwu Meng leg.; IZAS; IOZ(E)1566693. ♂, China, **Yunnan Province**, Xishuangbanna, Menghun; 1200 m a. s. l.; 2 Jun. 1958; Xuwu Meng leg.; IZAS; IOZ(E)1566699. ♂, China, **Yunnan Province**, Xishuangbanna, Menga; 1000 m a. s. l.; 20 May 1958; Fuji Pu leg.; IZAS; IOZ(E)1566695. ♀, China, **Yunnan Province**, Xishuangbanna, Mengzhe; 870 m a. s. l.; 5 Sep. 1958; Shuyong Wang leg.; IZAS; IOZ(E)1566694. ♀, China, **Yunnan Province**, Xishuangbanna, Mengzhe; 870 m a. s. l.; 6 Jul. 1958; Fuji Pu leg.; IZAS; IOZ(E)1566697. ♂, China, **Yunnan Province**, Xishuangbanna, Xiaomengyang; 850 m a. s. l.; 5 Jul. 1958; Lingchao Zang leg.; IZAS; IOZ(E)1566696. ♂, China, **Yunnan Province**, Xishuangbanna, Damenglong; 650 m a. s. l.; 6 May 1958; Chunpei Hong leg.; IZAS; IOZ(E)1566698. ♀, China, **Yunnan Province**, Cheli, Damenglong; 600 m a. s. l.; 29 Apr. 1957; Dahua Liu leg.; IZAS; IOZ(E)1566700.

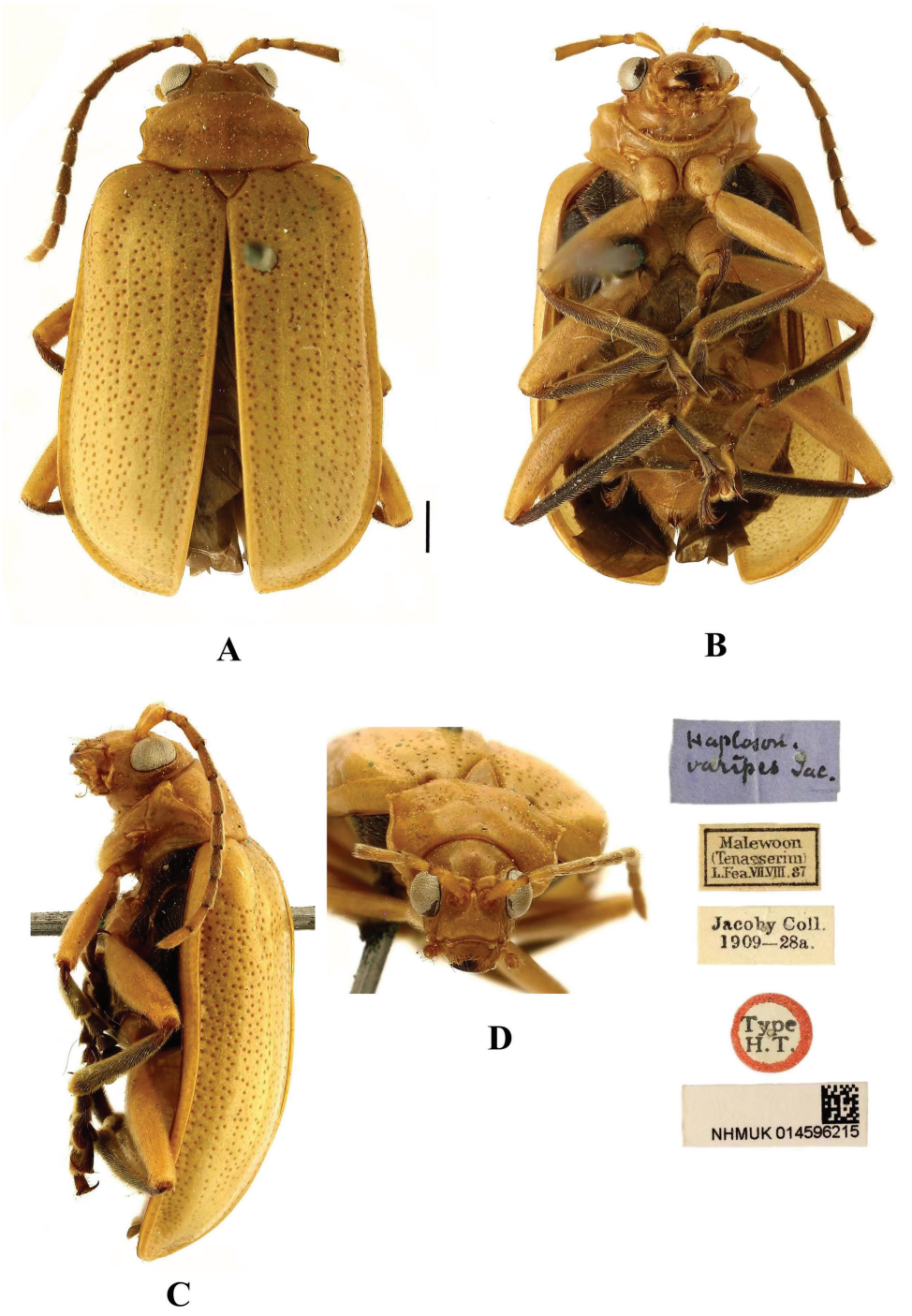

Figure 15. *Aplosonyx orientalis* **A–D** habitus of syntype, NHMUK **A** dorsal view **B** ventral view **C** lateral view **D** head view. Scale: 1 mm (**A–D**).

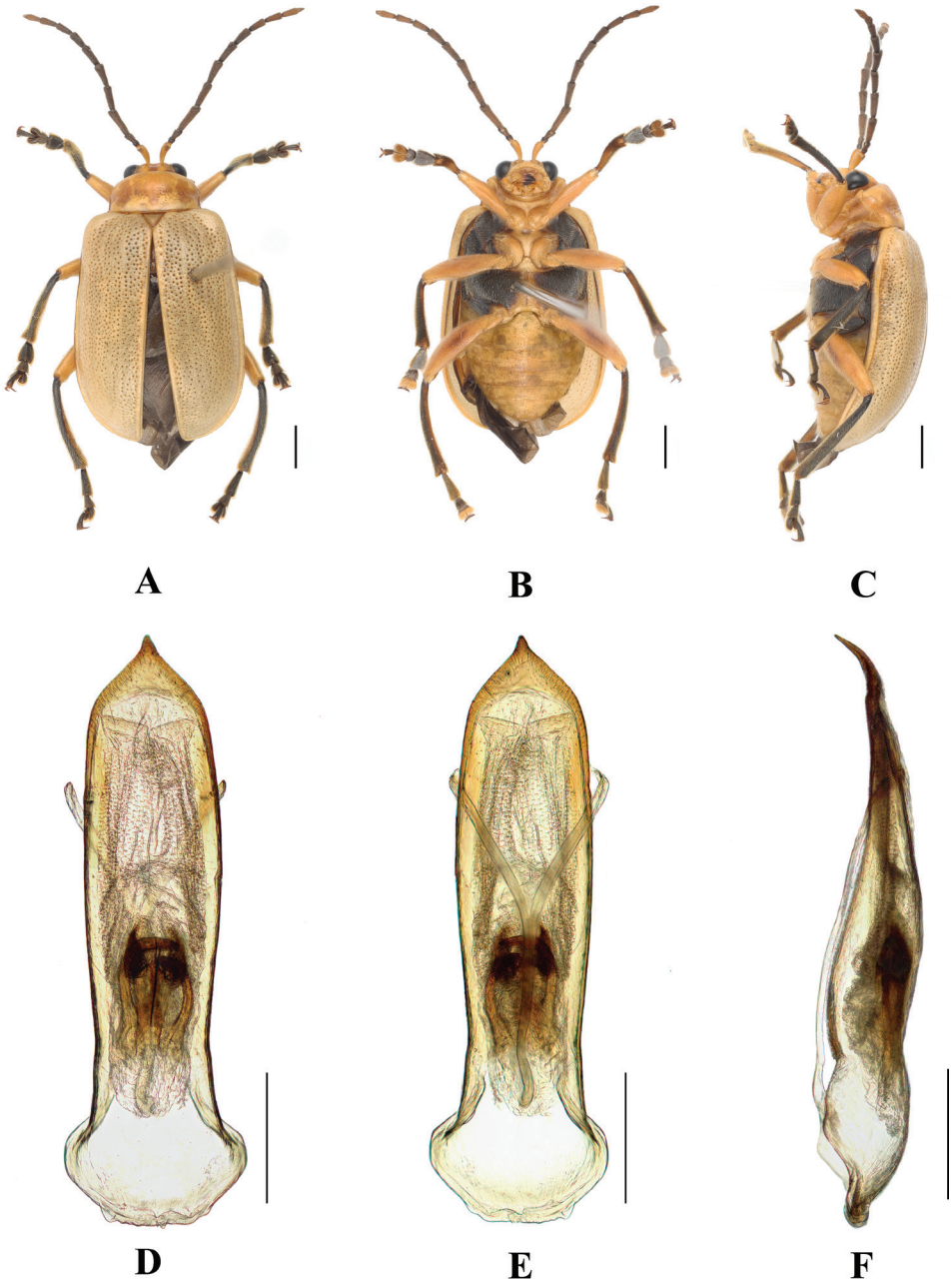

Figure 16. *Aplosonyx orientalis* **A–C** habitus **D–F** aedeagus **A, D** dorsal views **B, E** ventral views **C, F** lateral views. Scale bars 0.5 mm (**D–F**); 1 mm (**A–C**).

Diagnosis. This species can be distinguished from other species by the antennae with first antennomere yellow, and antennomeres 2–11 black; the legs are black with yellow femurs. This species differs from *A. cinctus* in having the aedeagus widened towards middle, in lateral view moderately bent.

Redescription. Male. Length 9.5–10.4 mm, width 5.0–5.8 mm.

Head, pronotum, elytra, scutellum, and abdomen yellow; antennae black with first antennomere yellow; ventral surface of thorax black and in middle area yellow; legs black with femur, inner sides of tibiae, coxae and trochanters are yellow.

Vertex finely covered with punctures. Interocular space 2 × as wide as transverse diameter of eye. Interantennal space 1.5 × as wide as transverse diameter of antennal socket. Frontal tubercles transverse, each separated by a deep furrow; antennae slender, 0.75 × as long as body; antennomeres 1–3 shiny; antennomeres 4–11 covered with pubescence, antennomere 2 shortest, antennomere 3 approximately 1.8 × as long as second; antennomere 4 longest, approximately 1.4 × as long as antennomeres 2 and 3 combined; antennomeres 5–10 gradually shortened, shorter than antennomere 4; antennomere 11 slightly longer than antennomere 10, pointed.

Pronotum approximately 2 × as wide as long, lateral border margined, widest at posterior corners; disc with deep transverse furrow, closely covered with large punctures in furrow and with sparse small punctures in other parts of pronotum, in furrow the interstices between the punctures equal to diameter of individual punctures.

Scutellum triangular, finely covered with punctures.

Elytra: wider than pronotum, 0.75 × as long as body, 1.55 × as long as wide, epipleura wide at anterior 1/4, posteriorly gradually narrowing towards apex, dorsal surface slightly convex, regularly covered with large and deep punctures, partially arranged in twenty rows in each elytron, the interstices of the punctures in rows approximately 2 × as wide as diameter of punctures and slightly covered with fine punctuation.

Metasternum 2 × as long as mesosternum. Ventral surface of abdomen with five ventrites, ventrite 1 longest, ventrites 2–4 gradually shortened, apical ventrite slightly longer than ventrite 3, with two subtriangular incisions.

Aedeagus gradually widening from base to middle, gradually narrowing from middle towards apex, at one tenth from apex strongly narrowing, ending in a pointed apex. in lateral view moderately bent, with distinctly bent apex.

Female. Length 9.2–10.5 mm, width 4.8–5.6 mm.

Antennae slightly thinner than in male, antennomere 2 shortest, antennomere 3 longer than antennomere 2, twice as long as second; antennomere 4 longest, 1.6 × as long as antennomeres 2 and 3 combined; apical sternite without incisions.

Distribution. China: Guangdong, Guangxi, Yunnan; Vietnam, Laos, Thailand, Myanmar, India.

***Aplosonyx ornatus* Jacoby, 1892**

Figs 11F, 17A–C, 18A–F

Haplosonyx ornata Jacoby, 1892: 963.
Aplosonyx ornata: Maulik, 1936: 622.

Type specimen examined. ♂ *Haploson. ornata* Jac.; Carin Chebà, 900–1100 m, L. Fea V XII-88; Jacoby Coll., 1909-28a.; syntype, NHMUK014596214.

Additional specimens examined. ♀, China, **Yunnan Province**, Xishuangbanna, Menga; 1050 m a. s. l.; 17 May 1958; Shuyong Wang leg.; IZAS; IOZ(E)1566589. ♀, China, **Yunnan Province**, Xishuangbanna, Menga; 1050 m a. s. l.; 12 May 1958; Shuyong Wang leg.; IZAS; IOZ(E)1566595. ♂, China, **Yunnan Province**, Xishuangbanna, Menga; 1080 m a. s. l.; 2 Jun. 1958; Fuji Pu leg.; IZAS; IOZ(E)1566596. ♂, China, **Yunnan Province**, Xishuangbanna, Menga; 1050 m a. s. l.; 2 Jun. 1958; Fuji Pu leg.; IZAS; IOZ(E)1566597. ♂, China, **Yunnan Province**, Xishuangbanna, Menga; 1050 m a. s. l.; 2 Jun. 1958; Fuji Pu leg.; IZAS; IOZ(E)1566596. ♂, China, **Yunnan Province**, Xishuangbanna, Menga; 1080 m a. s. l.; 2 Jun. 1958; Fuji Pu leg.; IZAS; IOZ(E)1566601. ♀, China, **Yunnan Province**, Xishuangbanna, Menghai, nuoshan; 1600 m a. s. l.; 24 Jul. 1958; Shuyong Wang leg.; IZAS; IOZ(E)1566613. 1♂1♀, China, **Yunnan Province**, Xishuangbanna, Menghai, nuoshan; 1200 m a. s. l.; 24 Apr. 1957; Lingchao Zang leg.; IZAS; IOZ(E)1566598. 1♂1♀, China, **Yunnan Province**, Xishuangbanna, Menghai, nuoshan; 1200 m a. s. l.; 28 Apr. 1957; Lingchao Zang leg.; IZAS; IOZ(E)1566600. 2♀♀, China, **Yunnan Province**, Xishuangbanna, Menghai, nuoshan; 1200 m a. s. l.; 24 Apr. 1957; Lingchao Zang leg.; IZAS; IOZ(E)1566617. ♀, China, **Yunnan Province**, Xishuangbanna, Menghun; 1400 m a. s. l.; 17 May 1958; Chunpei Hong leg.; IZAS; IOZ(E)1566590. ♂, China, **Yunnan Province**, Xishuangbanna, Menghun; 1200 m a. s. l.; 24 May 1958; Chunpei Hong leg.; IZAS; IOZ(E)1566591. ♂, China, **Yunnan Province**, Xishuangbanna, Menghun; 1200 m–1400 m a. s. l.; 19 May 1958; Yiran Zhang leg.; IZAS; IOZ(E)1566593. ♀, China, **Yunnan Province**, Xishuangbanna, Menghun; 1200 m a. s. l.; 21 May 1958; Xuwu Meng leg.; IZAS; IOZ(E)1566614. ♀, China, **Yunnan Province**, kunluo; 1050 m a. s. l.; 26 Apr. 1957; Qiuzhen Liang leg.; IZAS; IOZ(E)1566610.

Diagnosis. This species can be distinguished from the other species by its black pronotum and yellow elytra with a broad blackish band in the middle, which extends along the suture and onto the base.

Redescription. Male. Length 4.6–5.4 mm, width 3.0–3.4 mm.

Head, antennae, pronotum, scutellum ventral surface of body black or brown; elytra yellow with a broad blackish band in middle, which extends along suture and expends on base.

Vertex finely covered with punctures. Interocular space 1.6 × as wide as transverse diameter of eye. Interantennal space 1.2 × as wide as transverse diameter of antennal socket. Frontal tubercles distinctly raised, hook-like, each separated by a deep furrow; antennae slender, 0.75 × as long as body; antennomeres 1–3 shiny; antennomeres 4–11 covered with pubescence, antennomere 2 shortest, antennomere 3 approximately 1.6 × as long as second; antennomere 4 longest, approximately 1.5 × as long as antennomeres 2 and 3 combined; antennomeres 5–10 gradually shortened, shorter than antennomere 4; antennomere 11 slightly longer than antennomere 10, pointed.

Pronotum approximately 1.5 × as wide as long, lateral border margined, widest at posterior corners; disc with deep transverse furrow, sparsely covered with large punctures in furrow.

Scutellum triangular, finely covered with punctures.

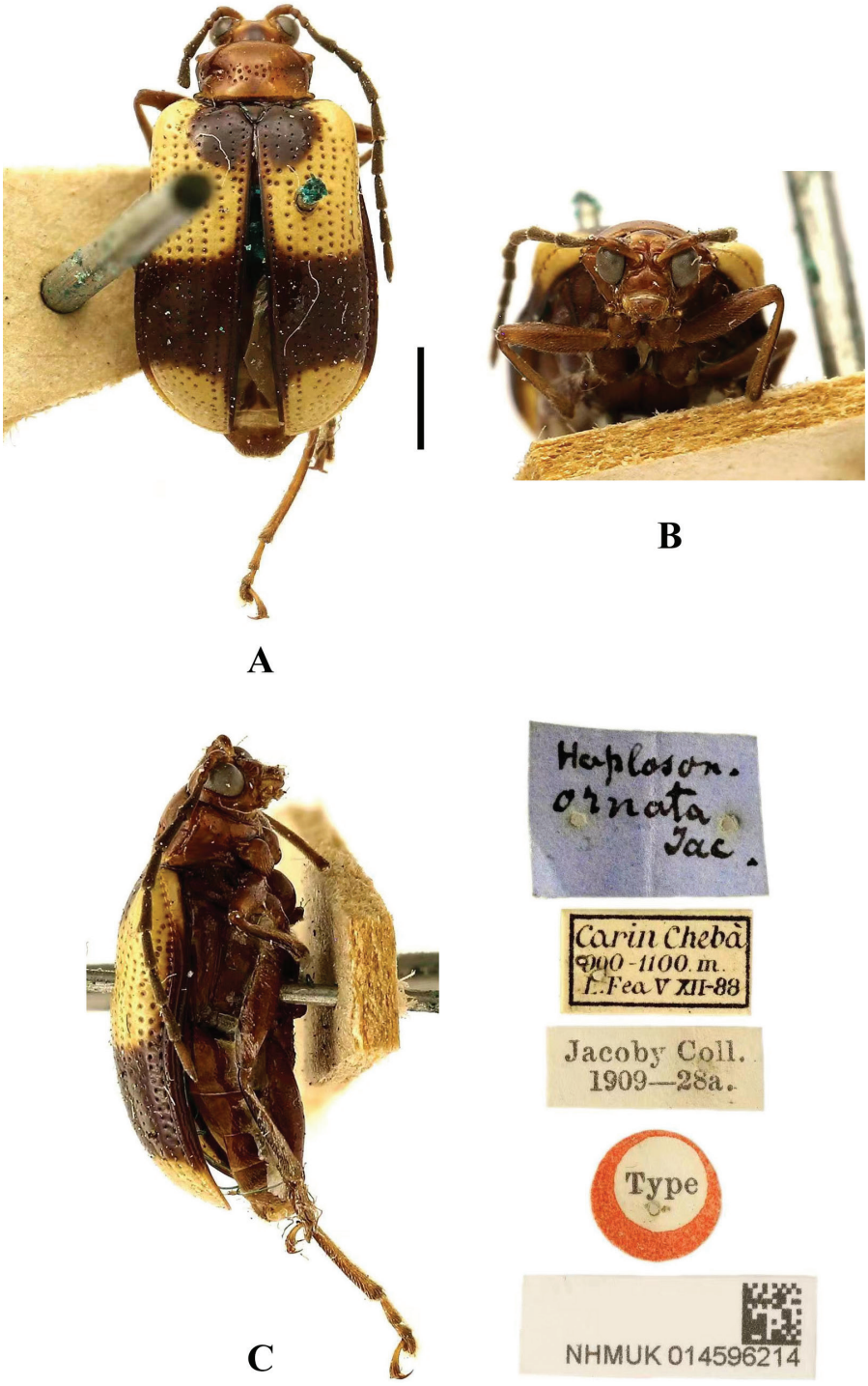

Figure 17. *Aplosonyx ornatus* **A–C** habitus of syntype, NHMUK014596214 **A** dorsal view **B** head view **C** lateral view. Scale bar: 1 mm (**A–C**).

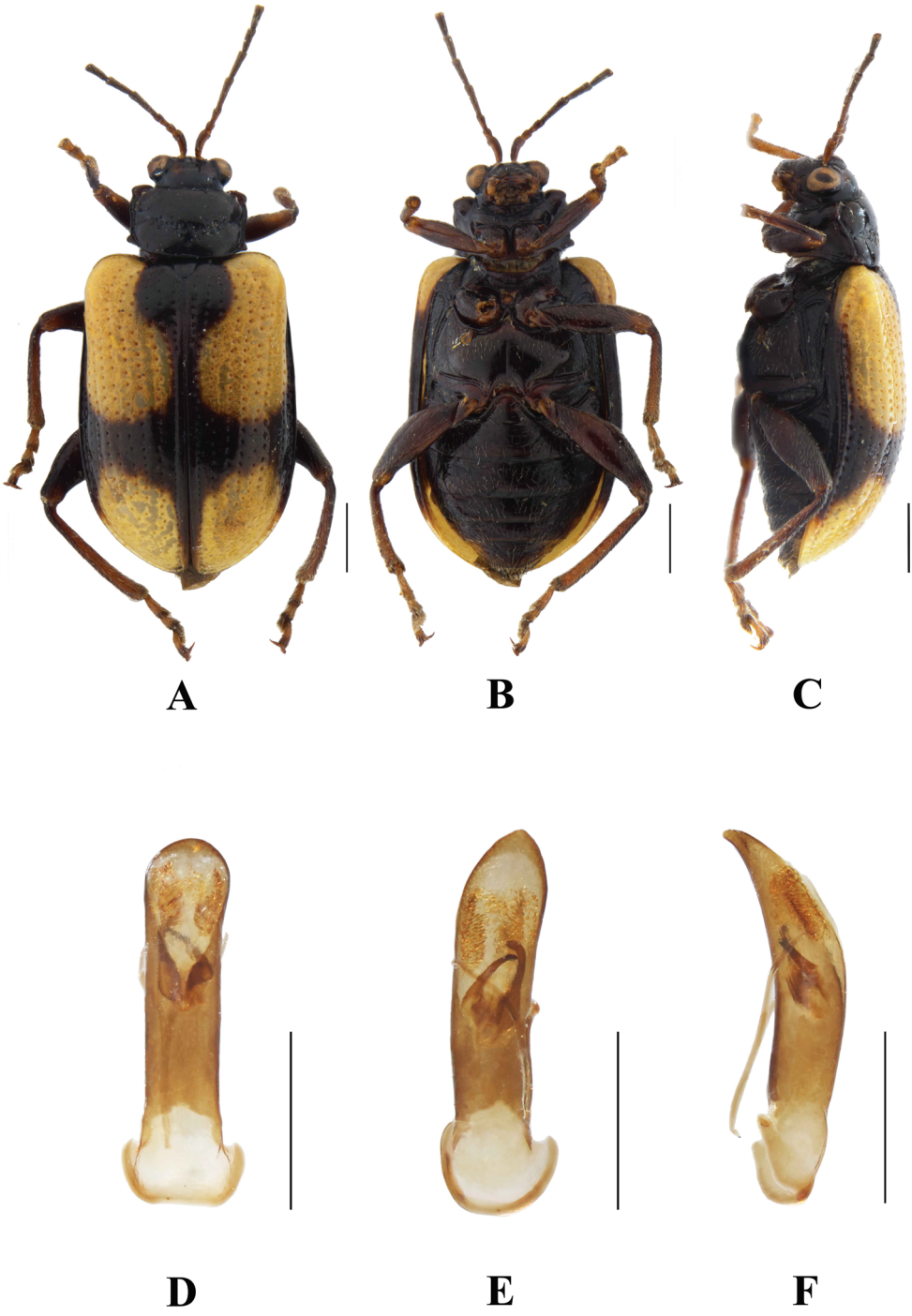

Figure 18. *Aplosonyx ornatus* **A–C** habitus **D–F** aedeagus **A, D** dorsal views **B, E** ventral views **C, F** lateral views. Scale bars 0.5 mm (**D–F**); 1 mm (**A–C**).

Elytra wider than pronotum, 0.75 × as long as body, 1.8 × as long as wide, epipleura wide at anterior 1/3, posteriorly gradually narrowing towards apex, dorsal surface slightly convex, regularly covered with large and deep punctures, partially arranged in ten rows in each elytron, the interstices between punctures wider than diameter of individual punctures, 2 × as wide as the diameter of individual punctures and lightly covered with small punctures in interstices.

Metasternum 2 × as long as the mesosternum. Ventral surface of abdomen with five ventrites, ventrite 1 longest, ventrites 2–4 gradually shortened, apical ventrite slightly longer than ventrite 3, with two subtriangular incisions.

Aedeagus slender, parallel-sided, basally widened, middle slightly narrowed, apex pointed, in lateral view obviously bent.

Female. Length 4.8–5.5 mm, width 2.8–3.2 mm.

Antennae slightly thinner than in male, antennomere 2 shortest, antennomere 3 longer than antennomere 2, twice as long as second; antennomere 4 longest, 1.6 × as long as antennomeres 2 and 3 combined; apical sternite without incisions.

Distribution. China: Yunnan; Laos, Myanmar.

Aplosonyx pictus Chen, 1942

Figs 19A–F, 20A

Aplosonyx pictus Chen, 1942: 39.
Sphenoraia picta: Lopatin 2002: 880.
Aplosonyx pictus: Zhang et al. 2008: 65.

Type specimens examined. ***Holotype*:** ♂, China, **Gansu Province**; 8 May 1919; IZAS; IOZ(E)215630.

***Paratype*:** ♂, China, **Gansu Province**; 8 May 1919; IZAS; IOZ(E)215633. ♀, China, **Gansu Province**; 8 May 1919; IZAS; IOZ(E)215634.

Additional specimens examined. ♂, China, **Gansu Province**, Qinghe; 1400 m a. s. l.; 7 Jul. 1999; Jian Yao leg.; IZAS; IOZ(E)1566618. ♂, same data as for preceding; 14 Jul. 1999; Decheng Yuan leg.; IZAS. ♂, same data as for preceding; 14 Jul. 1999; Shuyong Wang leg.; IZAS; IOZ(E)1566619. ♀, same data as for preceding; IOZ(E)1566620. ♂, China, **Shannxi Province**, Taibai Mt; 1850 m a. s. l.; 30 May 1981; IOZ(E)1566622. ♂, same data as for preceding; IOZ(E)1566623. ♀, **Shannxi Province**, Taibai Mt, Haopingsi; 18 Jun. 1981; Xuhui Chai leg.; IOZ(E)1566624.

Diagnosis. This species can be distinguished from other species by each elytron with two longitudinal black stripes, and the apex with one black spot. This species differs from *A. tianpingshanensis* in the aedeagus apex being distinctly pointed; in lateral view the apex is moderately bent.

Redescription. Male. Length 4.6–4.9 mm, width 2.5–3.0 mm.

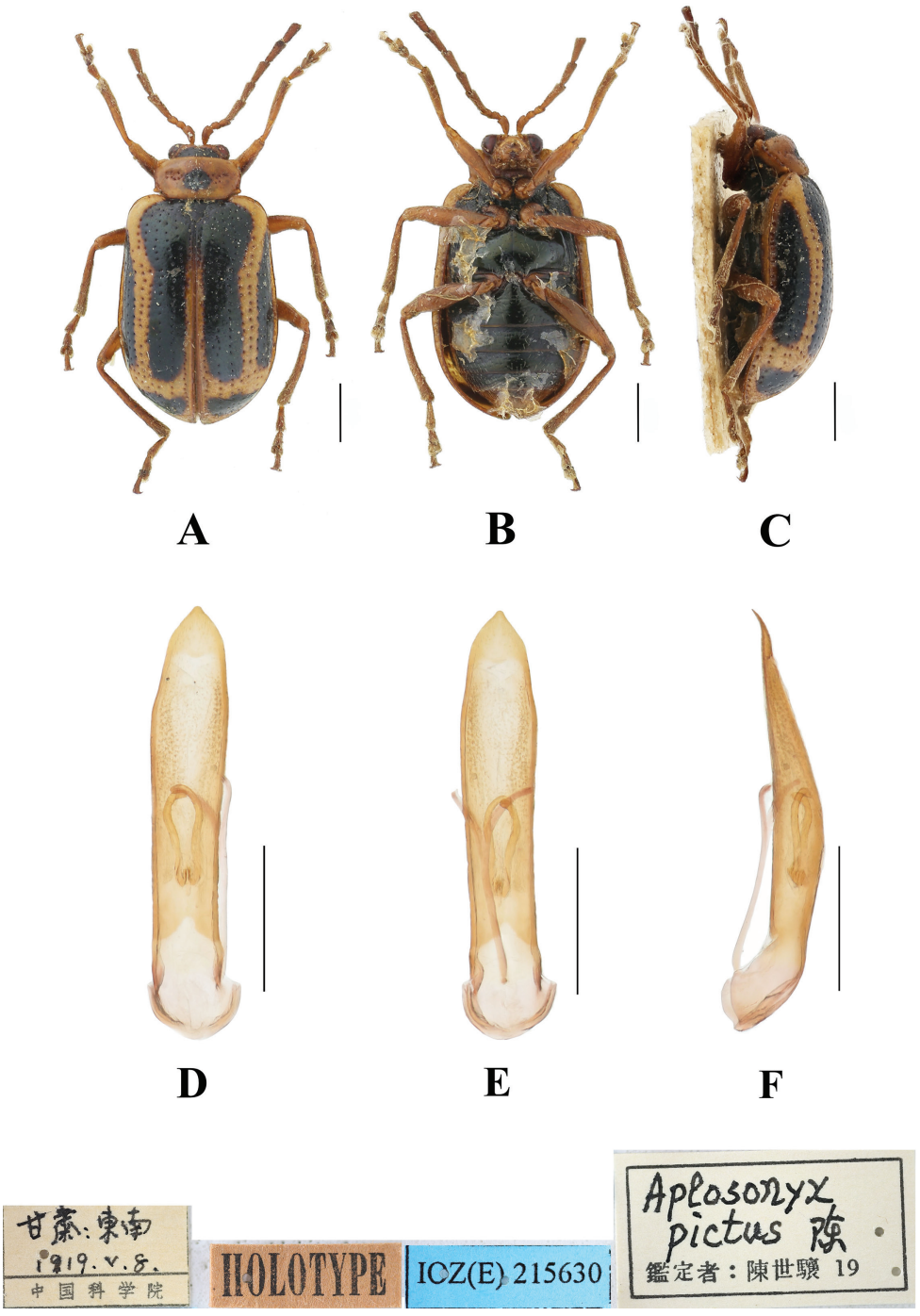

Figure 19. *Aplosonyx pictus* **A–C** habitus of holotype, IZAS IOZ(E)215630 **D–F** aedeagus **A, D** dorsal views **B, E** ventral views **C, F** lateral views. Scale bars 0.5 mm (**D–F**); 1 mm (**A–C**).

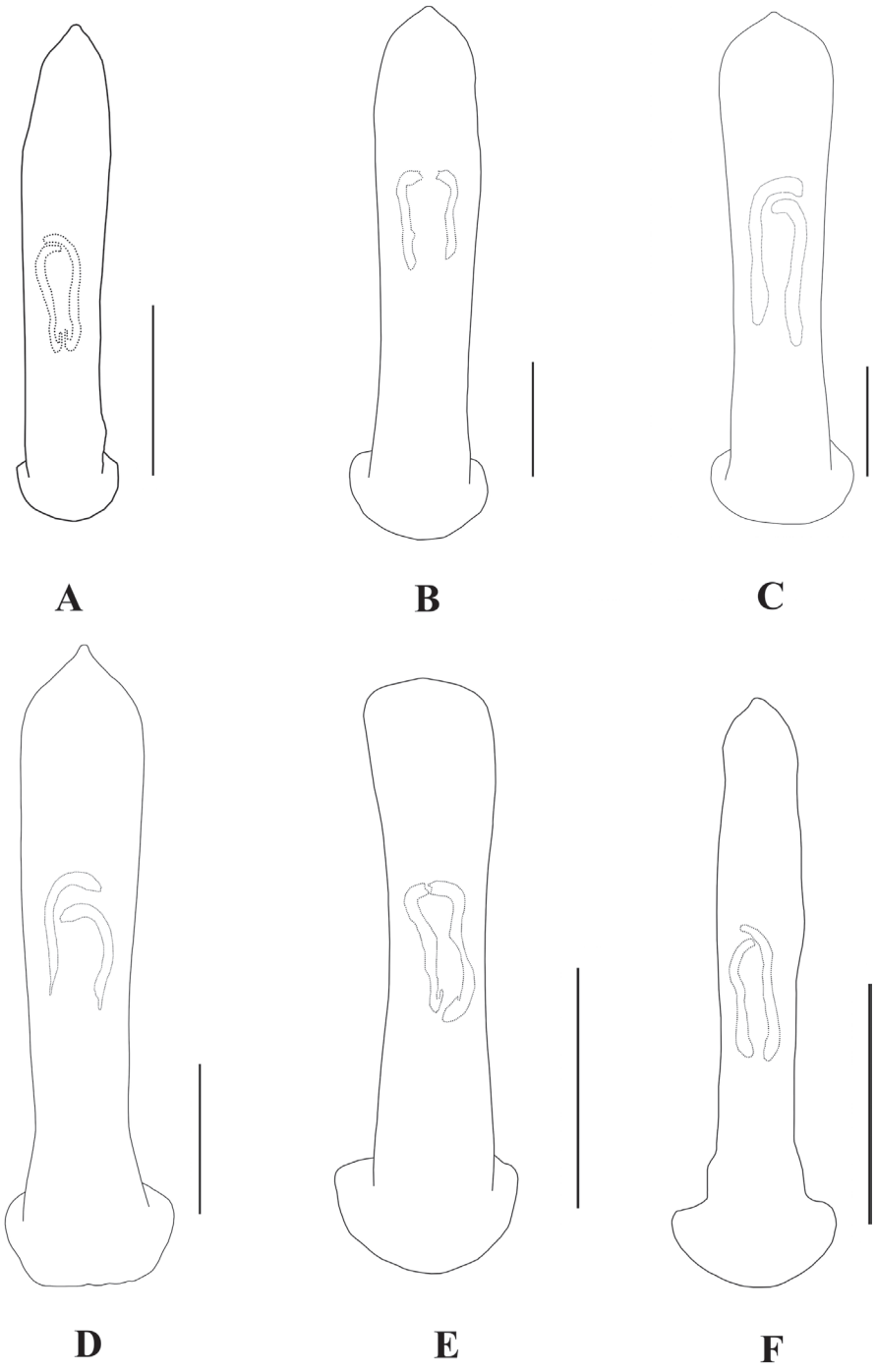

Figure 20. Aedeagus (dorsal view) **A** *A. pictus* **B** *A. robinsoni* **C** *A. rufipennis* **D** *A. sublaevicollis* **F** *A. tianpingshanensis* **E** *A. yunlongensis*. Scale bars 0.5 mm (**A–F**).

Head, antennae, pronotum, elytra and leg yellow, vertex, scutellum, and ventral surface of the body black, pronotum with a black spot in middle, each elytron with two longitudinal black stripes, and apex with one black spot.

Vertex finely and sparsely covered with punctures. Interocular space 1.5 × as wide as transverse diameter of eye. Interantennal space 1.2 × as wide as transverse diameter of antennal socket. Frontal tubercles transverse, each separated by a deep furrow; antennae slender, 0.7 × as long as body; antennomeres 1–3 shiny; antennomeres 4–11 covered with pubescence, antennomeres 2 and 3 shortest, antennomere 3 nearly equal in length and shape to antennomere 2, antennomere 4 longest, approximately 1.8 × as long as antennomeres 2 and 3 combined; antennomeres 5–10 gradually shortened, shorter than antennomere 4; antennomere 11 slightly longer than antennomere 10, pointed.

Pronotum 1.8 × as wide as long, lateral border margined, widest at posterior corners; disc with deep transverse furrow, covered with closely large punctures in furrow and with sparsely small punctures in other parts of pronotum.

Scutellum triangular, with rounded apex, smooth, impunctate.

Elytra: wider than pronotum, 0.75 × as long as body, 1.65 × as long as wide, epipleura wide at anterior 1/3, posteriorly gradually narrowing towards apex, dorsal surface slightly convex, regularly covered with large and deep punctures, partially arranged in ten rows in each elytron, the interstices of punctures in rows wider than diameter of punctures, approximately 2 × as wide as diameter of punctures and lightly covered with small punctures in interstices.

Metasternum 2 × as long as the mesosternum. Ventral surface of abdomen with five ventrites, ventrite 1 longest, ventrites 2–4 gradually shortened, apical ventrite slightly longer than ventrite 4, with two subtriangular incisions.

Aedeagus slender, parallel-sided, basally widened, apex distinctly pointed, in lateral view apex moderately bent.

Female. Length 4.4–5.0 mm, width 2.6–3.2 mm.

Antennae slightly thinner than in male, without short hairs, antennomere 2 shortest, antennomere 3 approximately 1.5 × as long as second; antennomere 4 longest, approximately 1.5 × as long as antennomeres 2 and 3 combined; apical sternite without incisions.

Distribution. China: Gansu, Shaanxi.

Aplosonyx robinsoni Jacoby, 1905

Figs 20B, 21A–D, 22A–F

Haplosonyx robinsoni Jacoby, 1905: 6.
Aplosonyx robinsoni: Maulik 1936: 618.

Type specimen examined. ♂ ***Syntype*** of *Haplosonyx robinsoni* Siamese Malay States. Nawngchik: Bukit Besar. 2500 ft. May 1901. Coll. N. Annandale and H. C. Robinson. No; Jacoby Coll. 1909-28a. NHMUK015014023.

Additional specimens examined. ♀, China, **Yunnan Province**, Xishuangbanna, Mengzhe; 870 m a. s. l.; 11 Jul. 1958; Shuyong Wang leg.; IZAS; IOZ(E)1566661. ♀, same data as for preceding; 7 Jul. 1958; Shuyong Wang leg.; IZAS; IOZ(E)1566654. ♂, same data as for preceding; 7 Jul. 1958; Fuji

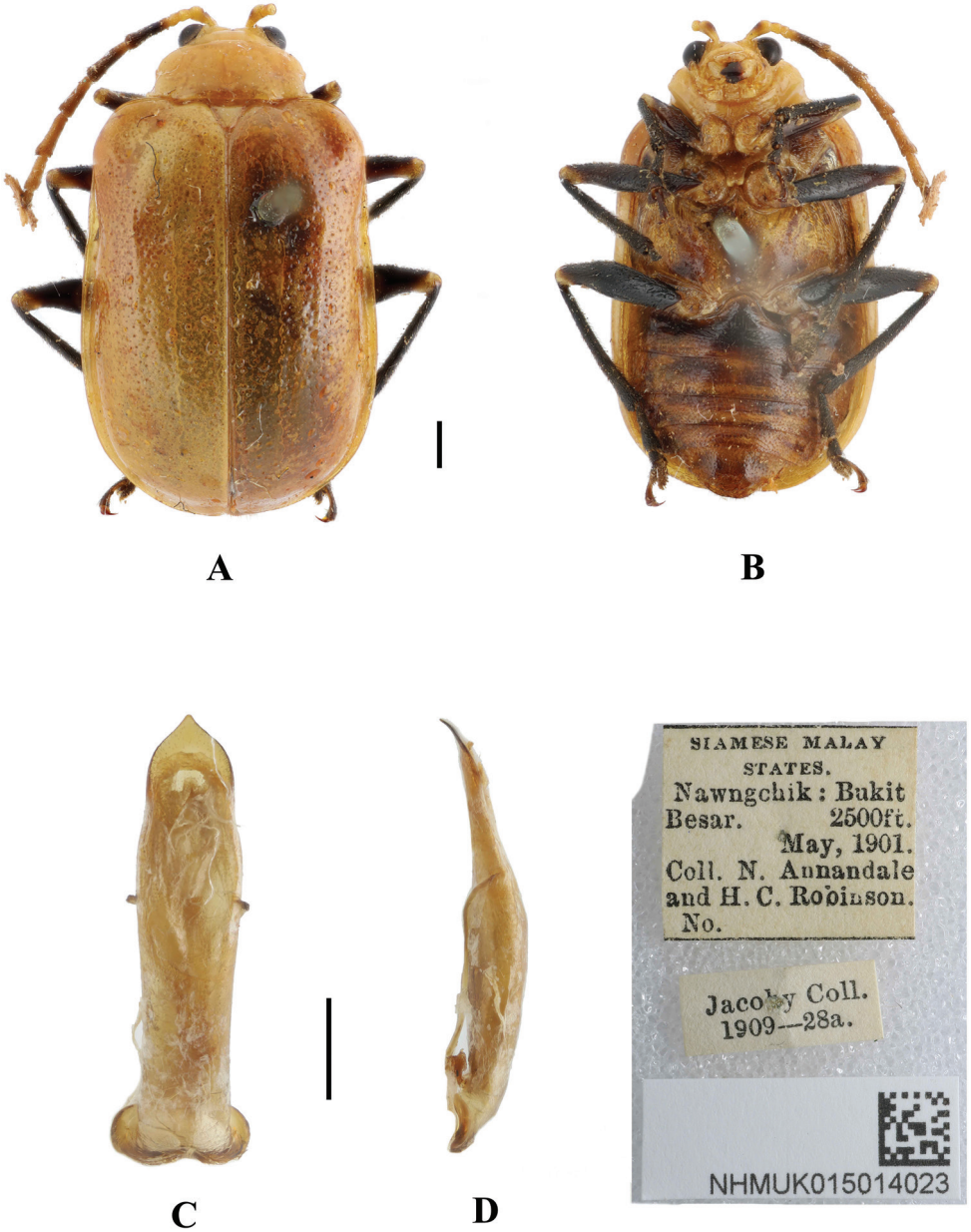

Figure 21. *Aplosonyx robinsoni* **A, B** habitus of syntype, NHMUK015014023 **C, D** aedeagus **A, C** dorsal views **B** ventral views **D** lateral views. Scale bars 0.5 mm (**C, D**); 1 mm (**A, B**).

Pu leg.; IZAS; IOZ(E)1566655. ♀, same data as for preceding; IOZ(E)1566657. ♂, China, **Yunnan Province**, Xishuangbanna, Mengzhe; 870 m a. s. l.; 7 Jul. 1958; Fuji Pu leg.; IZAS; IOZ(E)1566660. ♂, same data as for preceding; IOZ(E)1566663. ♀, China, **Yunnan Province**, Xishuangbanna, Mengzhe; 870 m a. s. l.; 7 Jul. 1958; Fuji Pu leg.; IZAS; IOZ(E)1566666. ♀, same data as for preceding; 5 Sep. 1958; Shuyong Wang leg.; IZAS; IOZ(E)1566667. ♀, same data as for preceding; 4 Jul. 1958; Shuyong Wang leg.; IZAS; IOZ(E)1566668. ♀, same data as for preceding; 11 Jul. 1958; Fuji Pu leg.; IZAS; IOZ(E)1566669. ♀, same data as for preceding; IOZ(E)1566670. ♀, China, **Yunnan Province**, Xishuangbanna, Mengzhe; 870 m a. s. l.; 8 Jul. 1958; Shuyong Wang leg.; IZAS; IOZ(E)1566672. ♂, same data as for preceding; 30 Jun. 1958; Shuyong Wang leg.; IZAS; IOZ(E)1566677. ♀, same data as for preceding; 3 Jul. 1958; Shuyong Wang leg.; IZAS; IOZ(E)1566681. ♂, same data as for preceding; 28 Jun. 1957; huyong Wang leg.; IZAS; IOZ(E)1566689. ♂, China, **Yunnan Province**, Jinping; 500 m a. s. l.; 12 May 1956; Keren Huang leg.; IZAS; IOZ(E)1566690. ♀, same data as for preceding; IOZ(E)1566691.

Diagnosis. This species can be distinguished from other species by the yellow body, black legs, and yellow antennae with the apical two or three antennomeres black.

Redescription. Male. Length 9.8–13.0 mm, width 6.5–7.4 mm.

Head, pronotum, scutellum, and elytra yellow; legs and ventral surface of the body black; antennae yellow with apical two or three antennomeres black.

Vertex finely covered with punctures. Interocular space 1.5 × as wide as transverse diameter of eye. Interantennal space 1.7 × as wide as transverse diameter of antennal socket. Frontal tubercles transverse, each separated by a deep furrow; antennae slender, 0.7 × as long as body; antennomeres 1–3 shiny; antennomeres 4–11 covered with pubescence, antennomere 2 shortest, antennomere 3 twice as long as second; antennomere 4 longest, 2 × as long as antennomeres 2 and 3 combined; antennomeres 5–10 gradually shortened, shorter than antennomere 4; antennomere 11 slightly longer than antennomere 10, pointed.

Pronotum approximately 2 × as wide as long, lateral border margined, widest at posterior corners; disc with deep transverse furrow, closely covered with large punctures in furrow and sparsely with small punctures in other parts of pronotum, the interstices of punctures equal to diameter of individual punctures in furrow, smooth and impunctate in middle of furrow.

Scutellum triangular, finely covered with punctures.

Elytra: wider than pronotum, 0.8 × as long as body, 1.7 × as long as wide, epipleura wide at anterior 1/4, posteriorly gradually narrowing towards apex, dorsal surface slightly convex, regularly covered with large and deep punctures, partially arranged in twenty rows in each elytron, the interstices of punctures wider than diameter of individual punctures, approximately 2 × as wide as diameter of punctures and lightly covered with small punctures in interstices.

Metasternum 2 × as long as the mesosternum. Ventral surface of abdomen with five ventrites, ventrite 1 longest, ventrites 2–4 gradually shortened, apical ventrite slightly longer than ventrite 3, with two subtriangular incisions.

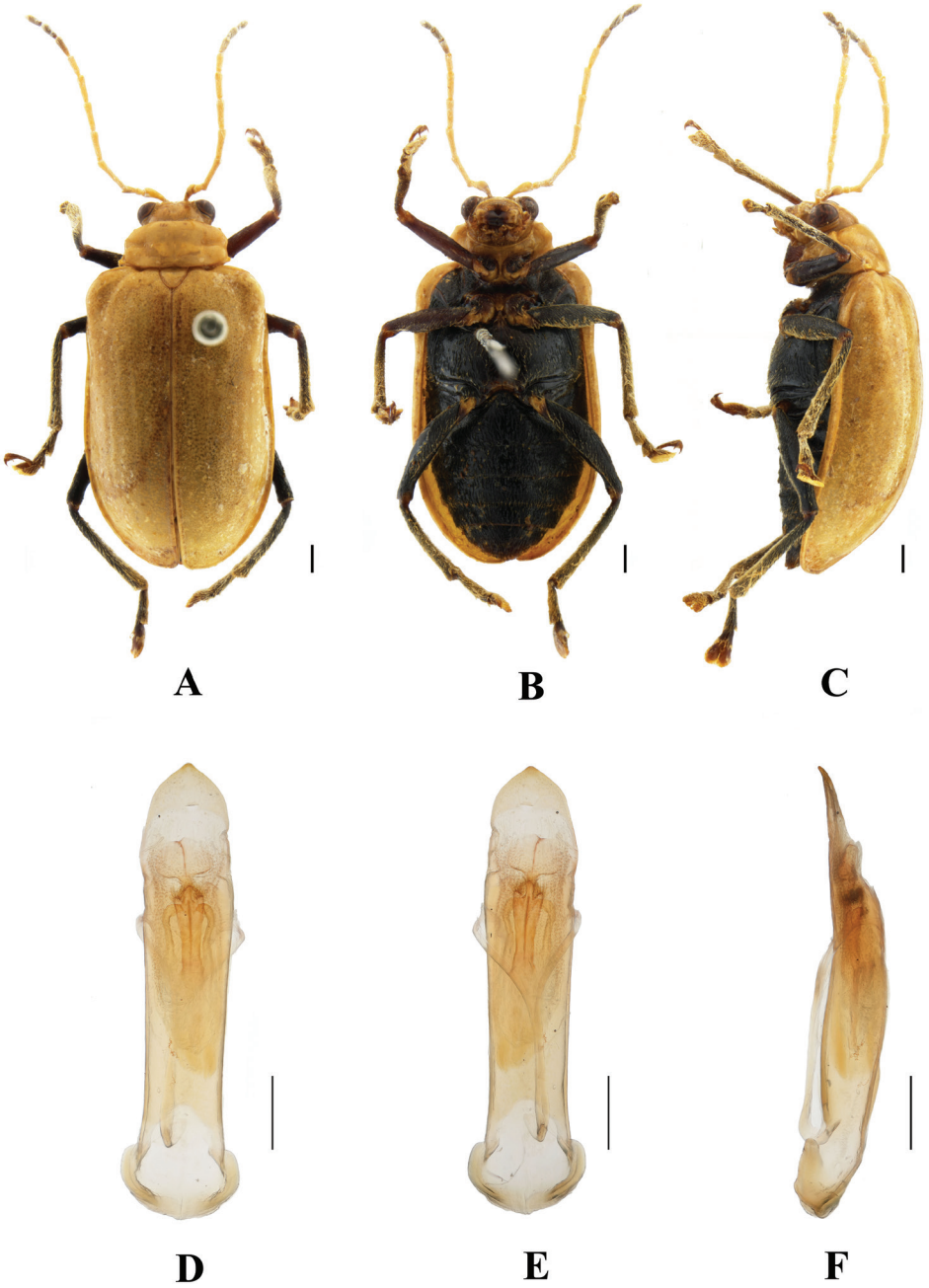

Figure 22. *Aplosonyx robinsoni* **A–C** habitus **D–F** aedeagus **A, D** dorsal views **B, E** ventral views **C, F** lateral views. Scale bars 0.5 mm (**D–F**); 1 mm (**A–C**).

Aedeagus slender, parallel-sided, basally widened, apex distinctly pointed, in lateral view base and apex moderately bent.

Female. Length 10.2–12.8 mm, width 6.6–7.2 mm.

Antennae slightly thinner than in male, antennomere 2 shortest, antennomere 3 twice as long as second; antennomere 4 longest, 1.6 × as long as antennomeres 2 and 3 combined; apical sternite without incisions.

Variability. The syntype studied has different coloration, antennae with antennomeres 1–3 yellow, ventral surface of the body, coxae, and trochanters yellow.

Distribution. China: Yunnan; Thailand, Myanmar, Malaysia, Indonesia.

Aplosonyx rufipennis Duvivier, 1892

Figs 20C, 23A–D, 24A–F

Haplosonyx rufipennis Duvivier, 1892: 439.
Aplosonyx rufipennis: Laboissière 1934: 110.
Aplosonyx rubra Maulik, 1936: 620. Synonymized by Laboissière 1940: 21.

Type specimen examined. ♂ ***Syntype*** of *Aplosonyx rubra*: Doherty, 64478, Birmah Ruby M[es]; Fry Coll., 1905. 100; *Aplosonyx rubra* M.; S. Maulik; Type 1935, NHMUK015014024.

Additional specimens examined. ♀, China, **Yunnan Province**, Pingbian; 700 m a. s. l.; 29 Jun. 1956; Bangfeiluofu leg.; IZAS; IOZ(E)1566821. ♂, China, **Yunnan Province**, Hekou; 80 m a. s. l.; 5 Jun. 1956; Keren Huang leg.; IZAS; IOZ(E)1566825. ♀, China, **Yunnan Province**, Pingbian; 800 m a. s. l.; 20 Jun. 1979; Baowen Zhang leg.; IZAS; IOZ(E)1566832. ♂, China, **Yunnan Province**; 1956; IOZ(E)1566822. ♀, China, **Yunnan Province**; 1956; IOZ(E)1566823. ♀, same data as for preceding; IOZ(E)1566824.

Diagnosis. This species can be distinguished from other species by its black head and pronotum, and the reddish brown elytra without any spots.

Redescription. Male. Length 8.4–10.6 mm, width 5.2–6.0 mm.

Head, antennae, pronotum, scutellum and leg black, elytra reddish brown, ventral surface of thorax yellow with lateral area black, abdomen yellow.

Vertex finely covered with punctures. Interocular space 1.6 × as wide as transverse diameter of eye. Interantennal space 1.5 × as wide as transverse diameter of antennal socket. Frontal tubercles transverse, each separated by a deep furrow; antennae slender, 0.65 × as long as body; antennomeres 1–3 shiny; antennomeres 4–11 covered with pubescence, antennomere 2 shortest, antennomere 3 approximately 1.5 × as long as second; antennomere 4 longest, approximately 1.8 × as long as antennomeres 2 and 3 combined; antennomeres 5–10 gradually shortened, shorter than antennomere 4; antennomere 11 slightly longer than antennomere 10, pointed.

Pronotum 1.8 × as wide as long, lateral border margined, widest at posterior corners; disc with deep transverse furrow, less distinct, smooth and impunctate in middle; covered with several large punctures in furrow and with sparsely small punctures in other parts of pronotum.

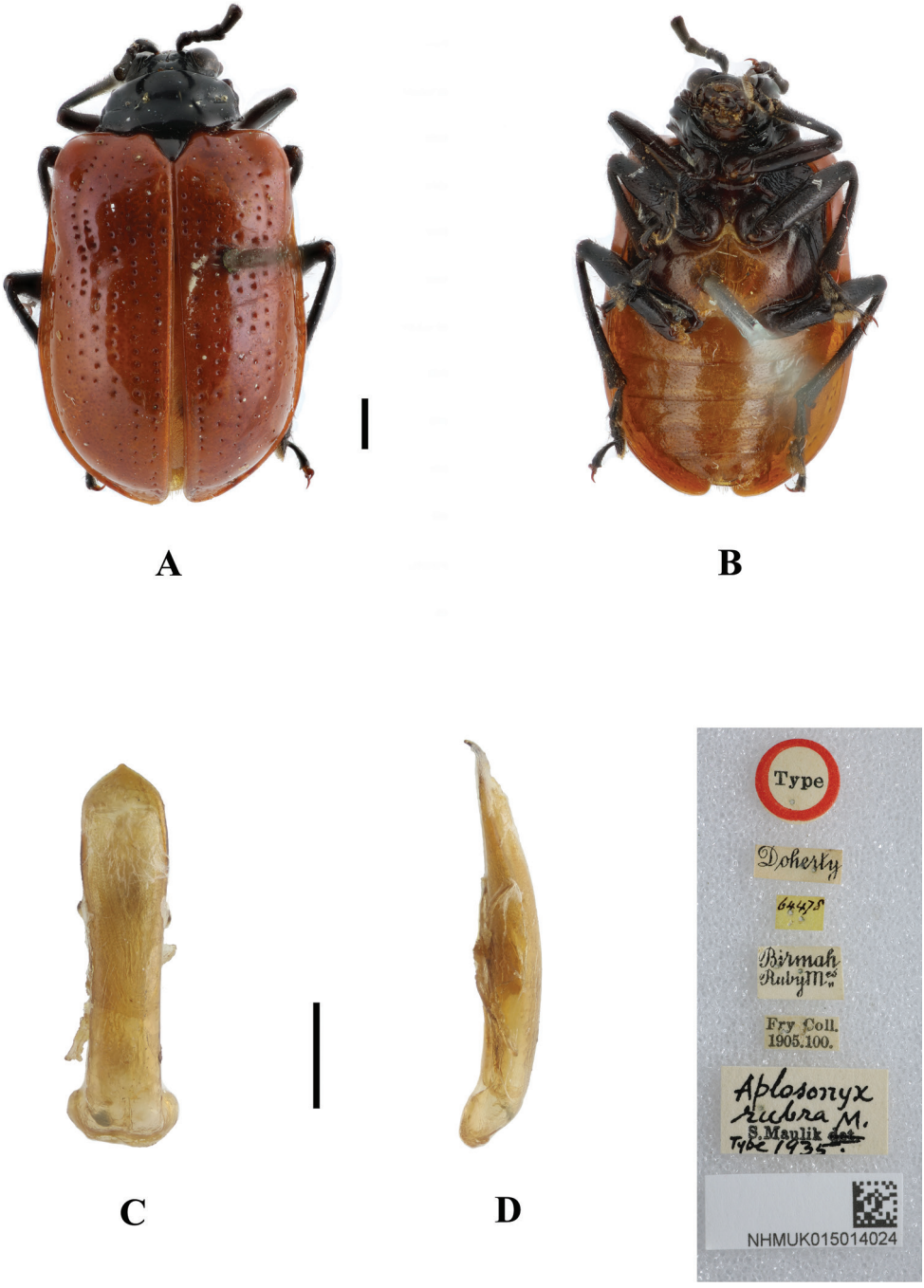

Figure 23. *Aplosonyx rufipennis* **A, B** habitus of syntype, NHMUK015014024 **C, D** aedeagus **A, C** dorsal views **B** ventral views **D** lateral views. Scale bars 0.5 mm (**C, D**); 1 mm (**A, B**).

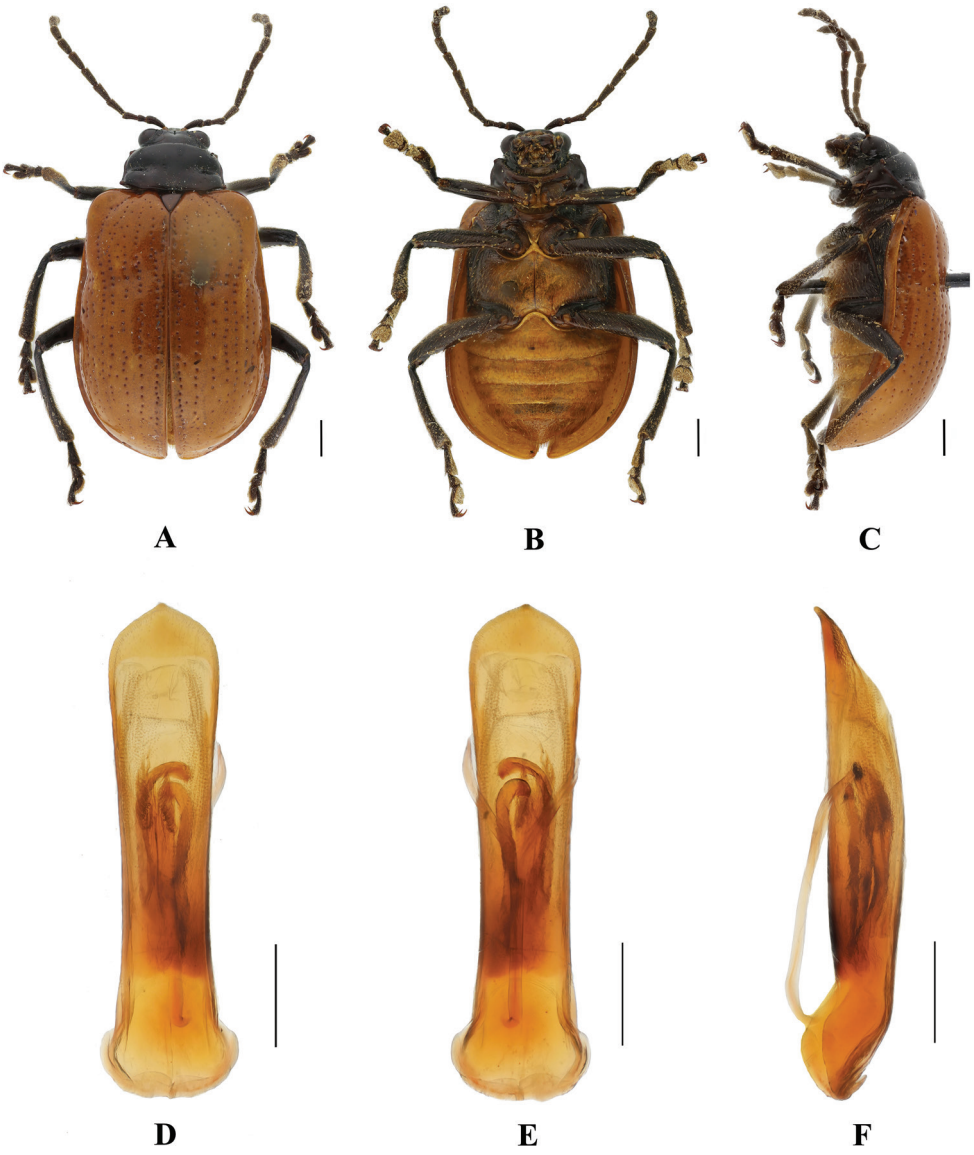

Figure 24. *Aplosonyx rufipennis* **A–C** habitus **D–F** aedeagus **A, D** dorsal views **B, E** ventral views **C, F** lateral views. Scale bars 0.5 mm (**D–F**); 1 mm (**A–C**).

Scutellum triangular, finely covered with punctures.

Elytra: wider than pronotum, 0.75 × as long as body, 1.65 × as long as wide, epipleura wide at anterior 1/4, posteriorly gradually narrowing towards apex, dorsal surface convex slightly, covered with large punctures regularly, partially arranged in ten rows in each elytron, the interstices of punctures wider than diameter of punctures, approximately 2 × as wide as diameter of punctures, covered with small punctures.

Metasternum 2 × as long as the mesosternum. Ventral surface of abdomen with five ventrites, ventrite 1 longest, ventrites 2–4 gradually shortened, apical ventrite slightly longer than ventrite 3, with two subtriangular incisions.

Aedeagus slender, parallel-sided, basally widened, narrowed in middle, apex round with slightly pointed, in lateral view base and apex slightly bent.

Female. Length 9.2–10.5 mm, width 4.8–5.6 mm.

Antennomere 2 shortest, antennomere 3 longer than antennomere 2, twice as long as second; antennomere 4 longest, slightly long than antennomeres 2 and 3 combined; apical sternite without incisions.

Distribution. China: Shanghai, Yunnan; Vietnam, India.

Aplosonyx sublaevicollis Jacoby, 1889

Figs 20D, 25A–F

Haplosonyx sublaevicollis Jacoby, 1889: 218.
Aplosonyx sublaevicollis: Maulik 1936: 615.

Additional specimens examined. ♂, China, **Yunnan Province**, Xishuangbanna, Xiaomengyang; 850 m a. s. l.; 25 Jun. 1957; Lingchao Zang leg.; IZAS; IOZ(E)1566505. ♂, same data as for preceding; 24 Jun. 1957; Lingchao Zang leg.; IZAS; IOZ(E)1566514. ♂, China, **Yunnan Province**, Xishuangbanna, Damenglong; 650 m a. s. l.; 6 May 1958; IZAS; IOZ(E)1566540. ♂, same data as for preceding; IZAS; IOZ(E)1566541. ♂, China, **Yunnan Province**, Xishuangbanna, Damenglong; 650 m a. s. l.; 7 May 1958; Chunpei Hong leg.; IZAS; IOZ(E)1566508. ♂, same data as for preceding; IOZ(E)1566510. ♂, China, **Yunnan Province**, Xishuangbanna, Damenglong; 650 m a. s. l.; 6 May 1958; Zhizi Chen leg.; IZAS; IOZ(E)1566513. ♂, same data as for preceding; Chunpei Hong leg.; IZAS; IOZ(E)1566517. ♂, China, **Yunnan Province**, Xishuangbanna, Damenglong; 650 m a. s. l.; 6 May 1958; Shuyong Wang leg.; IZAS; IOZ(E)1566518. ♀, same data as for preceding; 7 Oct. 1958; Zhizi Chen leg.; IZAS; IOZ(E)1566534 ♂, same data as for preceding; 7 Oct. 1958; Zhizi Chen leg.; IZAS; IOZ(E)1566535. ♀, China, **Yunnan Province**, Xishuangbanna, Menghun; 750 m a. s. l.; 2 Jun. 1958; Chunpei Hong leg.; IZAS; IOZ(E)1566507. ♂, same data as for preceding; 5 Jun. 1958; Chunpei Hong leg.; IZAS; IOZ(E)1566512. ♂, same data as for preceding; 30 May 1958; IZAS; IOZ(E)1566515. ♂, same data as for preceding; 30 May 1958; IZAS; IOZ(E)1566516. ♂, same data as for preceding; 30 May 1958; Chunpei Hong leg.; IZAS; /IOZ(E)1566519. ♀, China, **Yunnan Province**, Xishuangbanna, Yunjinghong; 900 m a. s. l.; 27 May 1958; Yiran Zhang leg.; IZAS; IOZ(E)1566509. ♂, China, **Yunnan Province**, Xishuangbanna, Mengla; 650 m a. s. l.; 18 May 1958; Fuji Pu leg.; IZAS; IOZ(E)1566520. ♀, China, **Yunnan Province**, Xishuangbanna, Menghun; 1400 m a. s. l.; 3 Jun. 1958; Shuyong Wang leg.; IZAS; IOZ(E)1566556.

Diagnosis. This species can be distinguished from other Chinese species by its purplish blue elytra, and the apex of the pronotum without a raised area. This species differs from *A. chalybeus* in the pronotum being widest at its posterior corners.

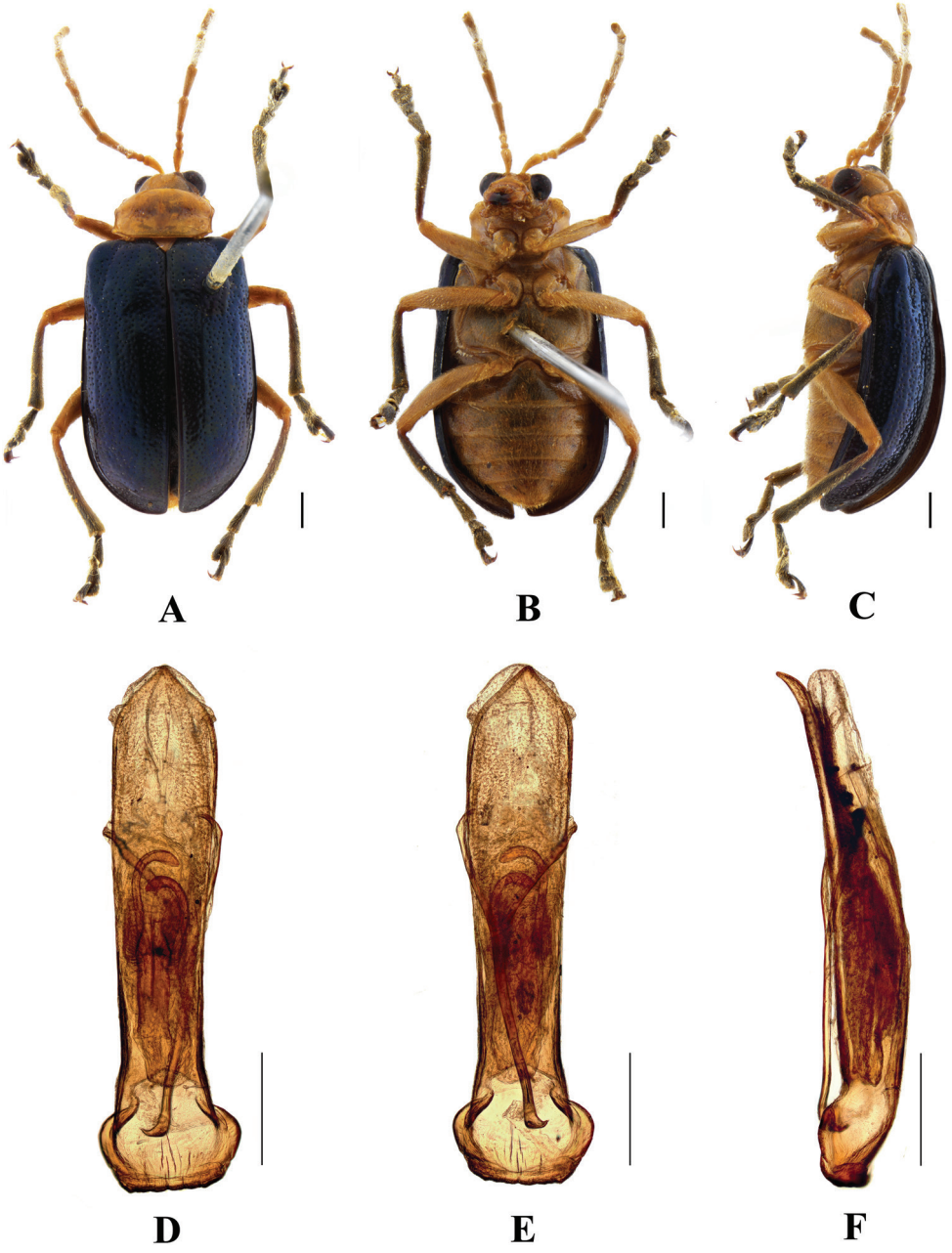

Figure 25. *Aplosonyx sublaevicollis* **A–C** habitus **D–F** aedeagus **A, D** dorsal views **B, E** ventral views **C, F** lateral views. Scale bars 0.5 mm (**D–F**); 1 mm (**A–C**).

Redescription. Male. Length 9.0–10.8 mm, width 4.8–5.2 mm.

Head, antennae, pronotum, scutellum and ventral surface of body yellow, legs brown with femur yellow, elytra purplish blue.

Vertex covered with several large punctures. Interocular space 1.65 × as wide as transverse diameter of eye. Interantennal space 1.4 × as wide as transverse diameter of antennal socket. Frontal tubercles distinctly raised, hook-like, each separated by a deep furrow; antennae slender, 0.75 × as long as body; antennomeres 1–3 shiny; antennomeres 4–11 covered with pubescence, antennomere 2 shortest, antennomere 3 twice as long as second; antennomere 4 longest, approximately 1.8 × as long as antennomeres 2 and 3 combined; antennomeres 5–10 gradually shortened, shorter than antennomere 4; antennomere 11 slightly longer than antennomere 10, pointed.

Pronotum approximately 2 × as wide as long, lateral border margined, widest at posterior corners; middle of disc with transverse furrow; closely covered with large punctures in furrow and with sparsely small punctures in other parts of pronotum.

Scutellum triangular, smooth, impunctate.

Elytra: wider than pronotum, 0.8 × as long as body, 1.7 × as long as wide, epipleura wide at anterior 1/4, posteriorly gradually narrowing towards apex, dorsal surface slightly convex, irregularly covered with large punctures, the interstices of punctures wider than diameter of individual punctures, approximately 2 × as wide as diameter of individual punctures and lightly covered with small punctures in interstices.

Metasternum 2 × as long as the mesosternum. Ventral surface of abdomen with five ventrites, ventrite 1 longest, ventrites 2–4 gradually shortened, apical ventrite slightly longer than ventrite 3, with two subtriangular incisions.

Aedeagus slender, parallel-sided, basally widened, narrowed in middle, apex distinctly pointed, in lateral view base and apex distinctly bent.

Female. Length 8.8–10.6 mm, width 4.6–5.4 mm.

Antennae slightly thinner than in male, antennomere 2 shortest, antennomere 3 approximately 1.5 × as long as second; antennomere 4 longest, 1.5 × as long as antennomeres 2 and 3 combined; apical sternite without incisions.

Distribution. China: Yunnan; Laos; Thailand; Myanmar; Malaysia; Indonesia.

Aplosonyx tianpingshanensis Yang, 1995

Figs 20E, 26A–F

Aplosonyx tianpingshanensis Yang, 1995: 91.

Type specimens examined. ***Holotype*:** ♂, China, **Hunan Province**, Sangzhi, Tianping Mt; 1640 m a. s. l.; 13 Aug. 1988; Xingke Yang leg.; IZAS.

***Paratype*:** ♀, same data as for holotype. ♀, China, **Hubei Province**, Hefeng, Fenshuiling; 1250 m a. s. l.; 3 Aug. 1989; Xiaochun Zhang leg.; IZAS. ♂, China, **Hunan Province**, Sangzhi, Tianping Mt; 1570 m a. s. l.; 13 Aug. 1988; Shuyong Wang leg.; IZAS. ♂, same data as for preceding; 1640 m a. s. l.; 13 Aug. 1988; Xingke Yang leg.; IZAS.

Additional specimen examined. ♀, China, **Hunan Province**, Sangzhi, Tianping Mt; 1640 m a. s. l.; 14 Aug. 1988; Xingke Yang leg.; IZAS; IOZ(E)1566662.

Diagnosis. This species can be distinguished from the other Chinese species by each elytron having two broad longitudinal black stripes, and the apex with two black spots. This species differs from *A. pictus* in the aedeagus being slightly narrowed in the middle, and the apex widened.

Redescription. Male. Length 5.0–5.3 mm, width 3.0–3.2 mm.

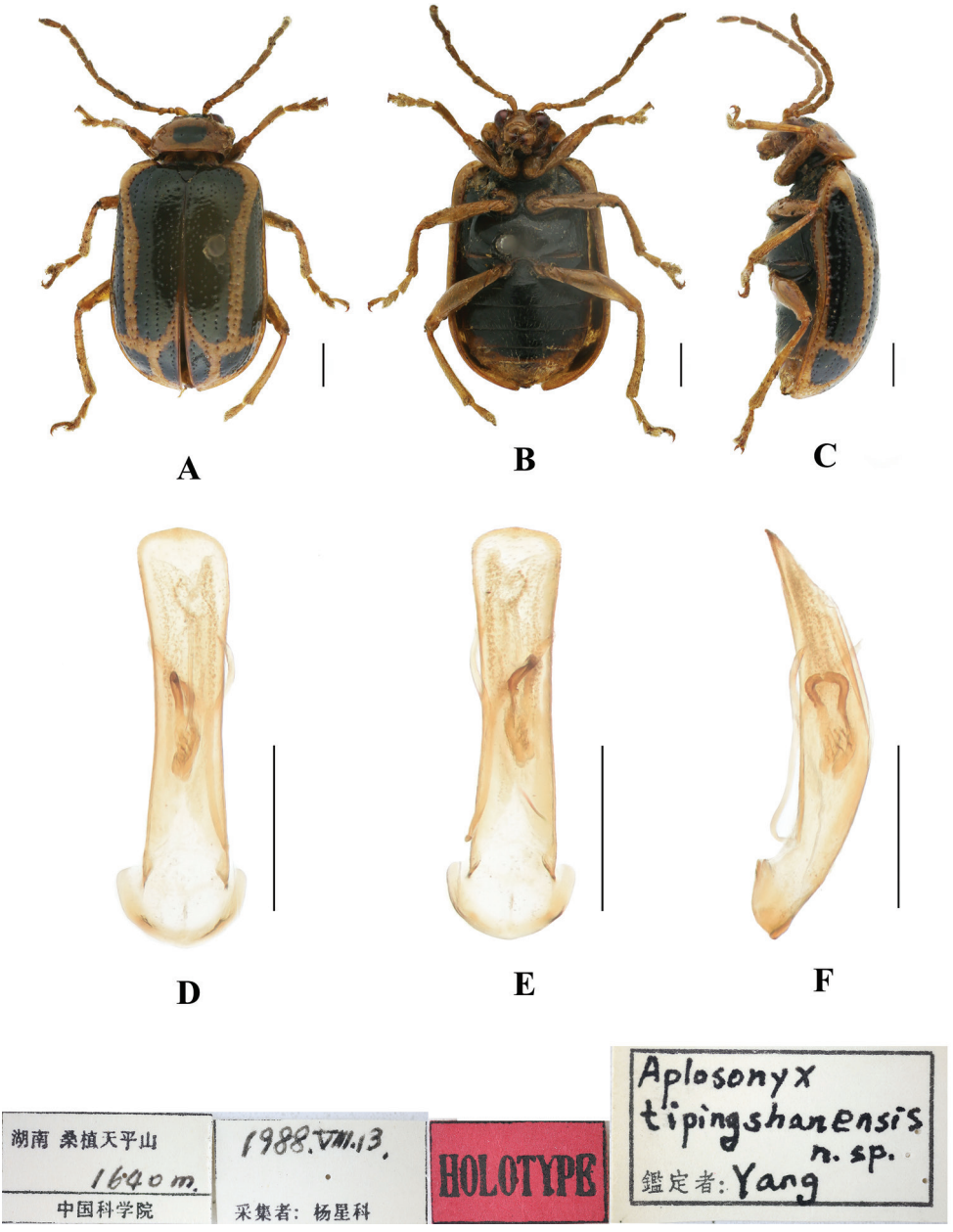

Figure 26. *Aplosonyx tianpingshanensis* **A–C** habitus of holotype, IZAS **D–F** aedeagus **A, D** dorsal views **B, E** ventral views **C, F** lateral views. Scale bars 0.5 mm (**D–F**); 1 mm (**A–C**).

Head, antennae, pronotum, elytra and legs yellow, vertex, scutellum and ventral surface of the body black, margin and apex of abdominal ventrite yellow, pronotum with a black spot in middle, each elytron with two longitudinal black stripes, and apex with one pair of black spots.

Vertex finely and sparsely covered with punctures. Interocular space 2 × as wide as transverse diameter of eye. Interantennal space 1.4 × as wide as transverse diameter of antennal socket. Frontal tubercles transverse, each separated by a deep furrow; antennae slender, 0.7 × as long as body; antennomeres 1–3 shiny; antennomeres 4–11 covered with pubescence, antennomere 2 shortest, antennomere 3 approximately 1.5 × as long as second; antennomere 4 longest, approximately 1.6 × as long as antennomeres 2 and 3 combined; antennomeres 5–10 gradually shortened, shorter than antennomere 4; antennomere 11 slightly longer than antennomere 10, pointed.

Pronotum approximately 1.8 × as wide as long, lateral border margined, widest at posterior corners; disc with deep transverse furrow, covered with several punctures in furrow and with sparsely small punctures in anterior angle.

Scutellum triangular, smooth, impunctate.

Elytra: wider than pronotum, 0.75 × as long as body, 1.75 × as long as wide, epipleura wide at anterior 1/3, posteriorly gradually narrowing towards apex, dorsal surface slightly convex, regularly covered with large and deep punctures, partially arranged in ten rows in each elytron, the interstices of punctures wider than diameter of punctures, approximately 2 × as wide as diameter of punctures and lightly covered with small punctures in interstices.

Metasternum 2 × as long as the mesosternum. Ventral surface of abdomen with five ventrites, ventrite 1 longest, ventrites 2–4 gradually shortened, apical ventrite slightly longer than ventrite 3, with two subtriangular incisions.

Aedeagus slender, parallel-sided, slightly narrowed in middle, basally widened, apex widened, in lateral view strongly bent.

Female. Length 5.0–5.2 mm, width 2.8–3.2 mm.

Antennae slightly thinner than in male, antennomere 2 shortest, antennomere 3 approximately 1.6 × as long as second; antennomere 4 longest, 1.4 × as long as antennomeres 2 and 3 combined; punctures densely in groove of pronotum, the interstices between punctures equal to diameter of individual punctures, apical sternite without incisions.

Distribution. China: Gansu, Shaanxi, Hunan, Hubei, Guizhou.

Aplosonyx yunlongensis Jiang, 1992

Fig. 27A–F

Aplosonyx yunlongensis Jiang, 1992: 664.

Type specimens examined. ***Holotype*****:** ♂, China, **Yunnan Province**, Yunlong, Zhiben Mt; 2250 m a. s. l.; 21 Jun. 1981; Shuyong Wang leg.; IZAS.

Paratype**:** ♀, China, **Yunnan Province**, Yunlong, Zhiben Mt; 2250 m a. s. l.; 21 Jun. 1981; Shuyong Wang leg.; IZAS.

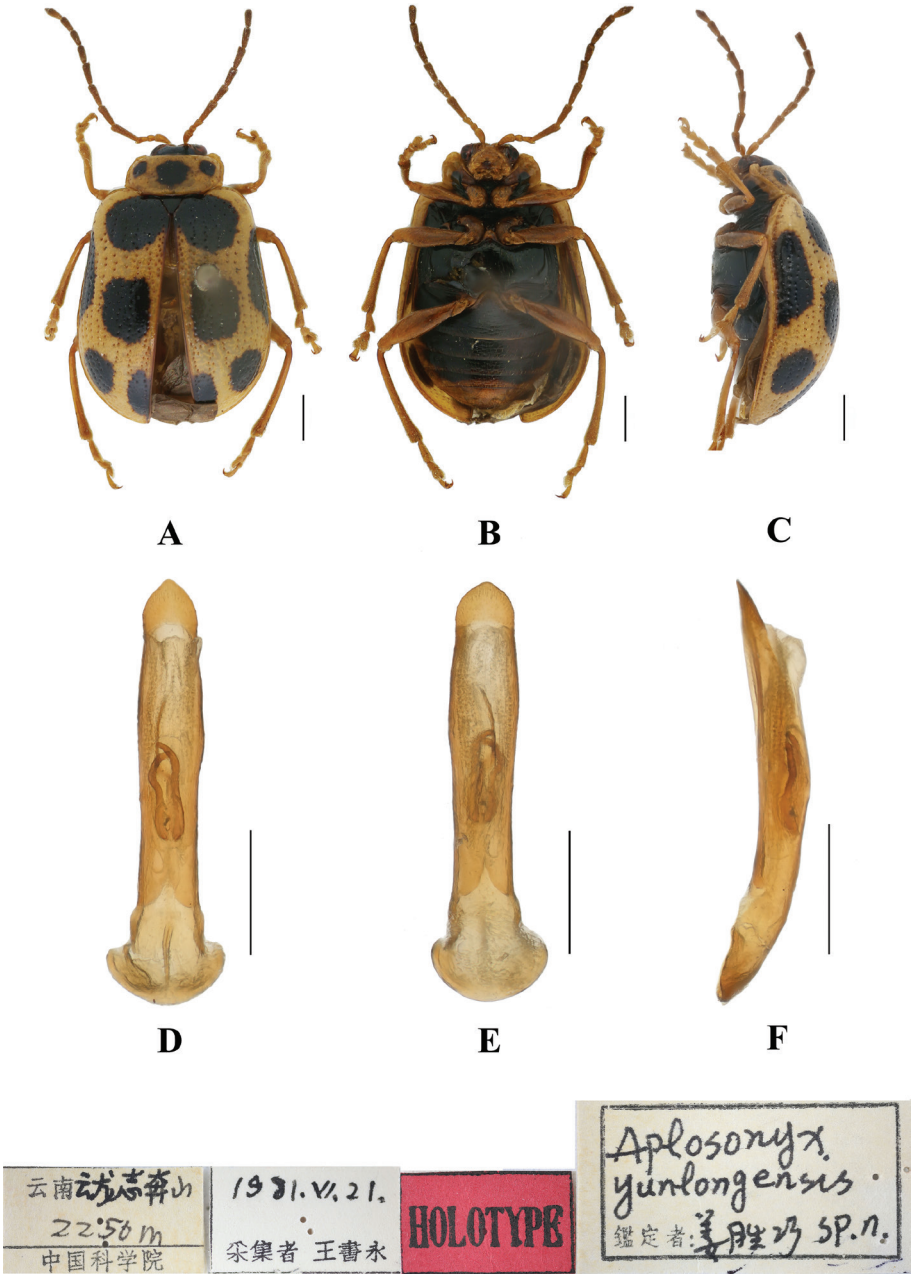

Figure 27. *Aplosonyx yunlongensis* **A–C** habitus of holotype, IZAS **D–F** aedeagus **A, D** dorsal views **B, E** ventral views **C, F** lateral views. Scale bars 0.5 mm (**D–F**); 1 mm (**A–C**).

Additional specimen examined. ♀, China, **Yunnan Province**, Yunlong, Zhiben Mt; 2250 m a. s. l.; 21 Jun. 1981; Shuyong Wang leg.; IZAS.

Diagnosis. This species can be distinguished from other Chinese species by each elytron having five black spots, the pronotum with three obvious black spots. This

species differs from *A. omeiensis* in the aedeagus being slightly widened at the middle, and the base expanded into a fan shape.

Redescription. Male. Length 5.4–5.8 mm, width 3.6–3.8 mm.

Head, antennae, pronotum, elytra, and leg yellow; vertex, scutellum, and ventral surface of the body black, apical ventrite of abdomen yellow, pronotum with three black spots, one large black spot in the middle, and one small black spot on each side; each elytron with five black spots, middle and apex with one pair of spots and base with one spot.

Vertex finely and sparsely covered with punctures. Interocular space 1.4 × as wide as transverse diameter of eye. Interantennal space 1.3 × as wide as transverse diameter of antennal socket. Frontal tubercles distinctly raised, hook-like, each separated by a deep furrow; antennae slender, 0.75 × as long as body; antennomeres 1–3 shiny; antennomeres 4–11 covered with pubescence, antennomere 2 shortest, antennomere 3 twice as long as second; antennomere 4 longest, approximately 1.6 × as long as antennomeres 2 and 3 combined; antennomeres 5–10 gradually shortened, shorter than antennomere 4; antennomere 11 slightly longer than antennomere 10, pointed.

Pronotum approximately 2 × as wide as long, lateral border margined, widest at posterior corner; disc with transverse furrow, less distinct in middle; sparsely covered with several large punctures in furrow.

Scutellum triangular, finely covered with punctures.

Elytra: wider than pronotum, 0.78 × as long as body, 1.7 × as long as wide, epipleura wide at anterior 1/3, posteriorly gradually narrowing towards apex, dorsal surface slightly convex, regularly covered with large and deep punctures, partially arranged in ten rows on each elytron, the interstices of punctures 2 × as wide as diameter of punctures and lightly covered with small punctures.

Metasternum 2 × as long as the mesosternum. Ventral surface of abdomen with five ventrites, ventrite 1 longest, ventrites 2–4 gradually shortened, apical ventrite slightly longer than ventrite 3, with two subtriangular incisions.

Aedeagus slender, slightly widened at middle, basally enlarged in a fan shape, apex pointed, in lateral view slightly bent.

Female. Length 5.6–6.0 mm, width 3.5–3.9 mm.

Antennae slightly thinner than in male, antennomere 2 shortest, antennomere 3 approximately 1.5 × as long as second; antennomere 4 longest, 1.3 × as long as antennomeres 2 and 3 combined; apical sternite without incisions.

Distribution. China: Yunnan.

***Aplosonyx ancorella* sp. nov.**

https://zoobank.org/1C9DA9C0-CDCD-44DA-9E5A-B9ADA4B2B32D

Figs 28A–F, 29A

Type material. ***Holotype*:** ♂, China, **Yunnan Province**, Menga; 1100 m a. s. l.; 18 Apr. 1982; Subai Liao leg.; IZAS; IOZ(E)1566748. ***Paratype*:** 1♂, China, **Yunnan Province**, Xiaomengyang; 850 m a. s. l.; 7 May 1957; Fuji Pu leg.; IZAS; IOZ(E)1566747.

Diagnosis. The new species closely resembles *A. ancora* and *A. fulvescens*. In *A. ancora*, the antennae with antennomeres 1–7 yellow and antennomeres 8–11 brown, abdomen with five pairs of black spots, the pronotum and elytra densely covered with large punctures, and the interstices of the punctures in the elytra are somewhat

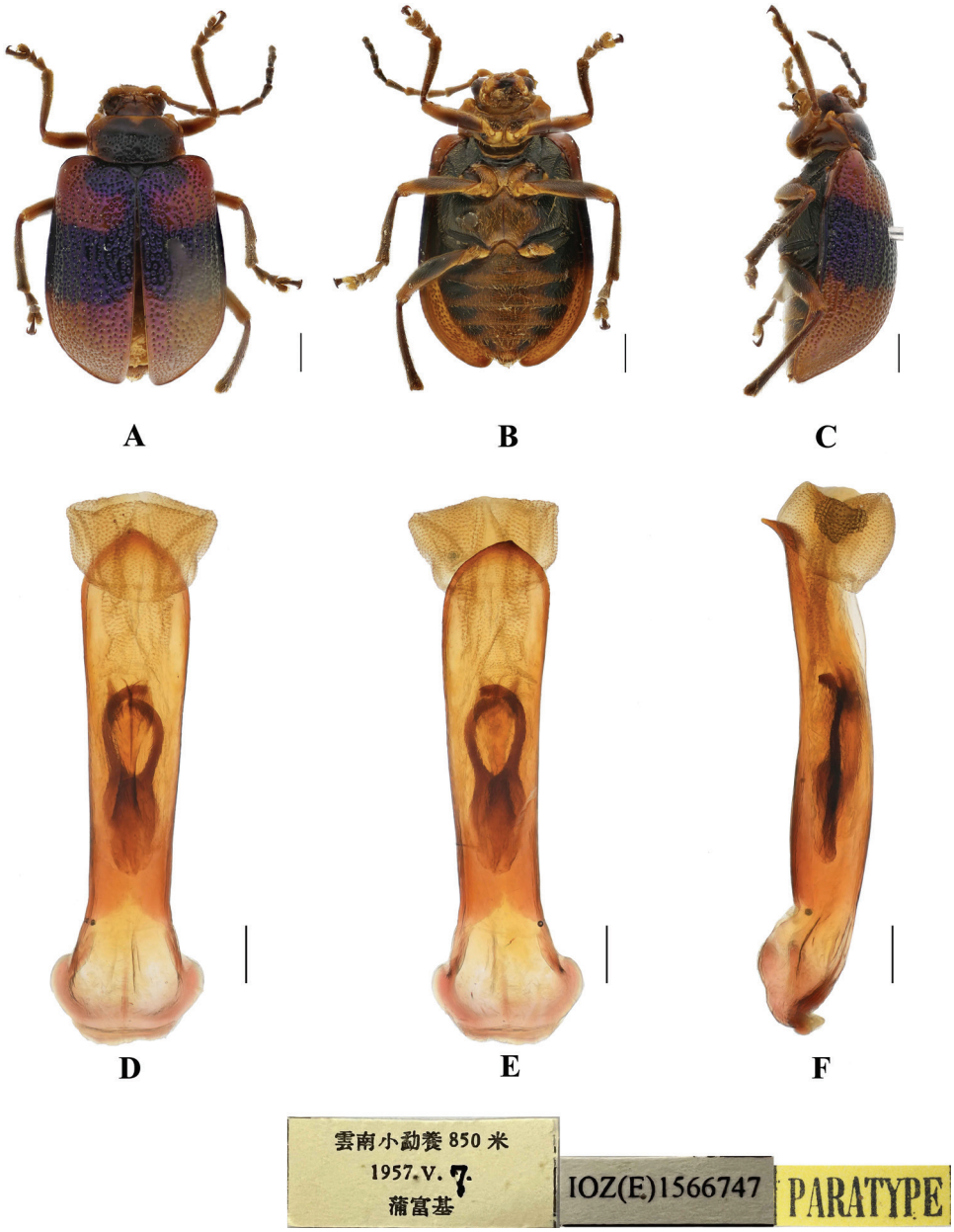

Figure 28. *Aplosonyx ancorella* sp. nov. **A–C** habitus of paratype, IZAS **D–F** aedeagus **A, D** dorsal views **B, E** ventral views **C, F** lateral views. Scale bars 0.5 mm (**D–F**); 1 mm (**A–C**).

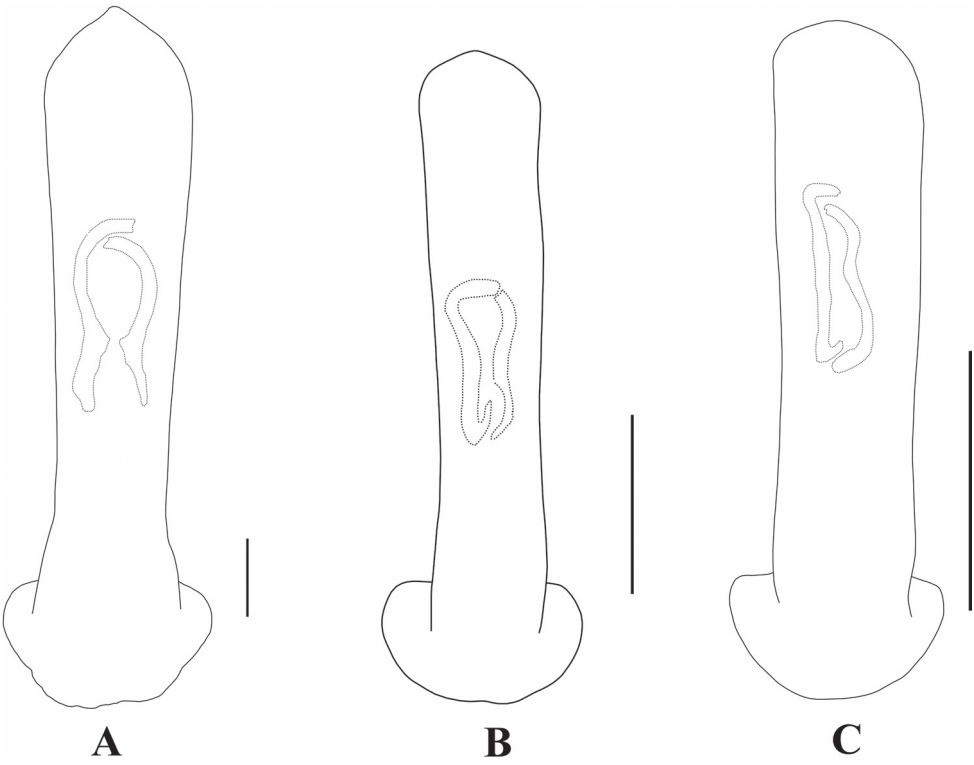

Figure 29. Aedeagus (dorsal view) **A** *A. ancorella* sp. nov. **B** *A. nigricornis* sp. nov. **C** *A. wudangensis* sp. nov. Scale bars: 0.5 mm (**A–F**).

wrinkled. In *A. fulvescens*, the antennae with antennomeres 1–3 yellow and antennomeres 4–11 brown, the pronotum and elytra are sparsely covered with small punctures.

Description. Male. Length 10.8–12.0 mm, width 5.8–6.2 mm.

Head, pronotum, abdomen and leg yellow, elytra reddish brown, antennae with antennomeres 1–7 yellow and antennomeres 8–11 brown, scutellum black, ventral surface of thorax black with yellow middle, pronotum purple or black, with lateral margin and anterior margin yellow, elytra with a broad purplish band from anterior to middle, which extends forward along suture and expends again on base, abdomen with five pair of black spots at side on each visible sternites.

Vertex finely and sparsely covered with punctures. Interocular space 1.9 × as wide as transverse diameter of eye. Interantennal space 1.3 × as wide as transverse diameter of antennal socket. Frontal tubercles transverse, each separated by a deep furrow; antennae slender, 0.7 × as long as body; antennomeres 1–3 shiny; antennomeres 4–11 with short hairs, antennomere 2 shortest, antennomere 3 approximately 1.5 × as long as second; antennomere 4 longest, approximately 2 × as long as antennomeres 2 and 3 combined; antennomeres 5–10 gradually shortened, shorter than antennomere 4; antennomere 11 slightly longer than antennomere 10, pointed.

Pronotum approximately 2 × as wide as long, disc with transverse furrow, densely covered with large punctures, the interstices of punctures distinctly narrower than diameter of punctures and with sparsely small punctures in apex of pronotum.

Scutellum triangular, finely covered with punctures.

Elytra: wider than pronotum, 0.7 × as long as body, 1.5 × as long as wide, epipleura wide at anterior 1/4, posteriorly gradually narrowing towards apex, dorsal surface slightly convex, irregularly covered with large and deep punctures, the interstices of punctures narrower than diameter of punctures and lightly covered with small punctures in interstices. their interstices somewhat wrinkled.

Metasternum 2 × as long as mesosternum. Ventral surface of abdomen with five ventrite, ventrite 1 longest, ventrites 2–4 gradually shortened, apical ventrite slightly longer than ventrite 3, with two subtriangular incisions.

Aedeagus slender, parallel-sided, basally widened, apex rounded, in lateral view apex distinctly bent.

Etymology. The name refers to the similarity with *Aplosonyx ancora*.

Distribution. China: Yunnan.

***Aplosonyx nigricornis* sp. nov.**

https://zoobank.org/59E394F3-D8A9-47A7-83D2-EA75A9544D1C

Figs 29B, 30A–F

Type material. ***Holotype*:** ♂, China, **Sichuan Province**, Qianjiang; 1750 m a. s. l.; 14 Jul. 1989; IZAS.

Diagnosis. The new species closely resembles *A. nigriceps* but differs due to each elytron with five black spots in *A. nigriceps*; in this new species each elytron has six black spots, and the aedeagus apex is rounded.

Description. Male. Length 5.0 mm, width 3.2 mm.

Head, antennae, pronotum, scutellum, ventral surface of thorax, abdomen, and legs black, elytra yellow, each elytron with six black spots, base, middle and apex with one pair of spots.

Vertex finely and sparsely covered with punctures. Interocular space 2.1 × as wide as transverse diameter of eye. Interantennal space 1.6 × as wide as transverse diameter of antennal socket. Frontal tubercles transverse, each separated by a deep furrow; antennae slender, 0.7 × as long as body; antennomeres 1–3 shiny; antennomeres 4–11 with short hairs, antennomere 2 shortest, antennomere 3 approximately 1.2 × as long as second; antennomere 4 longest, approximately 1.5 × as long as antennomeres 2 and 3 combined; antennomeres 5–10 gradually shortened, shorter than antennomere 4; antennomere 11 slightly longer than antennomere 10, pointed.

Pronotum 2 × as wide as long, lateral border margined, widest at anterior 1/3; disc with transverse furrow, less distinct in middle; covered with several large punctures in furrow and with sparsely small punctures in other parts of pronotum.

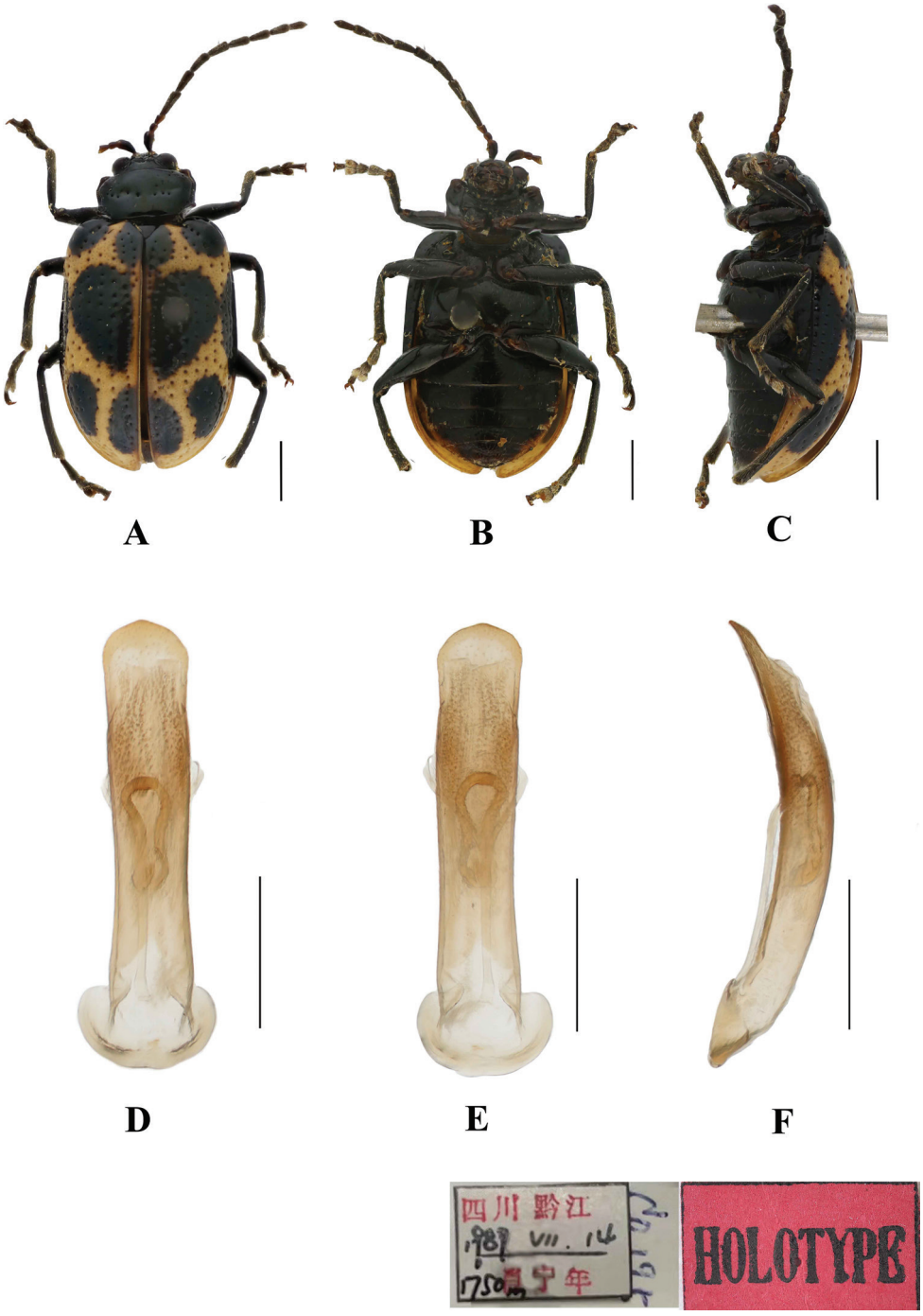

Figure 30. *Aplosonyx nigricornis* sp. nov. **A–C** habitus of holotype, IZAS **D–F** aedeagus **A, D** dorsal views **B, E** ventral views **C, F** lateral views. Scale bars 0.5 mm (**D–F**); 1 mm (**A–C**).

Scutellum triangular, only on base sparsely covered with small punctures.

Elytra wider than pronotum, 0.7 × as long as body, 1.65 × as long as wide, epipleura wide at anterior 1/3, posteriorly gradually narrowing towards apex, dorsal surface slightly convex, regularly covered with large punctures, partially arranged in ten rows in each elytron, the interstices of punctures in rows approximately 2.5 × as wide as the diameter of punctures and lightly covered with small punctures in interstices.

Metasternum 2 × as long as the mesosternum. Ventral surface of abdomen with five ventrites, ventrite 1 longest, ventrites 2–4 gradually shortened, apical ventrite slightly longer than ventrite 3, two subtriangular incisions.

Aedeagus slender, parallel-sided, basally widened, apically rounded, in lateral view distinctly bent.

Etymology. The species name refers to the black antennal color.

Distribution. China: Sichuan.

***Aplosonyx wudangensis* sp. nov.**

https://zoobank.org/14B1F164-283A-4223-AAC4-BB505F9C5CD4

Figs 29C, 31A–F

Type material. ***Holotype*:** ♂, China, **Hubei Province,** Wudang; 15 Aug. 1984; IZAS; IOZ(E)1566640.

Diagnosis. The new species closely resembles *A. yunlongensis* in spots of elytra, but the pronotum of *A. yunlongensis* has three obvious black spots. The new species is different in that the black spots on both sides of pronotum are small and almost invisible. The new species also closely resembles *A. tianpingshanensis* in the aedeagus, where the apex is wide and flat in *A. tianpingshanensis*, while the new species is round and slightly pointed. The interstices of punctures on elytra of new species are narrower than that on the elytra of *A. yunlongensis* and *A. tianpingshanensis*.

Description. Male. Length 5.0 mm, width 3.1 mm.

Head, antennae, pronotum, elytra and leg yellow, vertex, scutellum, and ventral surface of the body black, apical ventrite of abdomen yellow, pronotum with a black spot in middle, the black spots on both sides are small and almost invisible. each elytron with five black spots, middle and apex with one pair of spots and base with one spot.

Vertex sparsely covered with punctures. Interocular space 2.1 × as wide as transverse diameter of eye. Interantennal space 1.5 × as wide as transverse diameter of antennal socket. Frontal tubercles transverse, each separated by a deep furrow; antennae slender, 0.75 × as long as body; antennomeres 1–3 shiny; antennomeres 4–11 covered with pubescence, antennomere 2 shortest, antennomere 3 slightly longer than antennomere 2, approximately 1.4 × as long as second; antennomere 4 longest, approximately 1.2 × as long as antennomeres 2 and 3 combined; antennomeres 5–10 gradually shortened, shorter than antennomere 4; antennomere 11 slightly longer than antennomere 10, pointed.

Pronotum approximately 1.8 × as wide as long, lateral border margined, widest at anterior 1/3; disc with transverse furrow, the punctures are evenly distributed on the disc.

Scutellum triangular, smooth, impunctate.

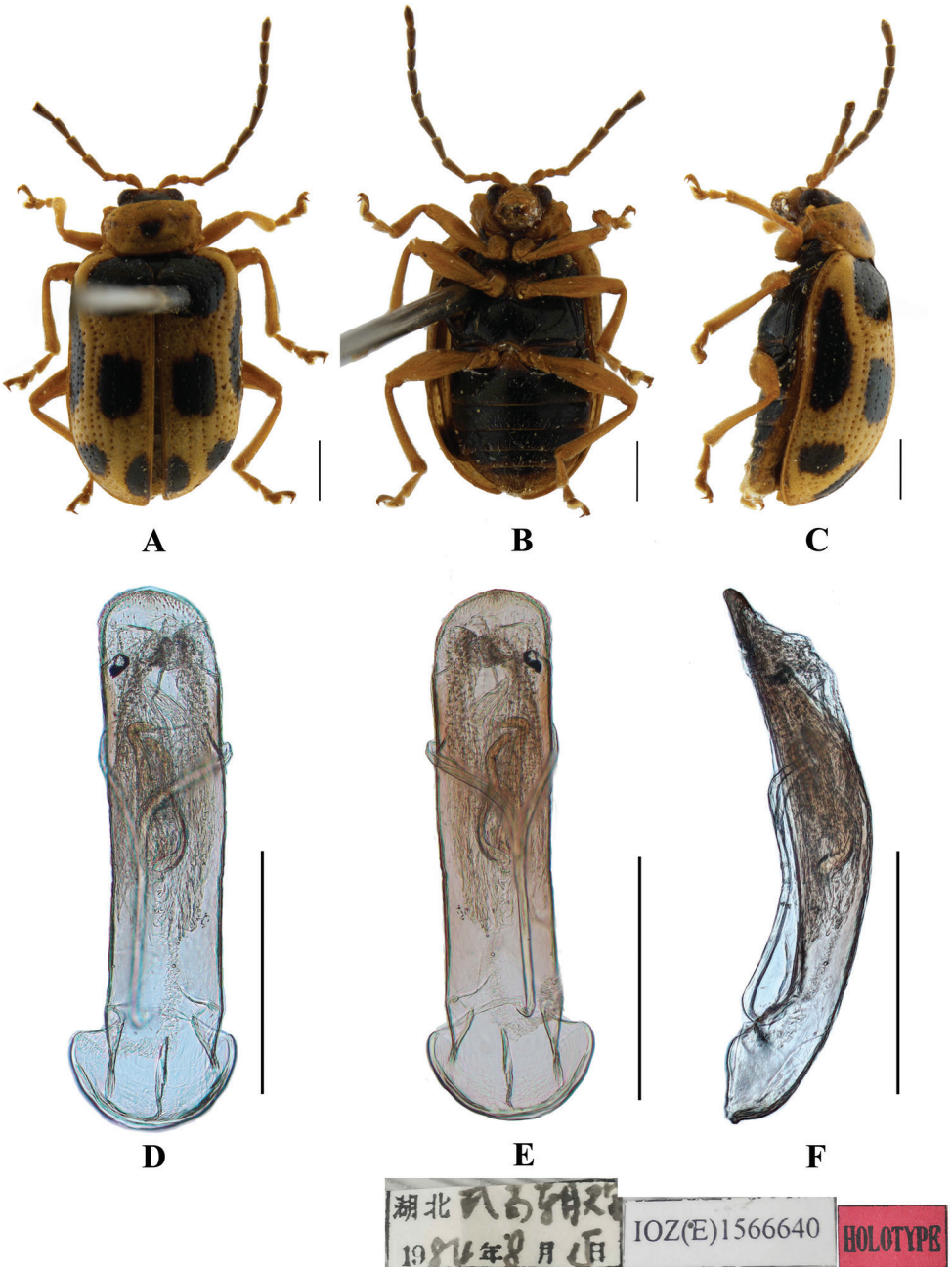

Figure 31. *Aplosonyx wudangensis* sp. nov. **A–C** habitus of holotype, IZAS IOZ(E)1566640 **D–F** aedeagus **A, D** dorsal views **B, E** ventral views **C, F** lateral views. Scale bars 0.5 mm (**D–F**); 1 mm (**A–C**).

Elytra: wider than pronotum, 0.8 × as long as body, 1.6 × as long as wide, epipleura wide at anterior 1/3, posteriorly gradually narrowing towards apex, dorsal surface slightly convex, regularly covered with large and deep punctures, partially arranged in

ten rows in each elytron, the interstices of punctures lightly wider than diameter of individual punctures and covered with small punctures in the interstices.

Metasternum 2 × as long as the mesosternum. Ventral surface of abdomen with five ventrites, ventrite 1 longest, ventrites 2–4 gradually shortened, apical ventrite slightly longer than ventrite 3, two subtriangular incisions.

Aedeagus slender, parallel-sided, basally widened, apex rounded, in lateral view moderately bent.

Etymology. This new species was named after the type locality.

Distribution. China: Hubei.

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